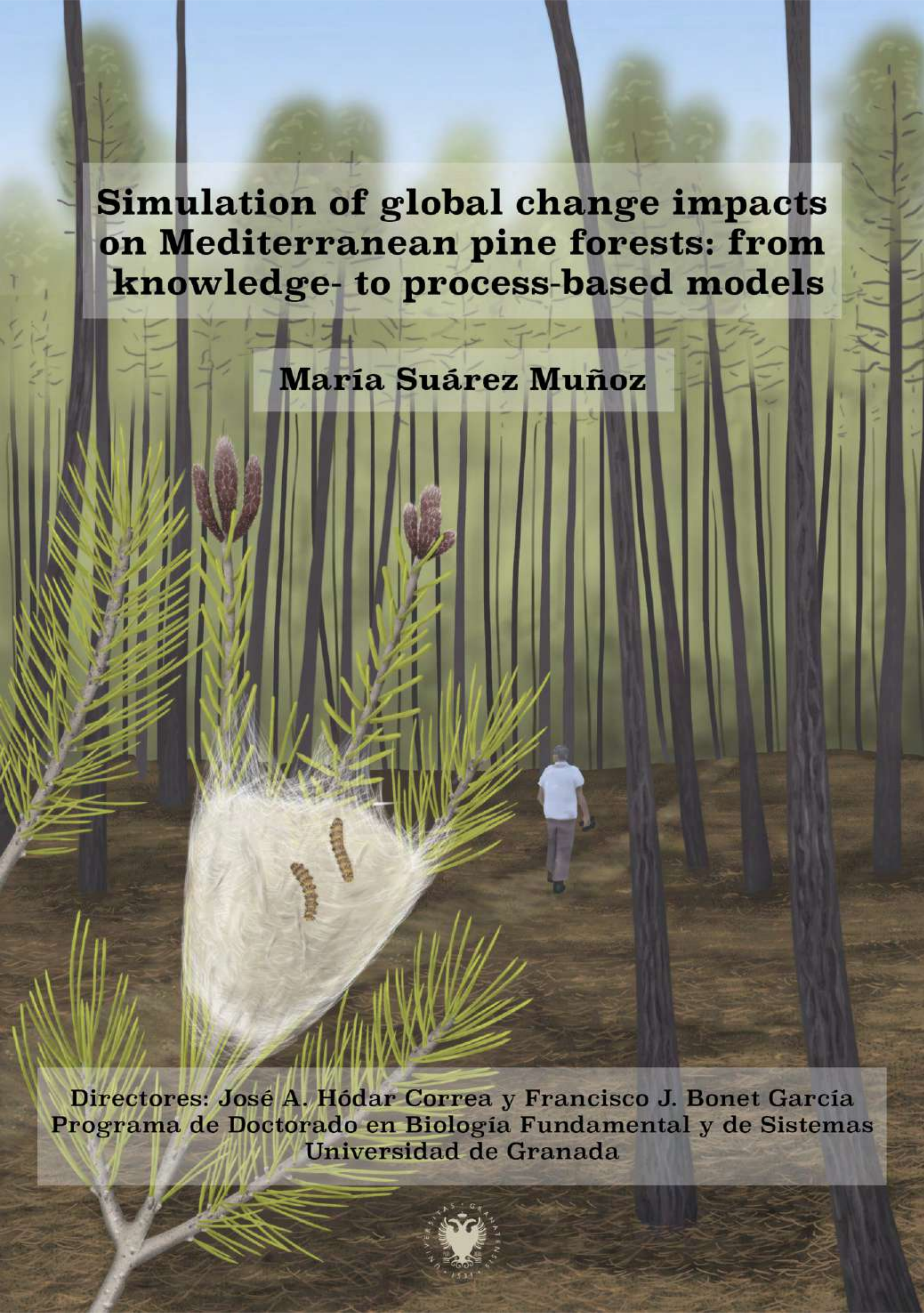

Simulation of global change impacts on Mediterranean pine forests: from knowledge- to process-based models

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Working team

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"Del rigor en la ciencia

En aquel Imperio, el Arte de la Cartografía logró tal Perfección
que el mapa de una sola Provincia ocupaba toda una Ciudad,
y el mapa del Imperio, toda una Provincia.
Con el tiempo, esos Mapas Desmesurados no satisficieron
y los Colegios de Cartógrafos levantaron un Mapa del Imperio,
que tenía el tamaño del Imperio y coincidía puntualmente con él.
Menos Adictas al Estudio de la Cartografía,
las Generaciones Siguientes entendieron que ese dilatado Mapa era Inútil
y no sin Impiedad lo entregaron a las Inclemencias del Sol y de los Inviernos..."

Suárez Miranda; Viajes de varones prudentes,
Libro Cuarto, Cap. XLV, Lérida, 1658. (José Luis Borges)

Modeling complex systems is challenging, but challenging is not the same thing as futile. Far from it, in fact. As far as I'm concerned, the only alternative to using a formal model is to use a verbal model, or worse, an unspoken mental model. In those cases it is much more difficult to identify implicit assumptions or show how the explicit assumptions lead to particular consequences, and therefore much easier to enter into the territory of unscientific vagueness. Everyone is using some model; but it is hard to know how good that model is without writing it down.

Smaldino (2020)

Contents

Summary

Pine forests are very abundant novel ecosystems in the Mediterranean Basin as a result of reforestation programmes aiming to reduce soil erosion problems. These forests often show high tree densities, low species diversity and high intraspecific competition, which makes them vulnerable to climate change and susceptible to forest pests outbreaks. Thus, these ecosystems are subject to intensive management due to their relevant role as providers of ecosystem services and the risks associated with global change.

The general aim of this thesis is to increase the understanding of pine plantation dynamics in southeastern Spain through the design and building of ecological models. Multiple ecological modelling approaches are applied in order to test different techniques, to experiment with them, and to promote their use in the study area, which constitutes the methodological objectives of this thesis. The different modelling techniques applied here study different compartments of pine plantations —the socio-ecological system, forest dynamics and defoliator dynamics—, which represent the ecological objectives of this thesis. The socio-ecological system is studied on a large scale taking into account the provinces of Granada and Almería. Forest dynamics are modelled on a medium scale by considering a 390,000 ha area covering the Protected Areas of Sierra Nevada, Sierra de Baza y Filabres and Sierra de Huétor. Finally, the population dynamics of the most common defoliator in these ecosystems are modelled on a local scale in a pine plot located in Sierra Nevada Protected Area.

Part I of this thesis aims to build a shared description of the socio-ecological system from the community of stakeholders within Mediterranean pine plantations in the study area. In this part we also aim to collect the most relevant management needs according to this community. The compilation of collective knowledge and management needs is addressed by applying a knowledge-based approach. For this purpose, a participatory modelling technique called Fuzzy Cognitive Mapping in combination with the "Drivers, Pressures, State, Impacts and Responses" framework is used. A total of 41 different individual perspectives were obtained in the form of cognitive maps and then aggregated, resulting in a social map which integrates the views of all participants and reveals that stand density influences central ecological processes. The complex relationships between regeneration of native vegetation, diversity and stand density are highlighted and point towards knowledge gaps which require further investigation. Thinning is revealed as the main action to regulate stand density according to all stakeholder groups. The social map also reveals that stakeholders demand a more effective knowledge transfer from science to management, increased economic investments and more participative decision-making processes. Our results highlight the potential benefits of multidisciplinary management approaches and advocate the creation of effective science-policy interfaces to serve as platforms for collaborative learning and the integrated management of these novel ecosystems.

Part II of this thesis focuses on the simulation of Mediterranean pine plantation dynamics under a context of climate change and the consideration of different management strategies aimed at adapting these forests to future climate. In order to simulate the most relevant forest functions of the target ecosystem, Forest Landscape Modelling is applied. Implementing a Forest Landscape Model requires substantial investments of time to develop the necessary input data and to calibrate model parameters and these processes are rarely reported thoroughly in application studies. Thus, we firstly document the process of calibrating and setting up an ecophysiologically-based forest landscape model (LANDIS-II). We describe the methodological process necessary to produce the required spatial inputs expressing initial vegetation and site conditions. We also test model behaviour on single-cell simulations and calibrate species parameters using local biomass estimates and literature information. We then test how different initialisation data influence the simulation of forest dynamics by applying the calibrated model at landscape level. Single-cell simulations reveal that the model was able to reproduce realistic biomass estimates and competitive effects for different forest types included in the landscape, as well as plausible monthly growth patterns of species growing in Mediterranean mountains. Our results also highlight the importance of considering shrub communities in forest landscape models, as they influence the temporal dynamics of tree species. In the absence of natural disturbances, harvesting or climate change, we observe that landscape-level simulations project a general increase of biomass over the next few decades but different spatio-temporal patterns among species due to differential competitive effects and landscape heterogeneity.

After model implementation and calibration, LANDIS-II model is used to simulate the future of Mediterranean pine plantations under different climate and management scenarios. The diversification of pine plantations to mixed forests is recommended to promote adaptation and increase the resilience of these ecosystems to climate change. Thus, different management strategies designed to assess their effects on the performance of planted pine forests and their change in terms of forest composition are tested. Climate change causes a shift in the phenological growth pattern of planted pine forests by reducing forest growth during summer and increasing photosynthetic productivity in spring and autumn, particularly under high emission scenarios. Biomass increases over time and more strongly under climate change, but this increase differs among species, resulting in changes of forest types across the landscape. Our results portray natural succession as the main driver of forest change, but also show that intensive management enforces this process by limiting pine growth and promoting the growth of oaks. The importance of active management on planted pine forests to favour mixed and climate-adapted ecosystems in shorter time scales than offered by succession alone is highlighted. Our spatially explicit modelling approach also helps to identify areas where lack of seed dispersal or competitive exclusion prevents diversification, providing useful recommendations for interventions.

Part III of this thesis focuses on the simulation of the biological cycle and population dynamics of the pine processionary moth (*Thaumetopoea pityocampa*), the most common forest defoliator in Mediterranean pine plantations. For this purpose, an Agent-Based Model called *INSTAR* is introduced and calibrated to simulate the biological cycle and population dynamics of the species in the study area. The model has been designed using a modular approach in which several interconnected submodels facilitate the incorporation of new knowledge about the species' biology. Firstly, *INSTAR* is described in detail using a standardised protocol. Then, different experiments are performed in order to calibrate and test model behaviour regarding temperature influence on species population dynamics. A consistency test of the submodules responsible for species development is performed by calibrating species phenology and a stress test is implemented by exposing the model to extreme climate inputs. As a result of calibration, the model successfully reproduces the phenology of the species in the simulated study area. Moreover, the stress test confirms that the model behaves as expected when exposed to extreme input values.

By focusing on different aspects of Mediterranean pine plantations from different approaches, we have attempted to show an overview of modelling techniques, providing a high level of detail on methodological aspects, ensuring transparency and promoting reproducibility over the modelling process. The ecological models presented in this thesis advance our understanding of the socio-ecological system, the forest dynamics and the pine processionary moth dynamics of Mediterranean pine plantations in southeastern Spain. Furthermore, we have outlined the methodological approaches to increase the usability of these models by forest managers. We therefore believe that this thesis constitutes a contribution towards a more integrated and participatory way of using modelling in forest management. Nevertheless, we consider that it is necessary to face multiple challenges before modelling becomes a common tool in ecosystem management.

Resumen

Los bosques de coníferas son ecosistemas noveles muy abundantes en la cuenca mediterránea que surgen como resultado de programas de reforestación orientados a disminuir problemas de erosión del suelo. Estos bosques a menudo muestran altas densidades, baja diversidad de especies y alta competencia interespecífica, lo que los hace vulnerables al cambio climático y susceptibles a brotes de plagas forestales. De ahí que, dada su importancia como proveedores de servicios ecosistémicos y teniendo en cuenta los riesgos asociados al cambio global, estos ecosistemas están sujetos a una gestión intensa.

El objetivo general de esta tesis es aumentar la comprensión que tenemos del funcionamiento de las repoblaciones de coníferas en el sudeste español a través del diseño y la construcción de modelos ecológicos. Se aplican múltiples aproximaciones a la modelización ecológica para testar diferentes técnicas, experimentar con ellas y promover su uso en el área de estudio, lo que constituye los objetivos metodológicos de esta tesis. Las diferentes técnicas aplicadas sirven para estudiar diferentes compartimentos de las repoblaciones —el sistema socio-ecológico, la dinámica forestal y la dinámica de los defoliadores—, los cuales representan los objetivos ecológicos de esta tesis. El sistema socio-ecológico es estudiado a gran escala, considerando las provincias de Granada y Almería. Los cambios en la estructura del bosque son modelados a una escala intermedia considerando un área de 390.000 hectáreas que cubre las áreas protegidas de Sierra Nevada, Sierra de Baza y Filabres, y Sierra de Huétor. Finalmente, se modelan a escala local las dinámicas poblacionales de la especie defoliadora más común en estos ecosistemas en una parcela de pinar en el Espacio Protegido de Sierra Nevada.

La Parte I de esta tesis pretende extraer una descripción compartida del sistema socio-ecológico de la comunidad de agentes en torno a las repoblaciones en el área de estudio. En esta parte también pretendemos recopilar las necesidades de gestión más relevantes de acuerdo a la comunidad. La recopilación del saber colectivo y las necesidades de gestión se aborda mediante una aproximación basada en el conocimiento. Con esta finalidad se utiliza una técnica de modelización participativa llamada *Fuzzy Cognitive Mapping* en combinación con el marco 'Drivers, Pressures, State, Impacts and Responses'. Se obtuvieron un total de 41 perspectivas individuales diferentes en forma de mapas cognitivos posteriormente agregados, resultando en un mapa social que integra la visión de todos los participantes y revela cómo la densidad influye en procesos ecológicos clave. Se destacan las complejas relaciones entre regeneración de vegetación nativa, diversidad y densidad y se señalan lagunas de conocimiento que requieren más investigación. El clareo se revela como la principal acción para regular la densidad de acuerdo a todos los grupos de agentes. El mapa social también revela que los agentes demandan una transferencia de conocimiento más efectiva de la ciencia a la gestión, mayores inversiones económicas y procesos de decisión más participativos. Nuestros resultados subrayan los beneficios potenciales de una gestión multidisciplinar y abogan por la creación de interfaces ciencia-gestión efectivas, que sirvan como plataformas para el aprendizaje colaborativo y la gestión integrada de estos ecosistemas noveles.

La Parte II de esta tesis se centra en la simulación de la dinámica de las repoblaciones de coníferas mediterráneas en un contexto de cambio climático, considerando distintas estrategias de gestión dirigidas a adaptar estos bosques al clima futuro. Para simular las funciones forestales más relevantes del ecosistema se aplica *Forest Landscape Modelling*. La implementación de un modelo de paisaje forestal requiere una inversión sustancial de tiempo en la preparación de los datos iniciales necesarios y en la calibración de los parámetros del modelo, y estos procesos raramente son reportados en detalle en los estudios de aplicación. De ahí que, en primer lugar, documentemos el proceso de calibración e implementación de un modelo ecofisiológico de paisaje forestal (LANDIS-II). A continuación, describimos el proceso metodológico necesario para producir las entradas espaciales requeridas, y que expresan las condiciones iniciales de la vegetación y del área de estudio. Además testamos el comportamiento del modelo a través de simulaciones con una sola celda y calibramos los parámetros de las especies usando estimaciones de biomasa locales e información científica. Llegado este momento, testamos cómo diferentes datos de inicialización influyen en la simulación de la dinámica forestal aplicando el modelo calibrado a escala de paisaje. Las simulaciones de una celda revelan que el modelo es capaz de reproducir estimaciones de biomasa y efectos de competencia realistas para distintos tipos de vegetación presentes en el paisaje, además de patrones mensuales de crecimiento de especies mediterráneas plausibles. En ausencia de perturbaciones naturales, gestión o cambio climático, observamos que las simulaciones a escala de paisaje proyectan un incremento general de la biomasa en las próximas décadas pero revelan patrones espaciales distintivos entre especies debido a efectos de la competencia y la heterogeneidad

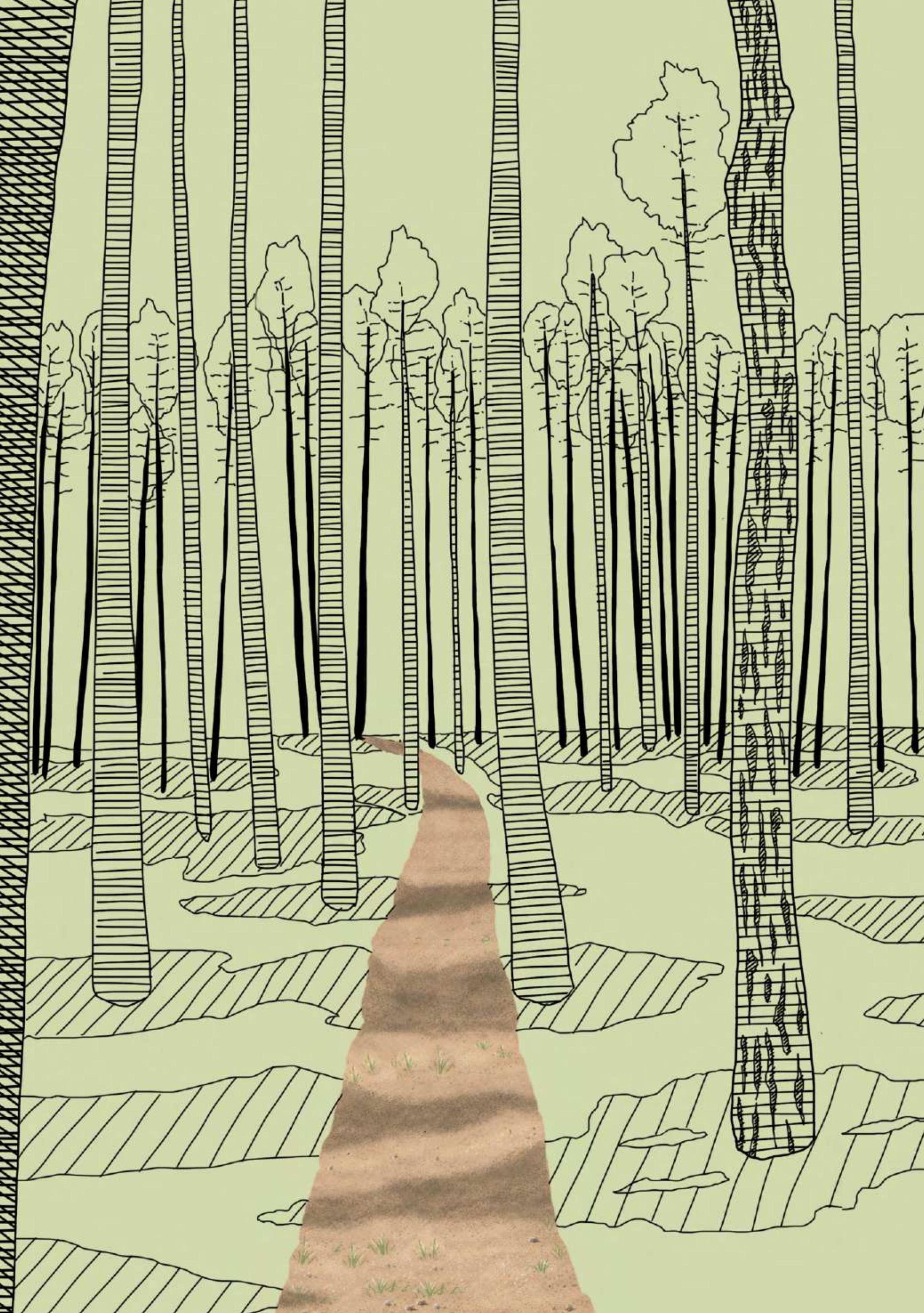
espacial.

Tras la implementación y calibración, se emplea el modelo LANDIS-II para simular el futuro de las repoblaciones de pinos bajo distintos escenarios de clima y gestión. Se recomienda la diversificación de las repoblaciones a bosques mixtos para promover la adaptación y aumentar la resiliencia de estos ecosistemas al cambio climático. Por lo tanto, se prueban diferentes estrategias de gestión diseñadas para evaluar sus efectos en el funcionamiento de estas plantaciones y sus cambios en términos de composición específica. El cambio climático causa un cambio en el patrón fenológico de crecimiento de estas plantaciones, reduciendo el crecimiento forestal durante el verano e incrementando la productividad fotosintética en primavera y otoño, particularmente bajo escenarios de altas emisiones. La biomasa aumenta a lo largo del tiempo y más intensamente bajo cambio climático, pero este incremento difiere entre especies, resultando en cambios de tipo de vegetación en el paisaje. Nuestros resultados muestran a la sucesión forestal como el principal impulsor de cambio, pero también que la gestión intensiva refuerza este proceso limitando el crecimiento de los pinos y promoviendo el de las quercíneas. Se subraya la importancia de una gestión activa de las repoblaciones para favorecer ecosistemas mixtos y adaptados al clima en plazos más cortos que sólo bajo sucesión. Nuestra aproximación espacialmente explícita también ayuda a identificar áreas en las que la falta de dispersión o exclusión competitiva impide la diversificación. Estos resultados nos permiten generar recomendaciones útiles para planificar futuras actuaciones forestales.

La Parte III de esta tesis está orientada a simular el ciclo biológico y las dinámicas poblacionales de la procesionaria del pino (*Thaumetopoea pityocampa*), la especie defoliadora más común en las repoblaciones de coníferas. Con este propósito, se describe un modelo de agentes llamado *INSTAR* y se calibra para simular el ciclo biológico y las dinámicas poblacionales de la especie en el área de estudio. El modelo ha sido diseñado con una estructura modular en la que varios submodelos interconectados facilitan la incorporación de nuevo conocimiento sobre la biología de la especie. En primer lugar, se describe *INSTAR* en detalle usando un protocolo estándar. Se aplica un test de consistencia de los submodelos responsables del desarrollo mediante la calibración de la fenología de la especie y se implementa un test de estrés mediante la exposición del modelo a series climáticas extremas. Como resultado de la calibración, el modelo reproduce de forma exitosa la fenología de la especie en el área de estudio. Además, el test de estrés confirma que el modelo se comporta de acuerdo a lo esperado cuando es expuesto a valores de entrada extremos.

Mediante las aproximaciones descritas anteriormente enfocadas a diferentes

aspectos de las repoblaciones mediterráneas hemos hecho un esfuerzo para mostrar una perspectiva general de las técnicas de modelización, aportando detalles metodológicos y asegurando la transparencia y claridad sobre todo el proceso de modelización. Los modelos ecológicos presentados en esta tesis avanzan nuestra comprensión sobre el sistema socio-ecológico, las dinámicas forestales y las dinámicas poblacionales de la procesionaria del pino en la repoblaciones forestales del sudeste español. Así, creemos que esta tesis supone una contribución hacia una gestión forestal más integrada y participativa a través de la modelización. No obstante, consideramos que es necesario afrontar múltiples retos para que la modelización sea una herramienta habitual en la gestión de los ecosistemas.



Preamble

Introduction

We are walking through a forest. Pine trees give us shade as we ascend a stony path. Here and there we can see oak seedlings and junipers. We stop by to collect some rosemary and thyme. As we reach the ridge, a valley opens before our eyes. On our way down the valley we see holm oaks growing in small groups and gall oaks starting to yellow in these early autumn days. Further down big brooms are the only ones challenging the blazing sun in those reddish dry soils. Why are those areas so different from each other? Why is a species present in one place and not in another?

We have been asking ourselves such questions since long before we could conceive what ecology is. Those “simple” questions, so necessary to solve basic problems such as where to find food, often require complicated and elaborated answers. This is because ecosystems are complex; they are systems composed of numerous components interacting with each other nonlinearly (Wu and Marceau, 2002). These systems exchange energy and mass with the environment, show great heterogeneity in time and space —as we just saw during our walk—and develop emergent properties as a result of interactions at multiple scales and, often to our surprise, self-organisation dynamics (Wu and Marceau, 2002).

To answer our questions we use models, which ultimately are abstract representations of reality (Mulligan and Wainwright, 2004). We use models to describe an ecosystem and explain our observations —pines grow in rocky soils—, but models are also used to make predictions —we will find brooms at low elevations—and finally, we also use models to take decisions —let’s avoid broom areas in summer afternoons (Blanco, 2013; Geary et al., 2020). Ecological models describe “the interactions between at least two ecosystem components (for example, a species or functional group), whereby the interactions are real ecological processes (for example, predation, dispersal or perturbations)" (Geary et al., 2020).

During our long history of creating ecological models, we have come up with different approaches to build them. One possible classification, among others, is that given by Twery (2004), who differentiates between the knowledge-based, the empirical and the mechanistic approach. The knowledge-based approach makes use of information captured in the form of logical statements or causal relationships. Models developed through this approach make use of symbolic representations of the system in order to describe their functioning (Twery, 2004). As such, these models are highly useful when quantitative information of the system is lacking or difficult to obtain. Knowledge-based models can be relatively simple, such as diagrams showing causal relationships, or quite sophisticated, as is the case of ontologies (e.g. Coetzer et al., 2017). In environmental management, these kinds of models are often built to simulate or support decision-making processes (Özesmi and Özesmi, 2004).

Under the empirical approach, relationships between variables are studied based on statistical analysis, traditionally assuming stationarity of site conditions (Fontes et al., 2010). These kinds of models are widely used in ecology and environmental sciences, fields with a long tradition of relating observations with explanatory variables. As an example, growth and yield models have long been developed in forest sciences to estimate wood production and other timber-related variables (Bravo et al., 2011; Burkhart and Tomé, 2012).

The mechanistic approach instead focuses on the processes influencing the system's dynamics. Mechanistic or process-based models (considered synonyms here, see Blanco, 2013; Schuwirth et al., 2019) emulate the functioning of ecological processes instead of studying the relationships between outcomes of these processes. As an example, photosynthesis can be modelled by analysing how much CO_2 and light is required to produce a certain amount of O_2 (empirical approach) or by simulating the physiological process of CO_2 absortion, electron excitement due to light and synthesis of organic matter (mechanistic approach). Process-based models have the advantage that they are better suited than empirical models to understanding system dynamics under new conditions (Fontes et al., 2010). Therefore, process-based models serve as virtual laboratories for where to perform *in silico* experiments that could not be performed otherwise (Blanco, 2013).

This classification into knowledge-based, empirical and mechanistic approaches is, nevertheless, a model itself, a way to structure our ideas, and there is a gradient among the different approaches. Statistical analysis applied to build empirical models is generally based on previous knowledge-based models of the system. And process-based models are never fully mechanistic but instead they often incorporate empirically-obtained parameters, since purely mechanistic models would be as complex as the system itself and would therefore become meaningless (Smaldino, 2020). This gradient can also reflect the mental process followed to describe and understand the world around us.

The above outlined classification of modelling approaches becomes more complex when the spatial component is present, as this happens when our target entity is an ecosystem. Ecological questions may have different answers depending on the spatial scale considered (Wiens, 1989). Moreover, analysing the processes occurring throughout the landscape may be required in order to reach satisfactory descriptions of our systems. Thus, ecological modellers consider non-spatially explicit and spatially explicit models, depending on whether they incorporate the spatial component into their models or not. Non-spatially explicit models such as Gap Models (e.g. JABOWA model, Botkin et al., 1972) do not consider spatial interactions but can be very useful to understand internal processes (e.g. stand growth).

Spatially explicit models, on the other hand, consider interactions based on maps and other spatial information of the system. The scale and accuracy of simulated processes is adjusted in these kinds of models considering the model purpose. Dynamic Vegetation Models (Bonan et al., 2003; Peng, 2000) are highly useful to study processes on a continental or global scale, but due to their coarse resolution they are not very suitable for detailed processes such as management applications. Landscape Models (Keane et al., 2015) are spatially-explicit simulation models —process-based models by definition—able to incorporate the spatial consideration at a higher resolution, which allows them to capture more detailed processes than previous techniques. Landscape Models usually represent an area or territory as a grid of cells with a series of state variables or attributes describing them, which has multiple advantages for ecological research (e.g. Sitch et al., 2003). The simplest of these kinds of models would be Cellular Automata models, in which a set of rules defines how a cell changes its state based on the state of neighbouring ones (e.g. Jeltsch and Wissel, 1994). However, some model purposes may require a higher level of detail, for example when ecosystem conditions arise from the interaction of system elements which move through the landscape. To overcome this limitation, Agent-Based Modelling incorporates discrete individuals or *agents* with the capacity to move and act over a continuous landscape (Grimm et al., 2005).

Any ecological modelling technique requires a system to ground ideas, raise relevant questions and develop answers. Pine forests are very abundant in the Mediterranean Basin and subject to intensive management due to their important role as providers of ecosystem services and the vulnerabilities they face under global change (Sánchez-Salguero et al., 2012b). Large areas of these pine forests can be considered novel ecosystems due to their anthropic origin and, furthermore, low species diversity (Gómez-Aparicio et al., 2009; Lindenmayer et al., 2015). Thus, the forest described above is just a small corner in the world, but a good example of a complex system, highly interesting for its socio-ecological aspects and landscape dynamics. In this thesis, multiple ecological modelling approaches are applied to study socio-ecological aspects of Mediterranean pine plantations in southeastern Spain.

Objectives

The general aim of this thesis is to increase the understanding of pine plantation functioning in southeastern Spain through the design, building and application of ecological models. The empirical approach has been traditionally used in ecology to describe the functioning of an ecosystem. However, other approaches are clearly underrepresented within ecological research. Thus, in this thesis we focus on novel ecological modelling approaches and specifically tackle the simulation of Mediterranean pine plantations based on knowledge-based and process-based approaches in order to test different modelling techniques, to experiment with them, and to promote their use in the study area. This aim serves a dual purpose: ecological and methodological learning of socio-ecological forest systems. Therefore, a set of ecological and methodological objectives are defined. Under each objective the developed model serves a different purpose, which explains the selection of the modelling approach (Table P.1).

Ecological objectives

To compile collective knowledge and management needs on Mediterranean pine plantations

Ecosystems are often studied from a biological perspective, in terms of population dynamics or nutrient fluxes. However, how a human community perceives the ecosystem in which it is inserted has important implications for the understanding and management of such ecosystems and this aspect is rarely modelled explicitly. In addition, Mediterranean pine plantations are highly anthropised ecosystems and therefore the community's understanding of the system and its expectations strongly defines future management and thus the ecological status of the system. Considering these aspects, under this objective we aim to extract

Table P.1: Overview of objectives, model purposes and modelling approaches. Model purpose *sensu* Mulligan and Wainwright (2004) and Chowdhury and Stauffer (2005).

Part	**Ecological objectives**	**Methodological objectives**	**Model purpose**	**Modelling approach**
I	To compile collective knowledge and management needs on Mediterranean pine plantations	To explore knowledge-based models as tools to approach socio-ecological systems	Tool for understanding, integrator within and between disciplines	Knowledge-based
II	To simulate Mediterranean pine plantation dynamics in relation to climate and management	To explore landscape process-based models as tools to simulate ecosystem dynamics	Tool for simulation and prediction, virtual laboratory where *in silico* experiments can be performed	Landscape process-based
III	To simulate the biological cycle of a relevant forest defoliator in Mediterranean pine plantations	To explore landscape process-based models as tools to simulate ecosystem dynamics	Research product, aid to research	Landscape process-based

a shared description of the socio-ecological system from the community of stakeholders around Mediterranean pine plantations in the study area. Moreover, within this objective we also intend to collect the most relevant management needs according to this community. Part I of this thesis focuses on this first socio-ecological objective.

To simulate Mediterranean pine plantations dynamics in relation to climate and management

Forests are highly sensitive ecosystems to climate change (Allen et al., 2015). The long time scales of forest processes and high dependence on climatic conditions makes them vulnerable to the rapid changes posed by global warming. Predicting the impacts of climate change on forest ecosystems therefore constitutes a challenge nowadays for ecologists and managers. Mediterranean pine plantations are especially vulnerable due to their structure, species composition and location in relatively dry areas where climate is expected to rapidly intensify arid conditions (Navarro-Cerrillo et al., 2019; Zittis et al., 2021). In this second objective, addressed in Part II, we focus on the simulation of Mediterranean pine plantation dynamics under a context of climate change and the consideration of different management strategies aiming to adapt these forests to climate change.

To simulate the biological cycle of a relevant forest defoliator in Mediterranean pine plantations

Forest defoliators are highly relevant drivers of change in coniferous forests, especially under climate change due to their interacting effects with climate (Seidl et al., 2017). In Mediterranean pine plantations, the pine processionary moth (*Thaumetopoea pityocampa*) is one of the most abundant defoliator species, causing massive defoliations and tree growth reductions, especially when co-occurring with drought (Jacquet et al., 2013; Linares et al., 2014). Under this third objective, covered in Part III, we therefore focus on increasing our understanding of pine processionary moth dynamics through the simulation of its biological cycle.

Methodological objectives

To explore knowledge-based models as tools to approach socio-ecological systems

Knowledge-based models can be very useful to understand the perception of a system according to the stakeholders' community or to obtain a description of a system in the absence of abundant quantitative information. Thus, in Chapter 1 of this thesis we address the compilation of collective knowledge and management needs on Mediterranean pine plantations by developing a knowledge-based model which serves as a *tool for understanding* as well as *integrator within and between disciplines* (*sensu* Mulligan and Wainwright, 2004).

To explore spatially-explicit landscape models as tools to simulate ecosystems dynamics

Landscape process-based models are effective tools to address the current challenges posed by climate change and to understand complex population dynamics influenced by multiple spatio-temporal factors. These models can serve as a *tool* *for simulation and prediction* as well as a *virtual laboratory* where *in silico* experiments simulating long-term dynamics can be performed (Chowdhury and Stauffer, 2005). Moreover, they can also be *research products* which can serve as an *aid to research* ecological processes such as the population dynamics of a forest defoliator (Chowdhury and Stauffer, 2005). In Chapter 2 of this thesis we describe the implementation of a Forest Landscape Model and in Chapter 3 its application to simulate the most relevant forest functions —among others growth, regeneration or tree mortality—of the target ecosystem. In Chapter 4, we introduce a detailed Agent-Based Model and its calibration to simulate the biological cycle and population dynamics of the pine processionary moth.

Methodology

A set of modelling techniques were selected for the development of knowledge- and process-based models. The selection was made considering the aim of each project as well as the available information about the socio-ecological system, the forest dynamics and the defoliator dynamics in Mediterranean pine plantations, respectively (Table P.2). The description of the socio-ecological system by the stakeholders' community is semi-quantitative, as it is a mental construction mainly composed of statements and causal relationships reported by the stakeholders themselves. Since the aim is to build a shared description of the socio-ecological system, a participatory modelling technique called *Fuzzy Cognitive Mapping* was chosen for this purpose. In the case of forest dynamics, a landscape approach was required to capture spatio-temporal patterns at scales relevant for forest management. In this case, quantitative aggregated information such as vegetation maps or forest inventory data were used for *Forest Landscape Modelling*. In order to simulate the defoliator dynamics, a higher level of detail was required and therefore detailed quantitative information such as field observations was used to apply *Agent-Based Modelling*.

Fuzzy Cognitive Mapping

The first part of this thesis focuses on the compilation of collective knowledge and management needs. For this purpose, we searched for a participatory modelling technique which would allow us to collect multiple perspectives in the least constrained way possible. In this regard, semi-structured individual interviews allow stakeholders to express their ideas at their own pace and in their own words, avoiding single individuals monopolising group discussions, or the highlighting of agreements and hiding of differences, as discussed by Jetter and Kok (2014) and Olazabal et al. (2018b). Moreover, we were interested in integrating the collected information into a shared description of the system, and therefore we searched for

Table P.2: Methodological aspects of this thesis. Type of information considered *sensu* Voinov et al. (2018).

Part	**Modelling approach**	**Type of information considered**	**Modelling technique**	**Elements defining the model**	**Scale considered**
I	Knowledge-based	Semi-quantitative	Fuzzy Cognitive Mapping	Concepts and relationships	Large
II	Landscape process-based	Quantitative (aggregated)	Forest Landscape Modelling	Cells, cohorts, state variables, parameters	Medium
III	Landscape process-based	Quantitative (detailed)	Agent-Based Modelling	Cells, agents, state variables, parameters	Detail

an interviewing method that would generate semi-structured information which could somehow be combined. Finally, our ideal technique should be as quantitative as possible to allow for a prioritisation of the most relevant aspects and be feasible to apply, given our limited experience as facilitators.

Considering these requirements, Fuzzy Cognitive Mapping was found to be the best alternative over other techniques such as Group Model Building or Bayesian Belief Networks which are more oriented towards decision-making rather than the description of the system and since they require group work instead of individual interviews. Fuzzy Cognitive Mapping constitutes a semi-quantitative modelling technique which allows the explicit representation of a system's functioning based on the views of one or multiple stakeholders (Voinov et al., 2018). Moreover, it can be applied following a systematic methodology, which simplifies the process and ensures transparency and reproducibility (Olazabal et al., 2018b).

Fuzzy Cognitive Mapping is a modelling technique broadly used in environmental and socio-ecological research (Olazabal and Pascual, 2016; Papageorgiou and Salmeron, 2013), that allows knowledge co-production by integrating diverse information sources into semi-quantitative models (Olazabal et al., 2018b). Fuzzy Cognitive Maps represent a system or situation and aim to capture the knowledge, experience and perception of one or multiple stakeholders on a certain topic (Kok, 2009). Fuzzy Cognitive Maps are mental schemes composed of a set of concepts which relate to each other through causal relationships, usually represented by nodes and arrows, respectively (Özesmi and Özesmi, 2004). Cause-effect relationships between concepts are characterised by a sign and a weight (Figure P.1). A positive sign means that an increase in concept A leads to an increase in concept

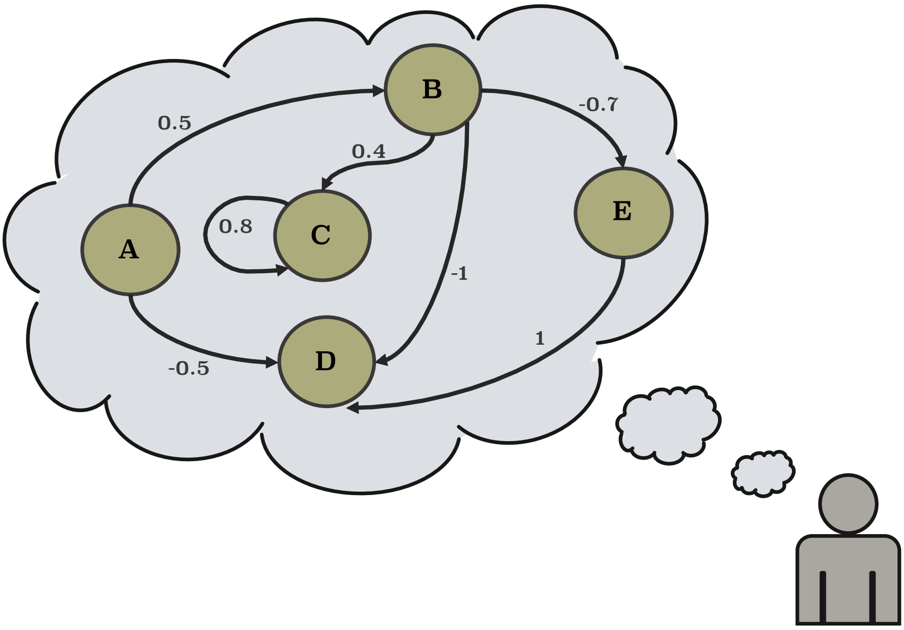


Figure P.1: Schematic representation of an example Fuzzy Cognitive Map in the form of a causal diagram.

B, while a negative sign means that an increase in concept A leads to a decrease in concept B. The associated measure or weight expresses the strength of the relationship, either in qualitative or quantitative terms. Fuzzy Cognitive Maps can be depicted graphically as a semi-quantitative causal diagram or numerically as an adjacency matrix.

In Chapter 1, FCM was applied in combination with the "Drivers, Pressures, State, Impacts and Responses" framework (DPSIR). Individual researchers, managers and socio-economic agents were interviewed to generate a set of 41 Fuzzy Cognitive Maps which were then aggregated. The collected concepts were subsequently classified into DPSIR categories and Responses were analysed as proposals for actions and reactions towards the current situation and management of pine plantations by the different stakeholder groups.

Forest Landscape Modelling

Forest Landscape Modelling is a modelling technique which simulates forest dynamics by considering factors responsible for forest structuring and interactions (Gustafson et al., 2020). Forest Landscape Models have evolved from earlier forest modelling techniques as computing power and availability of forest data for calibration have become less constraining, therefore allowing for the simulation of large areas at a relatively high resolution (Shifley et al., 2017).

In Forest Landscape Modelling a landscape is generally represented as a group of cells, each of them assigned with a series of variables which are used to define ecological processes taking place at cell level or at landscape level (Shifley et al., 2017, Figure P.2). A group of functions, submodels, behaviours or processes define how variables change with time in order to mimic ecological processes such as species growth, reproduction, dispersal or death. In order to start a simulation, Forest Landscape Models usually require a series of data describing the initial conditions of the landscape to simulate, a series of parameters defining species behaviour and, often, data such as climate time series or disturbances regimes (e.g. probability of fire occurrence, management interventions frequency and characteristics, probability of pest outbreak). Thus, calibration, parameterisation and preparation of all required input data (e.g. species-specific parameters, spatialised climate series, up-to-date vegetation data) is one of the greatest challenges when building Forest Landscape Models (Scheller, 2018).

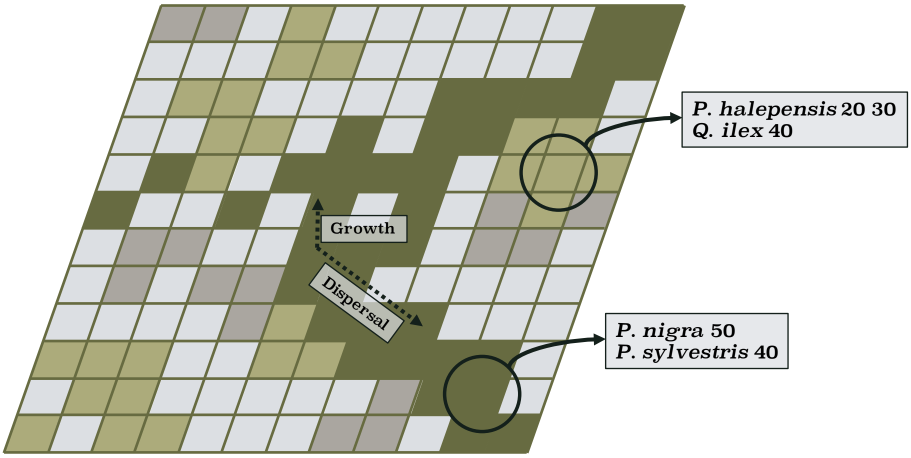


Figure P.2: Schematic representation of a general Forest Landscape Model. Continuous arrows represent cell variables, in this case species cohorts occurrence and age, while dashed arrows indicate submodels or processes.

Numerous Forest Landscape Models exist, with a wide range of complexity in their submodels as well as various approaches to the simulation of ecological processes, ranging from more empirical to more mechanistic ones (Shifley et al., 2017). To select the most suitable Forest Landscape Model for the purposes of this thesis, we compared several potential models against modelling aim requirements and evaluated them based on their specific applicability. For example, the process-based GOTILWA+ model (Gracia et al., 1999) has been parameterised in numerous studies in Spain (e.g. Nadal-Sala et al., 2017; Sperlich et al., 2020) but it only allows simulating mono-specific stands and is therefore not suitable for studying forest diversification, a key process in our study area. SORTIE model (Coates et al., 2003) is an hybrid stand model that could be upscaled to small landscapes, but we considered that it required too much effort to fine-tune its detailed neighbourhood processes across a large complex forest landscape. ForClim model (Bugmann, 1996) is a convenient model to capture the influence of climate change on forest dynamics, but it is not spatially explicit, making it impossible for us to capture landscape scale processes. The Agent-Based forest landscape model iLand (Seidl et al., 2012) constituted a promising option, but the level of complexity in the initialisation (highly detailed input data: high resolution soil data, carbon pools and climatic variables) and parameterisation (newly simulated species) prevented us from using this model.

For the purpose of this thesis, models derived from the LANDIS family constituted the best alternatives in our opinion. The original LANDIS model (Mladenoff, 2004) simulates landscape processes such as seed dispersal and harvesting activities and has been further developed into multiple models: LandClim, LANDIS Pro or LANDIS-II, among others. LandClim model (He and Mladenoff, 1999) was developed from LANDIS and ForClim by integrating tree competition processes, climatic and edaphic aspects and forest fire dynamics (Schumacher et al., 2004; Schumacher et al., 2006). However, its application has remained limited to Alpine regions and Central Europe (Bugmann and Solomon, 2000; Didion et al., 2009), thus significant efforts would have been required in model calibration for Mediterranean ecosystems. LANDIS Pro model (Wang et al., 2014b) incorporates the number of trees per cell to the previous data model structure, but its application has so far been limited to North America (e.g Iverson et al., 2017). LANDIS-II is a model that tracks biomass for each species-age cohort across large landscapes. It has also been developed from the original LANDIS model, but it has been built with a modular structure, promoting the development of multiple model extensions making it possible to represent ecological processes and forest succession with different levels of complexity (Scheller et al., 2007). This allowed the integration of the tree physiology PnET-II model as a new extension simulating forest succession in a more mechanistic way than previous ones (De Bruijn et al., 2014). Even though LANDIS-II and PnET extension had not been applied in Mediterranean areas before, it offered high flexibility to simulate multiple processes using different approaches (mechanistic succession simulation, rule-based management) in large areas, which encouraged us to use this model. Moreover, LANDIS-II is maintained by a large community of scientists and developers, who help maintain exhaustive model documentation, guidance materials and training activities for new users.

Thus, LANDIS-II was chosen for the simulation of forest dynamics in Mediterranean pine plantations. In Chapter 2, the initialisation and calibration process followed to implement the model in a 390,000 ha area in southeastern Spain is described. Data from the Third Spanish National Forest Inventory (IFN3, 2007), the Spanish Forestry Map (MFE, 2006) and the Andalusian Vegetation Map (REDIAM, 2007) were combined to generate a map of current vegetation communities in the study area, representing the starting point of model simulations. Lastly, different climate datasets (Cornes et al., 2018; Karger et al., 2020; Meinhardt and Centre, 2020; REDIAM, 2019) and regional soil maps (Rodríguez, 2008) were used to generate the biophysical inputs required by the model. Moreover, the calibration of species parameters is described and a simulation comparing different initialisation data —with and without shrub communities—is presented.

In Chapter 3, LANDIS-II is applied to evaluate future scenarios under different climatic conditions and management strategies. Climate scenarios represent the projected climate under different emission scenarios: current climate, moderate emissions (RCP4.5) and high emissions (RCP8.5). Management scenarios, designed in cooperation with forest managers, are oriented to diversify pine plantations in order to drive these forests towards more mixed and, therefore, climate-adapted forest ecosystems. They represent divergent viewpoints towards the management of pine plantations based on different balancing of the precautionary principle and the availability of resources allocated for management. This study allowed us to evaluate the possible impact of climate change and management scenarios across the landscape by looking at the multiple model outputs.

Agent-Based Modelling

Agent-Based Modelling, or Individual-Based Modelling, is a modelling technique which combines a landscape environment with discrete elements or *agents* (Table P.2). This technique is usually used for spatially-explicit models where landscape represents a simplified environment. As in Forest Landscape Modelling, landscape is generally divided into cells which have a series of variables describing the landscape in terms of, for example, environmental conditions (e.g. temperature, elevation). However, in contrast to Forest Landscape Modelling, in Agent-Based Modelling a set of agents representing individuals (e.g. a person, a tree, a company) are also present throughout the landscape. These agents also have a series of variables defining them (e.g. age, value) and usually have the capacity to move from one cell to another. Thus, Agent-Based Modelling is very appropriate for problems where the focus is on temporal and spatial interactions among independent agents and their environment (Railsback and Grimm, 2011).

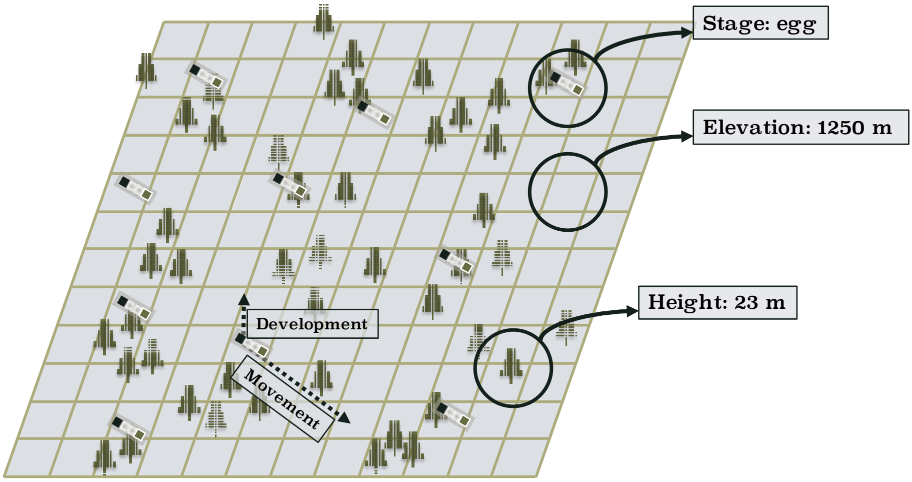


Figure P.3: Schematic representation of a general Agent-Based Model. Continuous arrows represent cells and agents' variables, in this case elevation (a cell state variable), height (tree state variable) and stage (colony state variable), while dashed arrows indicate submodels or processes, in this case movement and development of colonies.

Agent-Based Modelling allows the simulation of landscape processes, for example forest dynamics, but unlike Forest Landscape Modelling, it focuses on elements of the landscape which can move or interact with the landscape or each other, such as insects and the vegetation or preys and predators (Figure P.3). In other words, Agent-Based Models simulate individual agents' behaviour instead of aggregated variables describing the state of the whole system (Railsback and Grimm, 2011). These agents may be different from each other (for example in size) and only interact with other close agents or the landscape around their location (Railsback and Grimm, 2011). As a result of the individual behaviour of these agents, emergent properties arise. Thanks to these peculiarities, Agent-Based Models can simulate processes occurring at different scales across the system

(Railsback and Grimm, 2011). For example, we could see a reduced pasture availability at landscape level as a consequence of a higher herbivores birth rate due to some individuals changing to a more successful mating strategy.

Due to these characteristics, Agent-Based Modelling was chosen to simulate the population dynamics of the pine processionary moth. Thus, in Chapter 4, an Agent-Based Model called *INSTAR* simulating the population dynamics of the pine processionary moth is presented. The model is described following the "Overview, Design Concepts and Details" (ODD) standard protocol (Grimm et al., 2010). The internal structure of *INSTAR* models the temperature-dependent lifecycle of the species and spatial aspects of the species dynamics. A consistency test of the model is performed in order to calibrate species phenology in the study area. Moreover, a stress test analyses the robustness of the model against extreme temperatures.

Data availability and reproducibility

Data and scripts generated in this thesis have been documented and stored in stable repositories in order to ensure the availability and reproducibility of the analysis presented here. Scripts, raw data, model outputs and processed results for each chapter can be found at:

- Chapter 1: https://zenodo.org/badge/latestdoi/277569033
- Chapter 2: https://doi.org/10.5281/zenodo.4584475 and https://zenodo.org/record/4580266#.Yl1VeLixX9Q
- Chapter 3: https://zenodo.org/badge/latestdoi/412398572
- Chapter 4: http://sl.ugr.es/github_instar

Regarding model codes and documentation, LANDIS-II technical documentation is available at https://www.landis-ii.org/ and its code is distributed under an open source licence at https://github.com/LANDIS-II-Foundation. The last *INSTAR* stable version can be freely downloaded from Chapter repository and run under a NetLogo free licence (https://ccl.northwestern.edu/netlogo). Besides this, a demo execution of *INSTAR* can be executed at https://vlab.geodab.org/workflows, a virtual laboratory promoted by the ECOPOTENTIAL project (https://ecopotential-project.eu).

Target ecosystem

Pine plantations are one of the most common vegetal formations in Spain and the main focus of this thesis. These plantations were established with two main objectives. On one hand, the reforestation policy conducted in Spain between 1940 and 1980 intended to halt the high soil erosion rates in large areas of the territory as a result of excessive agricultural and pasture use in rocky topographies under a semiarid climate (Navarro Gómez-Menor and Medina Achirica, 2009). Subsequent abandonment of marginal low-productive areas was causing acute soil erosion, which constituted a threat of silting for newly built water reservoirs within a process of intense economic transformation of the agricultural sector (Iriarte Goñi, 2017). On the other hand, the reforestation activity represented certain economic revitalisation in highly depressed areas, either directly by the rise in value of areas with low revenues or indirectly by generating employment through reforestation activities (Sánchez Martínez et al., 2008). In some areas, the production of timber and forest products was also intended (Pérez-Soba Diez del Corral and Pemán García, 2017).

Almost 4 million hectares were reforested in Spain and approximately 250,000 ha were planted in the provinces of Granada and Almería, being among the most intensively reforested provinces (Vadell Guiral et al., 2017). These figures consider reforestations with multiple species groups, which differed among areas and climatic conditions, but conifers were the main taxonomic group considered in all cases (Figure P.4). In Granada and Almería, different pine species —*Pinus sylvestris* L. (Scots pine), *P. nigra* Arnold. (Black pine), *P. pinaster* Aiton (Maritime pine) and *P. halepensis* Miller. (Aleppo pine)—were selected depending on the altitude and thus the climatic conditions of each location (Mesa Garrido, 2019). These species were chosen over other late successional ones due to the poor condition of soils, their high growing rates and, in some cases, due to their expected capacity to generate products of economic value (Vadell Guiral et al., 2017).

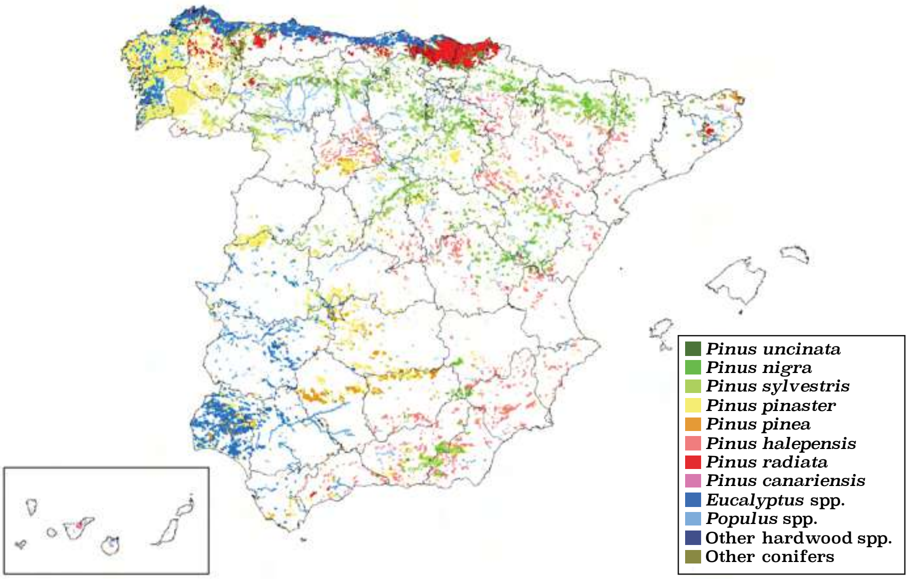


Figure P.4: Planted surface in Spain by species (1997). Map developed by Vadell Guiral et al. (2019) based on Ceballos (1966) and Ruiz de la Torre, J. (1990). Adapted from Vadell Guiral et al. (2019, page 120) and reproduced with permission.

Plants used in the reforestations were mostly produced locally in order to ensure their acclimatisation to their future growing conditions. Seedlings were finally planted at high densities (up to 5000 holes per hectare), often with multiple seedlings in the same hole (Picos Martín, 2017). Areas with steep slopes were usually prepared before planting by terracing, which caused significant impacts on already highly degraded soils (Figure P.5). The high planting densities, a benign climatic period during the 1950s and the protection against grazing through exclusion zones contributed to the establishment of numerous saplings and the development of extended forest covers (Figure P.6). The history of the Spanish reforestation programme is analysed in more detail in Pemán García et al. (2017), where a description of the planning process, the execution, and different aspects of the reforestations after establishment (pastures, relationship with protected areas, forest fires and silviculture) are reviewed in detail by an array of experts in the Spanish forestry field.

The high establishment rates achieved and the limited silvicultural interventions applied on pine plantations (Serrada Hierro, 2017) has nowadays resulted in wide areas covered by dense, homogeneous and monospecific pine woodlands

Figure P.5: Pictures of representative pine plantations in the study area. Top picture: Jerez del Marquesado (Granada), November 2021. Bottom picture: Lanteira (Granada), May 2018. Terracing can be observed in the second picture.

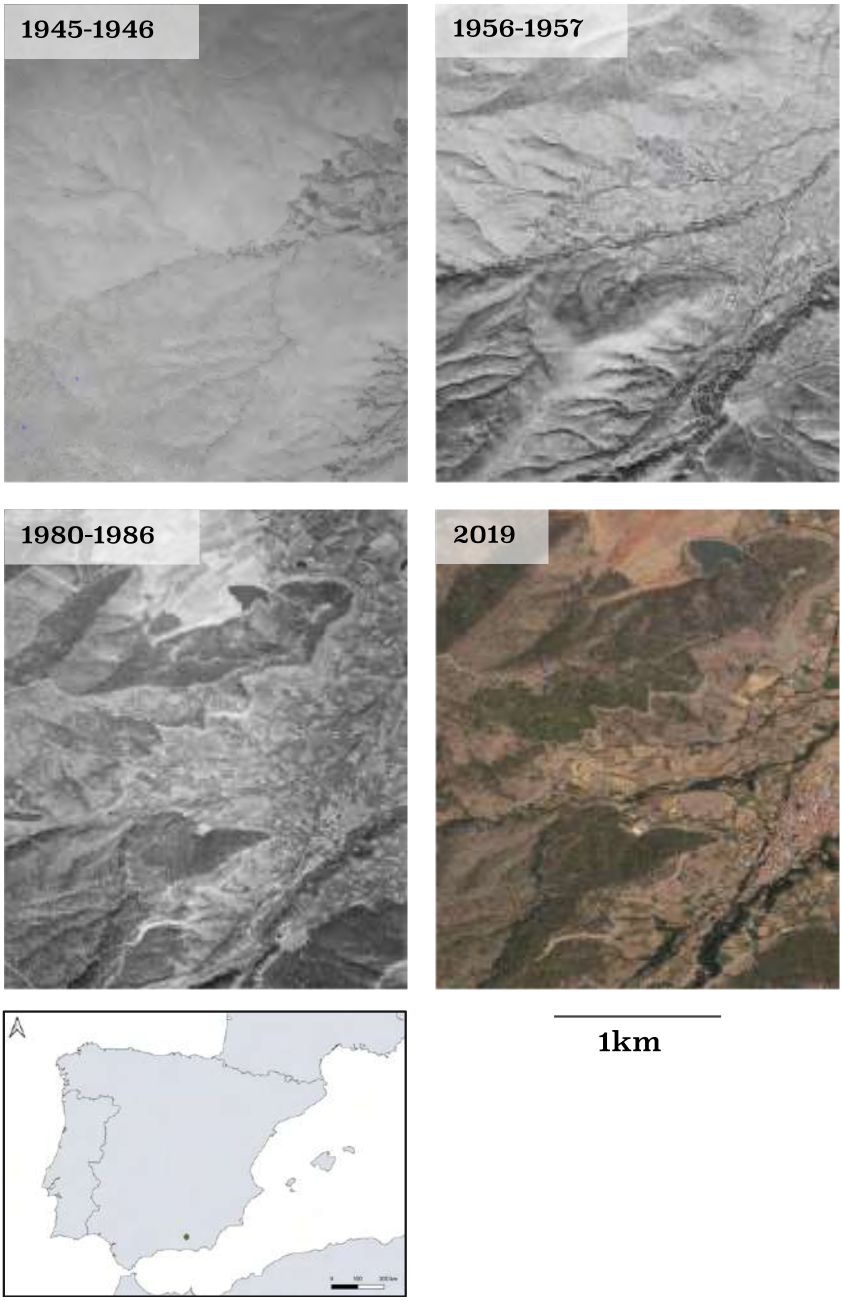


Figure P.6: Aerial pictures of the Jerez del Marquesado area (Granada, Spain) taken at different times: years 1945-1946 (so called "American Flight"), 1956-1957 (so called "American Flight"), 1980-1986 (National Flight) and 2019 (PNOA, *Plan Nacional de Ortografía Aérea*). Map below shows the exact location. Source: Digital photo library of *Instituto Geográfico Nacional*.

(Figure P.5). These stands currently present densities as high as 2,800 trees ha^{-1}, which limits tree growth and prevents regeneration of native vegetation due to high intraspecific competition (Gómez-Aparicio et al., 2009). Plant species diversity is generally low compared to native forest stands, although differences are found along climate, elevation and stand density gradients (Gómez-Aparicio et al., 2009). Moreover, these ecosystems pose multiple challenges for forest management, such as high vulnerability to forest fires (Pausas et al., 2004) and climate change impacts as a result of increased competition under water shortage (Fares et al., 2015; Navarro-Cerrillo et al., 2019; Sánchez-Salguero et al., 2012b) as well as high susceptibility to pest outbreaks (Hódar et al., 2003).

Numerous defoliators affect Mediterranean pine plantations since defoliator species find plenty of feeding resources in these homogeneous dense forests. Among other species, the pine processionary moth (*Thaumetopoea pityocampa*) is one of the most abundant and the one which receives most attention due to the urticating reactions it causes (Rodriguez-Mahillo et al., 2012). *T. pityocampa* is a Lepidoptera species belonging to the Notodontidae family. Together with *T. wilkinsoni*, it forms the processionary moth species complex (Auger-Rozenberg et al., 2015). The species is present all over the Mediterranean Basin, mainly feeding on *Pinus* genus but also on some *Cedrus* species (Sbabdji et al., 2015). Minimum winter temperatures limit the distribution of the species, since the larval stage occurs during this season (Buffo et al., 2007; Hoch et al., 2009). Therefore, increasing winter temperatures are expected to favour the expansion of this species, with some studies already reporting potential presence and higher frequency of outbreaks at higher altitudes and latitudes than before (Battisti et al., 2005; Pimentel et al., 2011).

The life cycle and mortality factor affecting the species have been described by several authors over time, with special attention to the larval stage (Démolin, 1987; Mirchev et al., 2015), while the nymph and moth phases remain less studied (but see Markalas, 1989; Torres-Muros et al., 2017). Other processes such as nymphs diapause, which can control population levels, or host selection, which determines survival probability and spatial distribution of the species, have also received relatively little attention (but see Niccoli et al., 2008; Paiva et al., 2011; Pérez-Contreras et al., 2008; Salman et al., 2016).

Several authors have studied the impact of *T. pityocampa* on their host, either at individual tree level (e.g. Arnaldo et al., 2010; Carus, 2009; Jacquet et al., 2013; Jacquet et al., 2012; Linares et al., 2014; Puri et al., 2015) and stand level (Damien et al., 2016; Dulaurent et al., 2012; Pimentel et al., 2017; Sangüesa-Barreda et al., 2014). These studies conclude that the species does not cause an irreversible growth loss on trees under normal conditions. Nevertheless, the combination with other stress factors such as drought is suspected to cause serious weakening of the host.

Foresters have dealt with this species for a long time and numerous chemicals and bioinsecticides have been proposed to control its population levels (Roversi et al., 2010; Sanchis et al., 1990). However, studies on the effectiveness of these methods find them ineffective to prevent pest outbreaks in severely affected areas (Cayuela et al., 2011). Therefore, scientists seem to agree that management measures aimed at increasing the resistance of the forest stands to the species are more appropriate in the long term. In this regard, some authors have attempted to simulate the distribution of *T. pityocampa* based on temperature constraints and make projections under global warming (Battisti et al., 2005; Robinet et al., 2007; Robinet et al., 2014). Their results show an expansion in the area suitable for the species, while current distribution is likely limited by the dispersal capability of the species.

Pine plantations are an interesting ecosystem to simulate forest dynamics for multiple reasons. Due to their anthropogenic origin they have a high impact in the socio-economic system around them. Both their creation and development has had significant consequences for society. For this reason, numerous stakeholders involved around these ecosystems are found, which facilitates the socio-ecological characterisation of the system. Moreover, by statutory imperative (*Plan Forestal Andaluz*) these forests are subject to intensive management aiming to increase their diversity in terms of structure and composition in order to adapt them to climate change and improve their resilience to multiple disturbances. Among other perturbations, defoliator insects —mainly the pine processionary moth—cause major impacts on these stands and therefore represent an interesting case study to simulate defoliator dynamics. Due to their anthropogenic origin they are especially sensitive to the impacts of climate change. In addition, they cover large surfaces, therefore their management is of key importance.

Study area

The study area considered in this thesis is located in the southeastern part of the Iberian Peninsula (Figure P.7). The models implemented in this thesis cover three spatial scales, and therefore the study area is described in relation to these different scales. On a large scale, the socio-ecological system encompasses the provinces of Granada and Almería. This area covers 2,142,200 ha and is home to 1,653,130 inhabitants (INE, 2021). A total of 277 municipalities are found, ranging from small rural ones (e.g. Carataunas with 200 inhabitants) to the large metropolitan areas of Granada (more than 500,000 inhabitants) and Almería (200,000 inhabitants).

The area shows a great variety of environmental conditions, ranging from desert areas to alpine ones, and is therefore an important biodiversity hotspot in the Mediterranean Basin (Médail and Quézel, 1999). For this reason, multiple and diverse Protected Areas have been declared in this area, such as the coastal Cabo de Gata-Níjar Natural Park and the Tabernas Desert Nature Reserve to various mountainous areas under diverse management and operating regimes. In the central part, the Sierra Nevada Protected Area (172,238 ha) shows a complex combination of uses due to its larger size, different protection regimes, diversity of ecosystems and presence of numerous settlements (Junta de Andalucía, 2011). Sierra de Baza Natural Park (53,649 ha), located in the northerneast part of the study area, has a strong livestock activity, while in Sierra de Huétor Natural Park (12,128 ha), in the northwest, recreational use predominates due to its vicinity to the city of Granada (Junta de Andalucía, 2004a; Junta de Andalucía, 2004b).

Forest dynamics are studied on a medium scale by considering an area of 390,000 ha containing the most relevant pine plantations within the larger study area (Figure P.8). The topography is complex, with several Baetic mountain ranges crossing it. In the southern part of the study area, Sierra Nevada crosses the area from east to west. In the northern part, Sierra de Arana is located in the west and Sierra de Baza y Filabres in the east. Between those two mountain formations lies

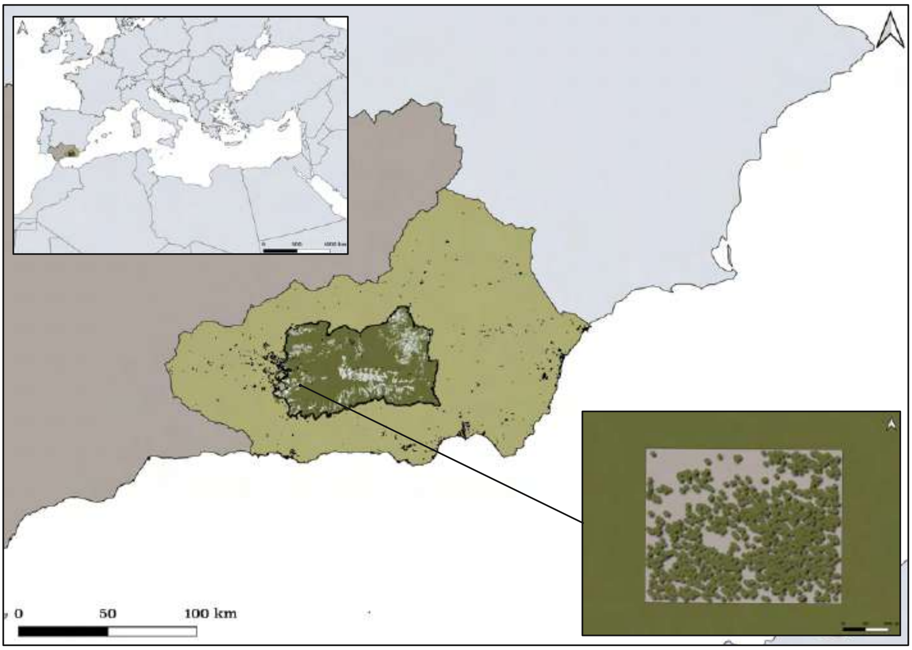


Figure P.7: Study area considered in this thesis. General location is shown in the panel on the top left corner. Three spatial scales are considered: the area covered by the provinces of Granada and Almería within the Andalusia region, which constitutes the socio-ecological system (in light green in the main panel); the mountainous area used to simulate the forest dynamics of pine plantations (in dark green in the main panel) and the sample plot used to simulate pine processionary moth dynamics (bottom left panel). Black areas denote urban areas and white areas denote pine plantations.

the Guadix Depression. In total, the area covers a wide altitudinal gradient, ranging from about 500 m a.s.l. to the 3,478 m of Mulhacén peak. Sierra de Arana is composed of diverse strips of sedimentary rocks. In Sierra de Baza y Filabres metamorphic rocks predominate, but limestones and dolomites are also found. Lastly, Sierra Nevada is mainly composed of metamorphic rocks such as amphibolite, serpentinite, mica-schists and marbles (Galdeano et al., 2007; IGME, 2015).

The medium scale study area is under a semi-arid Mediterranean climate, with broad differences depending on altitude and orientation resulting in multiple bioclimatic areas (REDIAM, 2018; Rivas Martínez, 1983). The lowest elevations of Sierra Nevada, connecting with Sierra de Arana, and also present in large surfaces of Sierra de Baza y Filabres, have an average annual temperature between 8-13 ℃

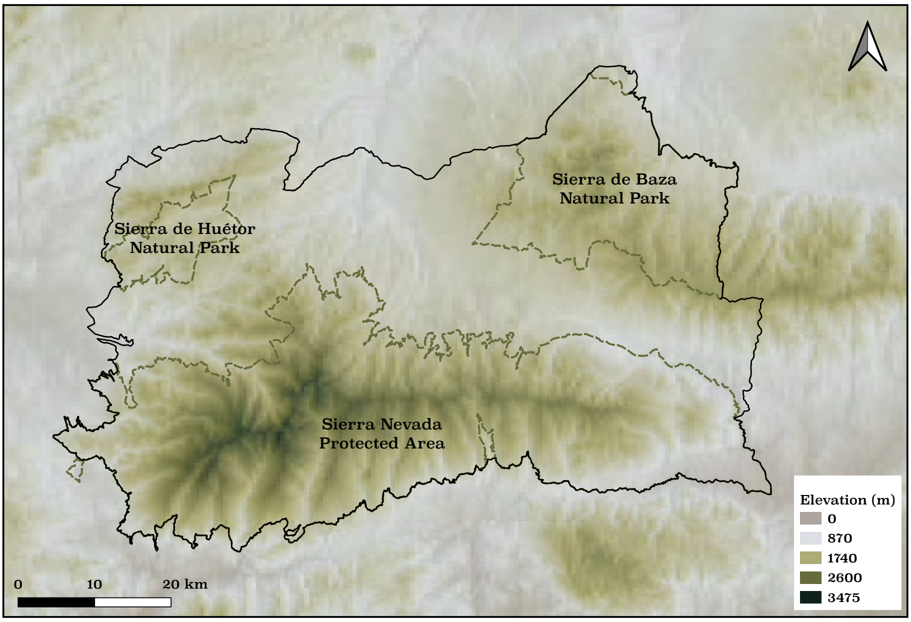


Figure P.8: Study area considered for the simulation of the forest dynamics of pine plantations. Dashed lines indicate the limits of Protected Areas within the study area.

and are mainly covered by a mosaic of pine plantations, mixed forests and sclerophyll shrublands. At higher elevations, with an average annual temperature of 4-8 °C, patches of pine plantations, shrublands and dispersed vegetation are found. The highest peaks of Sierra Nevada (average annual temperature below 4 °C) are covered by sparse vegetation adapted to the extreme conditions of these altitudes. The rest of this medium scale study area, mostly below 1,000 m a.s.l., shows an average annual temperature between 13-17 °C except for a small patch at the southeast whose average annual temperature is even higher (17-19 °C). In these warmer areas, diverse natural vegetation formations and crops form a mosaic.

Finally, the dynamics of the pine processionary moth are studied at a detailed scale by simulating a 16-ha plot within pine plantations. The plot is located in the eastern part of the Sierra Nevada Protected Area at an elevation of 1,796±34 m a.s.l. and contains 1,128 *P. halepensis* individuals according to LiDAR analysis. This area was selected as it constitutes a representative pine plantation stand with a constant presence of pine processionary moths with cyclic defoliation outbreaks (see Ros-Candeira et al., 2019, for details).

Part I

The socio-ecological system

Chapter 1

Participatory modelling for effective policy and management of Mediterranean pine plantations

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Manuscript

Key words participatory modelling, Fuzzy Cognitive Mapping, DPSIR framework, pine plantation, forest management, novel ecosystem

Resumen

Las plantaciones de pinos son usadas en todo el mundo como herramientas para prevenir la erosión del suelo y restaurar ecosistemas degradados. Estas plantaciones pueden ser consideradas ecosistemas noveles cuya gestión sostenible sigue siendo un tema de debate. De ahí que planteemos la necesidad de considerar estos ecosistemas desde una perspectiva múltiple que permita clarificar objetivos y proponer estrategias de gestión efectivas. En este trabajo aplicamos una técnica de modelización participativa para recopilar información sobre cómo la comunidad alrededor de las plantaciones de pinos mediterráneos entiende su estructura y funcionamiento. Concretamente, planteamos: i) construir una descripción compartida del funcionamiento del sistema de acuerdo a las percepciones, conocimientos y experiencias de los agentes involucrados; ii) revelar acciones de gestión propuestas por los diversos perfiles considerados. A tal fin combinamos la técnica 'Fuzzy Cognitive Mapping' con la clasificación 'Drivers, Pressures, State, Impacts and Responses' en un caso de estudio realizado en el sudeste español, en el que un total de 41 perspectivas individuales diferentes han sido plasmadas en forma de mapas cognitivos y posteriormente agregadas. El mapa social resultante integra las visiones de todos los participantes y revela cómo la densidad de árboles influye en procesos ecológicos esenciales. Se resaltan las complejas relaciones entre regeneración de la vegetación natural, la diversidad y la densidad, señalando lagunas de conocimiento que requieren más investigación. Las actividades forestales de claras y clareos son la principal acción propuesta para regular la densidad de los pinares de repoblación. Este mapa también muestra que los agentes demandan una transferencia de conocimiento más efectiva entre ciencia y gestión, mayores inversiones económicas y procesos de toma de decisiones más participativos. Nuestros resultados subrayan los beneficios potenciales de una gestión multidisciplinar y abogan por la creación de interfaces ciencia-gestión que puedan servir como plataformas eficaces de aprendizaje y gestión integrada de ecosistemas noveles.

Abstract

Pine plantations are used worldwide as a way to prevent soil loss and restore degraded landscapes. Plantations can be considered novel ecosystems for which sustainable management remains a topic under debate. We argue that a multiple knowledge perspective is required to clarify management objectives and propose effective strategies for these ecosystems. We apply a participatory modelling technique to gather information on how the community understands the structure and functioning of Mediterranean pine plantations. We specifically aim to: i) build a shared description of the system functioning according to stakeholder perceptions, knowledge and experience; ii) reveal preferred policy and management actions from diverse stakeholder profiles. To this end we combine Fuzzy Cognitive Mapping with the "Drivers, Pressures, State, Impacts and Responses" framework. For a case study from southern Spain, 41 different individual perspectives are obtained in the form of cognitive maps and then aggregated. The resulting social map integrates the views of all participants and reveals how stand density influences central ecological processes. The complex relationships between regeneration of native vegetation, diversity and stand density are highlighted and point towards gaps of knowledge which require further investigation. Thinning is revealed as the main action to regulate stand density in pine plantations. This map also reveals that agents demand a more effective knowledge transfer from science to management, increased economic investments and more participative decision-making processes. Our results highlight the potential benefits of multidisciplinary management approaches and advocate the creation of effective science-policy interfaces to serve as platforms for learning and integrated management of novel ecosystems.

1.1 Introduction

Afforestations and plantations with conifer species are natural resource management tools used for a broad range of goals such as carbon sequestration, economic development, land restoration or fuel production (EEA, 2016; Pausas et al., 2004; Pemán García et al., 2009; Quiroz Dahik et al., 2018). These plantations have been extensively used in dry areas of Europe as a means to halt soil erosion in disturbed areas within a context of agricultural land abandonment (EEA, 2016; Ruiz-Navarro et al., 2009). In the case of the Mediterranean, some authors describe these afforestations as novel socioecological systems, especially with respect to pine plantations (Lindenmayer et al., 2015). Novel or emerging ecosystems are those where previously unknown species assemblages are found as a result of natural ecosystems degradation or abandonment of highly anthropized systems (Hobbs et al., 2006).

How to adequately manage these systems is a debated issue. Often, traditional management and conservation strategies have aimed to restore a modified ecosystem to its previous conditions (Jordan III and Lubick, 2011; Palmer et al., 2016). However, there are concerns about the desirability of these strategies, given the limited resources available for conservation (Hobbs et al., 2006). Moreover, the large extent of novel ecosystems worldwide and the new conditions posed by global change represent additional challenges. Some experts therefore argue for a more pragmatic approach and the need to establish clear management objectives (Lindenmayer et al., 2015) that explicitly take into account these challenges. In either case, the management of such novel ecosystems can be challenging since they present new conditions where outcomes of commonly used management measures are uncertain.

Here we suggest a methodology to explore novel ecosystem functioning and management options from the perspective of local stakeholders. Illustratively we examine this for the Mediterranean case study of southeastern Spain pine plantations. The rocky topography as well as the semiarid climate of southeastern Spain, combined with intense deforestation in the first half of the twentieth century, caused a high rate of soil erosion (Navarro Gómez-Menor and Medina Achirica, 2009). This situation led to the implementation of a very ambitious reforestation programme in the 1940s with two main goals: reducing soil erosion in the short term and restoring original ecosystems (mainly broadleaf forests) in the long term (Pemán García et al., 2017). Even though the short term goals have been achieved (Chirino et al., 2006; Martín-Peinado et al., 2016; PFA, 2002), the long term goals are far from completion. The general lack of appropriate forest management has resulted in very dense, monospecific and coetaneous stands, and to a stagnant ecological succession. As a consequence, various environmental problems have emerged: high susceptibility to forest pest outbreaks and forest decay (Hódar et al., 2003), high risk of catastrophic forest fires (Pausas et al., 2004) and, more recently, increased exposure to climate change impacts such as droughts and wildfires (Fares et al., 2015; Sánchez-Salguero et al., 2012b).

Acknowledging the complexity of these socio-ecological systems, we argue that multiple knowledge approaches, in particular, the use of participatory system modelling, could be helpful in order to identify more sustainable and effective management options for these novel ecosystems. Specifically for pine plantations, this could support the long-term goal of ecosystem restoration. In this study, we aim to: i) build a shared description of the system functioning according to stakeholder perceptions, knowledge and experience and; ii) identify the preferred policy and management actions revealed from the diverse stakeholder profiles.

1.2 Methods

1.2.1 Methodological approach

In this work we apply a participatory approach, Fuzzy Cognitive Mapping (FCM), in combination with the Drivers, Pressures, State, Impacts and Responses (DPSIR) framework to describe southeastern Spain pine plantations as novel ecosystems and extract views and proposals for their management. A detailed description of the study area can be found in Supplementary Material S1.1.

Fuzzy Cognitive Mapping (FCM) is a technique that allows integrating diverse sources of information into a semi-quantitative model. FCM has been broadly used in environmental and socio-ecological research (Özesmi and Özesmi, 2003) and is especially suitable for situations where lack of data hampers the use of other more quantitative modelling techniques (Reckien, 2014). FCM is often used for knowledge sharing and knowledge integration and to promote group-developed solutions to problems, among other uses and benefits (Gray et al., 2018; Gray et al., 2015; Jetter and Kok, 2014; Olazabal et al., 2018a; Papageorgiou and Salmeron, 2013; Singh and Chudasama, 2021).

Fuzzy Cognitive Maps consist of a set of concepts which relate to each other through causal relationships. Cause-effect relationships between concepts are characterised by a sign and a weight. A positive sign means that an increase in concept A leads to an increase in concept B, while a negative sign means that an increase in concept A leads to a decrease in concept B. The associated weight expresses the strength of the relationship, either in qualitative or quantitative terms. The final result can be depicted graphically as a semi-quantitative causal diagram or numerically as an adjacency matrix (see Supplementary Material S1.2). Graph theory indices are commonly used to structurally analyse FCM results and to compare maps (Devisscher et al., 2016; Kok, 2009; Özesmi and Özesmi, 2004). Among the most common indices, centrality measures the relevance of a concept in the map, by showing how connected the concept is with other concepts. The cognitive maps intend to capture the knowledge, experience and perception of stakeholders on a certain topic and in this way also reveal their main interests or concerns (Kok, 2009). For more details on FCM and the diversity of methodological approaches, the readers are referred to (Glykas, 2010; Gray et al., 2015; Lopolito et al., 2020; Özesmi and Özesmi, 2004).

Since we are especially interested in (a) obtaining a description of the system and (b) collecting proposals for policy and management, we implemented FCM in two phases: a first phase to obtain the description of the system and the second phase to elicit potential actions. However, based on previous evidence (Olazabal et al., 2018a; Tepes and Neumann, 2020), we acknowledge that interviewees tend to incorporate management proposals or actions (b above) during the phase of description (a). Because of this, and after concluding the mapping exercise, we decided to apply a classification of concepts based on the DPSIR framework, as proposed by Hobbs et al. (2002), Mehryar et al. (2017), and Vanermen et al. (2020). This framework was proposed in EEA (1999) in the context of policy and environmental indicators. Under this scheme, "social and economic developments (Driving Forces) exert Pressures on the environment and, as a consequence, the State of the environment changes" (Maxim et al., 2009, p. 12). As the State changes, Impacts arise in ecosystems, human health or society and may lead to societal Responses that mitigate, adapt or avoid them (Maxim et al., 2009). In this work, the concepts classified as "Responses" allow us identify the actions and reactions from the different stakeholder profiles. Figure 1.1 shows a schematic view of the methodology applied in this work.

1.2.2 Interviews and maps building

In this study, individual maps were elicited through face-to-face interviews, and were later analysed and processed so as to develop a common terminology and level of detail. The individual processed maps were then merged into a social map following the procedure outlined in Olazabal et al. (2018b).

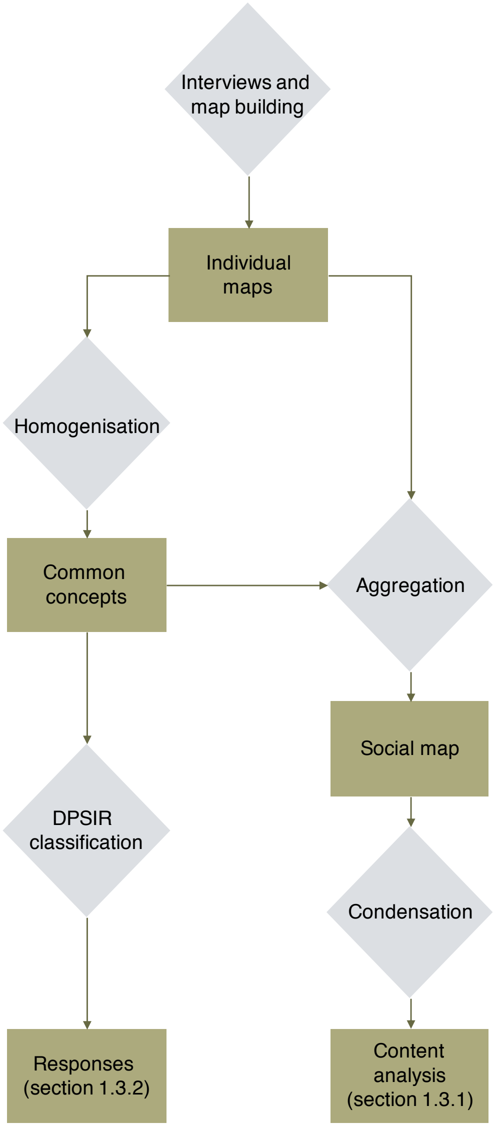

Figure 1.1: Schematic view of the workflow applied in this study. Rectangles depict products or results while rhombus represent analytical procedures.

The interviews were designed in a way to be able to collect the most comprehensive information possible from the most diverse stakeholders with a recognised role in southeastern Spain pine plantations. Experts specialising in different fields, working for different institutions and at different levels of responsibility were involved. Applying the snowball technique (Bonjean et al., 1967), an initial set of potential interviewees was contacted and asked to recommend other persons. A description of interviewed stakeholders is provided with this article (Supplementary Material S1.3). A total of 46 maps were elicited, and a final set of 41 individual maps were found suitable to be included in this study. The reasons for map discarding include stakeholder's knowledge and expertise being lower than previously expected (3 maps) and lack of understanding, commitment and/or motivation to follow the methodology (2 maps). Stakeholders are classified into three types:

- Forestry managers: 18 agents whose work is directly related to forest areas and pine plantations management;
- Researchers: 13 scientists based in nearby universities and institutes that conduct research within the study area in different fields;
- Socio-economic agents: 10 stakeholders who have a relationship with the system, either because they are influenced by it or because they influence it with their actions, such as non-governmental organisations, environmental associations, civil representatives, local administrators, farmers and media.

Interviews took place in Spanish, allowing an easy and detailed exchange of information between interviewee and interviewer. The entire process was recorded and all interviews were conducted by the same analyst to ensure a standard procedure. Each interview started with a general introduction on the area under consideration, the project objectives and the methodology and was supported through printed material (see Supplementary Material S1.4). Then, in the elicitation process, interviewees were asked to describe the system (a) *If we talk about pine plantations in this area and its surroundings, what comes to mind? How would you describe their state?*. Then, interviewees were asked to provide proposals for policy and management (b): *What could be done to improve the situation?*. Following the same technique proposed by Olazabal et al. (2018b), new concepts and new relationships arising from the answer to the second question were included in the map. The analyses and data processing reported in this study refer to the final individual maps produced through the set of the two questions addressing the description of the system and the potential actions.

The analyst led the discussion in a way to be able to capture the explanations in the form of cause-effects relationships. For this purpose, relevant concepts were collected and then relationships among them identified and drawn on paper leading to a causal network. Causality was understood as a relationship between two concepts implying that, if one concept changes (i.e. increases or decreases), it provokes a change in another concept. Further explanation was often required regarding cause-effect relationships that might be different in different locations. In this case, relationships were expressed as: "in spots where concept A is high, concept B is high/low." When the interviewee was satisfied with the map, he/she assigned a weight to each relationship. Interviewees were offered to draw the map themselves or, a mostly preferred option, they guided the interviewer in the drafting process.

1.2.3 Data processing, homogenisation and aggregation

Elicited maps were processed, digitised, homogenised and aggregated. Data processing includes concept annotation, translation, corrections and documentation of changes, for which the interview recordings were used.

The original individual maps and the social map were analysed based on graph theory indices such as number of concepts, number of relationships and concept centrality (see Özesmi and Özesmi, 2004, for a detailed description). The 41 elicited individual original maps contain an average of 14.5±3.3 concepts and 19.6±7.6 relationships.

In order to be able to aggregate the individual maps, a common terminology across all maps is required. This is achieved by homogenisation (Olazabal et al., 2018b) or qualitative aggregation (Vasslides and Jensen, 2016). Homogenisation reduces the complexity and scale variability of concepts contained in the individual maps to a common terminology and common level of detail defined by the analyst. Homogenisation is a sensitive step in FCM, highly dependent on project objectives and which can reduce the transparency and reproducibility of the methodology. We follow the recommendations from Olazabal et al. (2018b) to address the challenges in this phase. Homogenisation took place with respect to both concept terminology and hierarchy. Homogenisation with regards to terminology consists of applying the same terminology to concepts that have the same meaning. Homogenisation with respect to hierarchy refers to the process of either combining or expanding concepts in order to achieve a common level of detail. As an example for expanding, maps that mentioned "thinning and pruning" as a single concept were modified in order for these to appear as two distinct concepts. Homogenisation was performed in an iterative process and all the decisions taken were documented in detail. The homogenisation step reduced the number of original concepts from 666 to 144.

After homogenisation, individual maps were aggregated. Weights of recurrent relationships (i.e. the same relationship appearing in multiple maps) were computed by calculating the average. In addition their standard deviation was provided as a means to capture the variability of views. Randomised accumulation curves showing the number of new concepts added per map added as well as the total accumulated number of concepts were used to validate the sample size (Özesmi and Özesmi (2004), Supplementary Material S1.5). Map analysis and aggregation was performed with R software and packages such as 'FCMapper' (R Core Team, 2020; Turney and Bachhofer, 2016). As an important innovation in this kind of analysis, instead of commonly applied matrix algebra the computational analysis was mainly carried out considering a relational database where concepts and relationships among them are listed in related tables. Scripts used in this study, raw data and processed results are available from https://zenodo.org/badge/latestdoi/277569033.

1.2.4 Content analysis: condensation and DPSIR classification

Then the social map was analysed in terms of its content. For this purpose, the identification of relevant information was based on relationships recurrence among the individual (homogenised) maps which build up the social map. Recurrence here refers to the number of times that a relationship was mentioned across all elicited individual maps. In this manuscript we analyse in more detail a condensed view of the social map, which is obtained by considering only those relationships with a recurrence higher than 5 (the maximum recurrence was 19). The obtained outcomes are described in section 1.3.1. In addition, all homogenised concepts were classified into DPSIR categories by two analysts in an iterative process in order to extract proposed responses. Collected responses are analysed per stakeholder group in section 1.3.2.

1.3 Results

1.3.1 A participatory description of pine plantations functioning

In this section we summarise the main findings obtained from the condensed social map (Figure 1.2). The condensed social map shows those relationships which are recurrent among five or more stakeholders. That is, five or more stakeholders have included these relationships (connection of concept A to concept B) in their individual maps. For this reason, the condensed map (16 concepts) is able to reveal shared understandings of the structure and functioning of the system.

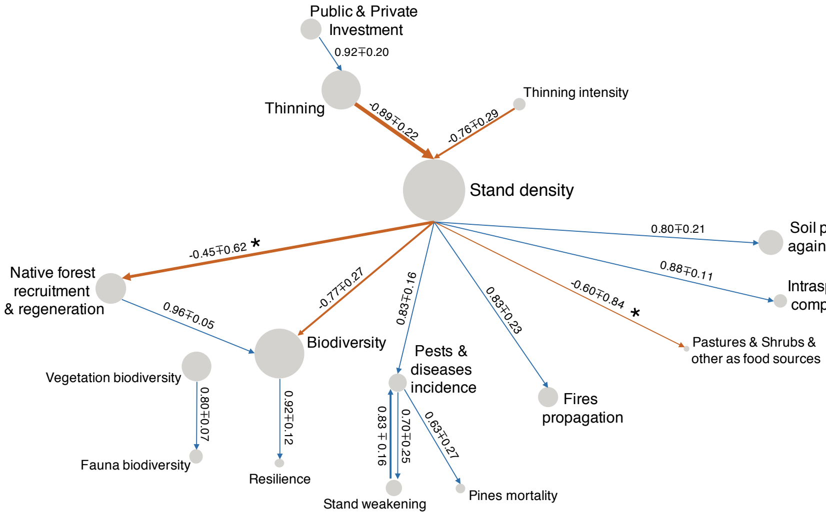

Figure 1.2: Condensed social map showing only relationships that appear in at least 5 of the 41 maps. Node size is proportional to the concept's normalized centrality. Arrow thickness is proportional to number of relationship recurrence across maps (maximum = 19). Relationships weights are indicated by mean (strength) and standard deviation (spread) across maps. Positive relationships are highlighted as blue arrows, while negative ones appear in red. Legend: asterisk (*) highlights relationships with opposite weight signs across individual maps.

Stand density is a structural component of the forest that emerges as the central concept with numerous outgoing and incoming arrows. This means that *stand density* controls a variety of other variables in the system under study and is simultaneously influenced by other concepts. The connection between *thinning* and *stand density* stands out as the most repeated relationship, which makes it the most agreed-upon aspect in the social map. Stakeholders also express similar understandings about the effect of *stand density* on ecological concepts such as *biodiversity* and *native forest recruitment & regeneration*. The map also highlights relationships centred around *biodiversity* aspects and forest *resilience*.

For each connection, the mean value (strength of causal relationship) as well as the spread of weights (a narrow spread indicates a high degree of consensus between stakeholders) can be assessed. We observe that only strong and intermediate relationships are present in the condensed social map, with average values higher than 0.60 for both positive and negative influences. The agreement between stakeholders is high with standard deviations below 0.30 in all cases except for two (marked with a star in Figure 1.2). These two exceptions, which are examined in more detail in the following section, show a high variability and even contain weights with different signs potentially indicating structural disagreement. The first exception is the influence of *stand density* on *native forest recruitment & regeneration*. In 11 cases increased *stand density* is reported to decrease *native forest recruitment & regeneration* whereas two stakeholders reported an increasing effect. In other words, a high number of stakeholders consider that a higher *stand density* causes a decrease in the regeneration of native species. However, two stakeholders reported a positive relationship of *stand density* to *native forest recruitment & regeneration*. This difference in viewpoint is explained when analysing the narratives provided by these two stakeholders regarding the nature of native species specific to the area. These two stakeholders mentioned that shade-tolerant species, and *Quercus ilex* seedlings in particular, benefit from a high *stand density* since it ensures a shaded soil surface. The consideration of these specific native forest species explains the disagreement.

Similarly, for the second exception, *stand density* is reported to negatively affect *food sources* by 5 stakeholders whereas one stakeholder posits a positive relationship. Upon closer examination we observe both a positive and negative arrow in one of the single maps. As explained by the interviewee, pastures are inhibited whereas mushrooms are favoured by increasing *stand density*, therefore resulting in two different signs and the apparent disagreement. When examining all of the recurrent relationships (i.e. mentioned at least twice by interviewees), 6 (4.2 %) of them included opposite signs indicating a low number of connections that contain disagreement.

1.3.2 Stakeholders responses

In this section, we analyse those concepts classified as Responses according to the DPSIR framework (see section 1.2.4 for details), which include both (passive) reactions and (pro-active) actions to impacts. A Venn Diagram shows which Responses are common across stakeholder groups; over 25 % are shared among all stakeholder groups (Figure 1.3).

According to its centrality, *thinning* is the main Response for all stakeholder groups. Other silvicultural actions are also among the most relevant Responses for all stakeholder groups (see Figure 1.3 for details). However, all stakeholder groups also highlight non-silvicultural actions such as *public and private investment*, *participative and democratic decision-making processes* and *social discontent*. The importance of *planning and projects quality* and *scientific activity and knowledge* are also mentioned by all stakeholder groups.

Although an important number of Responses are shared among all stakeholder groups, clear differences also emerge. Socio-economic agents and forest managers share some Responses which were not mentioned by researchers. This is the case of *science-management transfer and feedback*, *promotion of local economy*, *biomass, wood and firewood use promotion*, *environmental education* and *pines planting*. Moreover, each stakeholder group also mentioned a set of Responses which are distinct from the other two groups. Researchers highlight conservation aspects and forestry and policy issues, while they also express concerns regarding forest fires. Socio-economic agents refer to forest uses and their regulation and they also highlight the importance of the *manager's bonding with territory*. Forest managers refer to actions closely linked to their daily management activity, such as to *promote natural vegetation*. Forest managers also give importance to *knowledge, experience and tools for management*. Finally, it is remarkable that there are no Responses shared exclusively by Researchers and Forest managers or by Researchers and Socio-economic agents.

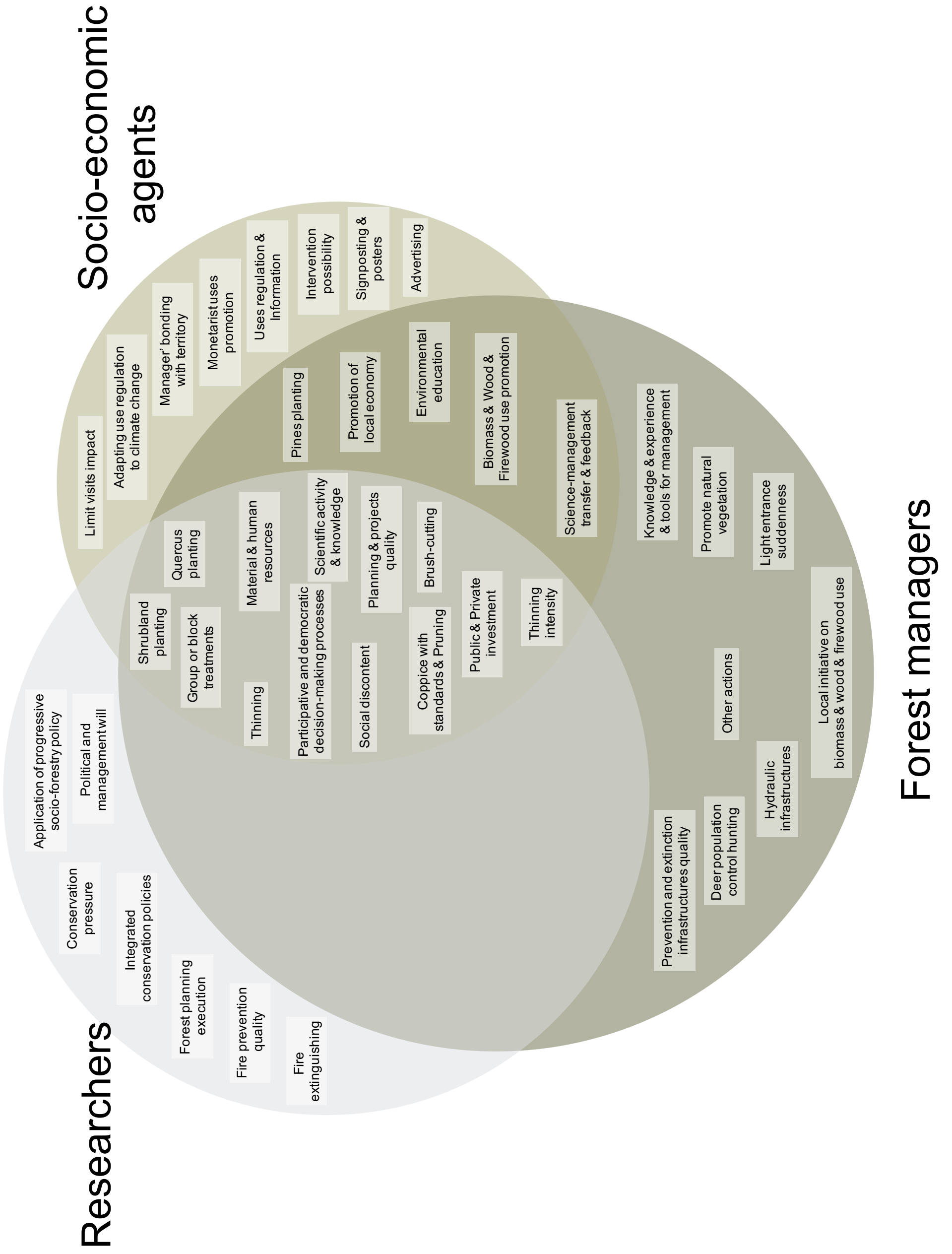

Figure 1.3: Responses collected among stakeholders' groups: forestry managers, researchers and socio-economic agents. Circles size is proportional to the number of persons interviewed in each stakeholder group.

1.4 Discussion

1.4.1 Structure and functioning of novel ecosystems: A shared system understanding emerges from combining individual perspectives

The results of this participatory exercise show the complex relationships involved in the structure, functioning and management of pine plantations and the agreements on what are deemed to be the most relevant cause-effect relationships. In this sense, we have applied FCM to extract a collective description of the functioning of the novel ecosystem under study, which provides more complex and holistic information than alternative approaches that focus on isolated processes or aspects (e.g. Vanermen et al., 2020).

Complex Fuzzy Cognitive Maps such as the one developed in this study can contain a high number of interrelated concepts, and therefore, synthesizing information from them can be challenging. To overcome this, we suggest a formal and transparent procedure to produce a condensed social map (16 concepts) that provides a synthetic description of the complete social map (144 concepts). As a result, a single variable —stand density—has emerged as a key concept to understand the functioning of pine plantations. This finding aligns with current scientific evidence where stand density is deemed to be one of the most important drivers explaining the structure and functioning of our pine plantations (Gómez-Aparicio et al., 2009).

In terms of how stakeholders perceive the strength of the cause-effect relationships between concepts, our study generally reveals a high level of agreement. The low variability in the weights given to the relationships can be seen as a measure of consensus. The few relationships exhibiting sign differences among participants were traced back to differences in interviewees' reasoning and did not indicate errors in the homogenisation process. The low percentage of connections exhibiting sign changes confirms the credibility of the information gathered as well as the consistency and robustness of the homogenisation process conducted in this study. One aspect of this robustness was to contemplate early on the possibility that non-monotonic relationships between two variables could give rise to opposite signs. Non-monotonic relationships are a common characteristic in environmental systems, such as changes along environmental gradients of temperature (Hobbs et al., 2002; Maestre et al., 2016; Vasslides and Jensen, 2016). FCM can be limited by these types of relationships (Carvalho, 2013; Reckien et al., 2013).

To overcome this, well-established non-monotonic relationships such as the one between herbivory pressure and biodiversity were identified during the interviews phase and correspondingly modelled by means of concept expansion. In this example, herbivory pressure was disaggregated in order to identify the effects of grazing on biodiversity under natural (herbivory) *versus* under overexploitation conditions (herbivory overuse).

Our social map reflects the complex interactions between stand density, regeneration and biodiversity as well as the uncertainties regarding these relationships. As expressed by the interviewees, the regeneration of one of the main native tree species in the area —*Quercus ilex*—is negatively affected by high stand densities (González-Moreno et al., 2011; Navarro-González et al., 2013) but at the same time requires shading from the tree canopy during the first years of development. Moreover, other factors such as distance to seed sources and past land use also play a role in the regeneration of native vegetation and related biodiversity levels in pine plantations (Gómez-Aparicio et al., 2009; González-Moreno et al., 2011; Navarro-González et al., 2013), which is reflected in the complexity reported in our social map.

1.4.2 Actions and reactions: Stakeholders demand silvicultural actions but also participative decision-making

We find that stakeholder groups share an important number of Responses obtained through the DPSIR classification, showing a relative agreement in terms of how to manage these novel ecosystems. The analysis of proposed responses highlights the importance of silvicultural actions for all stakeholders but also reveals other responses that are worth discussing. Thinning is revealed as the most influential (most central) silvicultural treatment but we also find that stakeholders demand more knowledge and an effective transfer from science to management in this respect. All stakeholder groups perceive a need to increase economic investments in the management of pine plantation and agree upon the need for more participative and democratic decision-making. The implementation of such participative decision-making could ideally reduce the existing social discontent reported by all groups.

By analysing the specific responses proposed by each group, some tension between stakeholders can be observed. Socio-economic agents and forest managers propose the promotion of the local economy through, for example, biomass use. However, forest managers wish for more local initiatives while socio-economic agents emphasise the need of stronger bonds of the managers with the territory.

In addition, researchers propose socio-forestry policies and envisage more willingness to act in the political and management domains. These demands and wishes may reflect a lack of communication among stakeholder groups, which could be hampering the implementation of integrated management solutions that could be supported by all groups. In this regard, researchers seem to be the most isolated group, as they do not share concepts with any of the other two groups individually, while managers and socio-economic agents share more concepts.

Considering the collected DPSIR Responses, ecological aspects seem more dominant in our community than socio-economic aspects, which do not seem to be completely embraced in the management of these ecosystems. This shows that the management of southeastern Spain pine plantations is still mainly conceived in relation to forest science (e.g. Mesa Garrido, 2019). The restoration of these systems towards fully functional forest ecosystems is a complex environmental challenge which requires more inter- and transdisciplinarity (Feliciano et al., 2019; Lang et al., 2012) and therefore further efforts to increase the diversity of experts involved in the management of these systems is recommended.

1.4.3 Implications for policy, management and research

Our results contain valuable insights on how pine plantations are conceived and managed in the study area. These ideas can be translated into direct implications for policy, management and research.

Our study has unveiled some unexpected needs. Despite the great research efforts carried out in the last decades to understand the functioning of pine plantations, there are still some knowledge gaps that should be covered. The most relevant one is the still uncertain relationship between stand density and regeneration and diversity (see Figure 1.2). In this regard, we argue that further research is required to quantify how different silvicultural treatments affect forest regeneration and diversity. This could be done by the implementation of thinning experiments that monitor native forest regeneration as well as diversity indices at local scales, as these variables may vary significantly at relatively small distances.

Another implication for research is directly related to the modelling and simulation of the functioning of complex socio-ecosystems. The suggested methodology provides a plethora of structural and functional insights that could be used to create new models or to improve existing ones by considering previously overlooked relationships.

Our results state the need to enrich both science and policy practice by integrating more disciplines. In our community, ecological aspects dominate and socio-economic considerations are not fully integrated.

Lastly, the stakeholders have explicitly mentioned some gaps and drawbacks in the governance of pine plantations as novel ecosystems. They request more integrated decision-making processes that would help to achieve the long term objectives of pine plantations management. This is in line with recent calls from the science for more involvement of local stakeholders in the decision-making process, a more effective knowledge transfer process between scientists and managers and the incorporation of more disciplines into the process. Based on this and the results from our study, we therefore advocate for the creation of effective science-policy interfaces (e.g. López-Rodríguez et al., 2015), which could serve as platforms for integrated management of novel ecosystems such as the studied pine plantations.

1.5 Conclusions

In this work, we applied Fuzzy Cognitive Mapping to extract a collective description of the functioning of pine plantations. Our results highlight the role of stand density as a key indicator explaining the functioning of these novel ecosystems, while thinning has been proposed as the main management action to control it. Our study points towards the need to study in more detail the relationships between stand density, regeneration and diversity.

By developing a more complex and holistic system characterisation than is typically obtained with traditional approaches, we were able to identify a very wide range of forest management actions. Our study reveals a demand by all stakeholder groups for a more integrative socio-ecological policy and points towards gaps and drawbacks in the current governance of pine plantations.

Based on these illustrative participatory modelling exercise, we conclude that, current approaches have been sufficient to satisfy the short-term goals of erosion control. However, to achieve the long-term goal of restoring the system to a fully functional forest ecosystem, our study points towards the need for a more integrative, multidisciplinary and socio-ecological approach.

Gathering, connecting and interpreting information on how a diverse stakeholder community understands the structure and functioning of the target system based on their perceptions, knowledge and experience is deemed to be a key step for the effective and sustainable management of Mediterranean pine plantations as novel ecosystems.

Part II

Forest dynamics

Chapter 2

A Step-by-Step Guide to Initialize and Calibrate Landscape Models: A Case Study in the Mediterranean Mountains

Suárez-Muñoz M., Mina M., Salazar P.C., Navarro-Cerrilo R.M., Quero J.L., Bonet-García F.J. (2021)
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Key words calibration, Mediterranean area, LANDIS-II; PnET-Succession, forest landscape model, forest succession, initial vegetation map, forest inventory

Resumen

El uso de modelos de paisaje forestal (Forest Landscape Models) espaciales interactivos ha aumentado en los últimos años. Estos modelos son herramientas muy valiosas para evaluar nuestro conocimiento sobre el funcionamiento y aprovisionamiento de servicios de los ecosistemas, además de aliados esenciales para la predicción de cambios futuros. Sin embargo, desarrollar y preparar los datos de entrada necesarios para aplicar estos modelos requiere una inversión sustancial de tiempo. Aunque la inicialización de modelos y su calibración, a menudo, suponen la mayor parte de los esfuerzos por parte de los modeladores, dichos procesos raramente son reportados con suficiente detalle. Nuestro trabajo documenta el proceso de calibración e implementación de un modelo de paisaje forestal ecofisiológico (LANDIS-II con PnET-Succession) en una bioregión donde dicho modelo no ha sido aplicado antes (montañas mediterráneas del sudoeste de Europa). En este artículo, describimos la metodología llevada a cabo con el fin de producir los datos de entrada necesarios para describir las condiciones iniciales de vegetación y de variables abióticas. Hemos testado el comportamiento del modelo en simulaciones con una sola celda y calibrado los parámetros del modelo usando estimaciones locales de biomasa e información bibliográfica de cada especie considerada. Finalmente, hemos testado la influencia de considerar diferentes condiciones iniciales —con y sin matorrales—en la simulación de la dinámica forestal mediante la aplicación del modelo calibrado a escala de paisaje. La combinación de datos a escala de parcela y de mapas de vegetación nos ha permitido generar un mapa detallado de las comunidades vegetales iniciales. Por otro lado, las simulaciones llevadas a cabo en celdas individuales revelaron que el modelo era capaz de reproducir estimaciones de biomasa y efectos de competencia realistas para los distintos tipos forestales presentes en el paisaje, así como unos patrones de crecimiento mensual plausibles para las especies de montaña mediterráneas. Nuestros resultados subrayan la importancia de considerar las comunidades de matorral en los modelos de paisaje forestal, ya que estas influyen en las dinámicas temporales de las especies arbóreas. Además, nuestros resultados muestran que, en ausencia de perturbaciones naturales, manejo selvícola o cambio climático, las simulaciones a escala de paisaje proyectan un aumento de la biomasa de varias especies a lo largo de las próximas décadas, aunque los patrones espacio-temporales de cada una son distintos debido a los efectos de competencia y la heterogeneidad paisajística. Mostrando un flujo de trabajo detallado para inicializar y calibrar un modelo de paisaje forestal, nuestro estudio promueve el uso de estas herramientas por parte de nuevos usuarios en aplicaciones forestales y de cambio climático. Por tanto, recomendamos una documentación transparente y reproducible de los procesos de inicialización en la modelización de paisaje forestal.

Abstract

The use of spatially interactive forest landscape models has increased in recent years. These models are valuable tools to assess our knowledge about the functioning and provisioning of ecosystems as well as essential allies when predicting future changes. However, developing the necessary inputs and preparing them for research studies require substantial initial investments in terms of time. Although model initialization and calibration often take the largest amount of modelers' efforts, such processes are rarely reported thoroughly in application studies. Our study documents the process of calibrating and setting up an ecophysiologically based forest landscape model (LANDIS-II with PnET-Succession) in a biogeographical region where such a model has never been applied to date (southwestern Mediterranean mountains in Europe). We describe the methodological process necessary to produce the required spatial inputs expressing initial vegetation and site conditions. We test model behaviour on single-cell simulations and calibrate species parameters using local biomass estimations and literature information. Finally, we test how different initialization data —with and without shrub communities—influence the simulation of forest dynamics by applying the calibrated model at landscape level. Combination of plot-level data with vegetation maps allowed us to generate a detailed map of initial tree and shrub communities. Single-cell simulations revealed that the model was able to reproduce realistic biomass estimates and competitive effects for different forest types included in the landscape, as well as plausible monthly growth patterns of species growing in Mediterranean mountains. Our results highlight the importance of considering shrub communities in forest landscape models, as they influence the temporal dynamics of tree species. Besides, our results show that, in the absence of natural disturbances, harvesting or climate change, landscape-level simulations projected a general increase of biomass of several species over the next decades but with distinct spatio-temporal patterns due to competitive effects and landscape heterogeneity. Providing a step-by-step workflow to initialize and calibrate a forest landscape model, our study encourages new users to use such tools in forestry and climate change applications. Thus, we advocate for documenting initialization processes in a transparent and reproducible manner in forest landscape modelling.

2.1 Introduction

Forests are indispensable ecosystems for human societies. Due to their role as climate regulators, soil protectors and biodiversity hotspots, forests provide a multitude of ecosystem services and are fundamental elements in the world's economy (Krieger, 2001; Martínez Pastur et al., 2018). The potential adverse impacts of global change on forest ecosystems emphasizes the need to understand how to manage them in the future (Hof et al., 2017; Lindner et al., 2014; Mina et al., 2017).

In recent years, the use of computational models has been increasing in forest ecosystem research (Gustafson et al., 2017; Shifley et al., 2017). Although empirical studies are of fundamental importance for process understanding, simulation models are nowadays recognized as useful tools to assess our knowledge about the functioning of ecosystems as well as essential allies when predicting future changes (Seidl, 2017). Over the past decades, a large range of models were developed to describe future dynamics in forest ecosystems (Keane et al., 2015), from stand-scale empirical simulators to more complex process-based models operating at landscape scale (Fontes et al., 2010). Because of computational constraints, models integrating fine-resolution processes (e.g., photosynthesis, specific growth functions) at large scales in a spatially explicit framework were rare, and smaller grain processes were often strongly simplified (Elkin et al., 2012). However, these constraints are constantly being reduced by the increase in computational power, allowing for the flourishing of Forest Landscape Models (FLMs) which integrate physiologically based processes from stand to landscape level (De Bruijn et al., 2014; Petter et al., 2020; Seidl et al., 2012; Shifley et al., 2017).

According to Jørgensen and Fath (2011), ecological models comprise five elements: state variables, external variables, parameters, mathematical equations, and universal constants. The mathematical equations and universal constants are implicit within the model structure, while the initial conditions of the state variables (e.g., species biomass, species age), external variables and parameter values are usually provided as inputs by the user for each simulation study. In the case of FLMs, they represent forests across the landscape in a spatially explicit way. The landscape is depicted as a set of cells for which a series of state and external variables are defined. These variables are used to define the ecological processes taking place at cell level (e.g., growth, mortality among others) and at landscape level (e.g., seed dispersal, fire spread). For comprehensive reviews on the development, structure and recent applications of FLMs see Shifley et al. (2017), Keane et al. (2015), and He et al. (2017).

The above-mentioned structural elements are essential to set up a simulation in a specific landscape. This requires the user to obtain, prepare and organise comprehensive datasets to address the two first key steps in applying FLMs: model initialization (initial conditions of state and external variables) and calibration of model parameters. The initial conditions of the state variables describe the ecosystem at the beginning of the simulation. In turn, external variables are those forces affecting the ecosystem without being internal parts of it (Jørgensen and Fath, 2011). Most FLMs require initial values of at least certain state and external variables to start a simulation. As an example, the FLM LandClim requires elevation or browsing intensity for initialization (Petter et al., 2020). In addition to biophysical conditions (e.g., soil types, climate maps or regions), essential initial conditions for FLMs are vegetation maps describing which species are present in the landscape at the beginning of the simulation time. Decisions regarding the inclusion or exclusion of certain species can be highly relevant in certain ecosystems (e.g., shrubs in the Mediterranean area). Thus, these vegetation maps are a keystone within these experiments since forest dynamics and properties (biomass, available light, regeneration, etc.) are highly driven by initial conditions and structure (Duveneck et al., 2015; Scheller and Swanson, 2015). For example, most FLMs require information of tree species and their age classes across the landscape. This information can be very challenging to obtain and estimate for large spatial scales without necessarily combining multiple and complex datasets (Zald et al., 2014). The generation of input data for FLMs can therefore require significant time and skills, and often demands complementarity with experimental research from long-term field studies (Scheller, 2018; Shifley et al., 2017).

The calibration of model parameters has been defined as one of the greatest challenges in modelling under environmental changes (Keane et al., 2015; Scheller, 2018). Model parameters are values used in model equations which represent processes (Jørgensen and Fath, 2011). Most models simulating the succession dynamics of vegetation require parameters describing the behaviour of the species present in the landscape. These parameters may differ for each model, but commonly refer to species growth characteristics, fruit and seed dispersal, reproduction strategies and absolute or relative measures of tolerance to stress factors (Huber et al., 2018). A broad range of sources can be used to fulfil these parameters, ranging from empirical case-specific data collected by the modeller to values of standard variables stored in global databases. In either case, an evaluation of model outputs to identify appropriate parameter values is usually required to ensure that the model produces plausible outcomes at the local scale (Duveneck et al., 2017; Gutiérrez et al., 2016). This evaluation of parameter values is known as calibration (Mulligan and Wainwright, 2013). During this phase, the different model sensitivity to some parameters over others should be considered (McKenzie et al., 2019).

Successional processes and long-term projections in FLM are highly sensitive to initial conditions and model parameters (Scheller, 2018). Estimation of initial condition and calibration procedures are typically described in the method section in literature studies (e.g. Boulanger et al., 2017; Scheller et al., 2005), but often not on a level of detail to allow full reproducibility or with enough information to help non-modellers to setup a new landscape from scratch. Even fewer provide access to inputs, outputs and scripts in public repositories. The aims of this study are twofold. First, documenting the process needed to initialize and calibrate a FLM step-by-step, as an example for analogous uses. Fulfilling this goal would encourage the application of FLMs as scientific tools to assess future forest dynamics and management adaptation under global change. Second, we aim at testing different initialization data —with and without shrub communities—by assessing the model ability to project forest landscape dynamics in a biome where the model has not been applied so far (Euro-Mediterranean region).

2.2 Materials and methods

2.2.1 Model description

In this manuscript, we chose LANDIS-II as our reference FLM. LANDIS-II[1] (Scheller et al., 2007) is a FLM designed to simulate forest dynamics at multiple spatial and temporal scales. It allows a wide degree of complexity depending on a set of extensions which can optionally be activated to simulate different processes such as succession, disturbances (fire, wind, herbivory, and pests) and management at different degrees of complexity (e.g., areas- and species-specific harvesting regimes, post-harvesting planting). The spatial scale (i.e., cell resolution) is defined by the user, which makes it very flexible and adaptable to a wide variety of simulation experiments. In LANDIS-II, the landscape is divided into ecoregions, which are subregions sharing similar climatic conditions and soil characteristics. Trees in each cell are represented as species-age cohorts, increasing the computational efficiency of the model (De Bruijn et al., 2014).

Particularly, we used the PnET-Succession extension v.3.4 (De Bruijn et al., 2014; Gustafson et al., 2015). This extension embeds the PnET-II ecophysiolog-

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[1] www.landis-ii.org/

ical model equations (Aber and Federer, 1992). PnET-Succession simulates forest succession in a more mechanistic way than previous approaches, representing an advantage for experiments where novel conditions such as climate change are being explored (Gustafson, 2013). In PnET-Succession, age is used to calculate cohort's biomass at the onset of the simulation (i.e., model spin-up) and cohorts with higher biomass are given priority access to light and water (Gustafson and Miranda, 2019). Cohort biomass is assumed to be homogeneously distributed in the cell and therefore shade conditions are also homogeneous within a cell (Scheller et al., 2007). Potential net photosynthesis rate is calculated as a linear function of foliar nitrogen (FolN) and biomass growth is a result of environmental conditions such as temperature, precipitation, photosynthetically active radiation (PAR), CO_2 concentrations and —optionally—ozone concentrations (De Bruijn et al., 2014). Biomass allocation depends on compartments turnover and fraction parameters. Mortality can occur at any time if carbon reserves become limiting (non-structural carbon <1%) or when age approaches species longevity (De Bruijn et al., 2014).

PnET-Succession requires a series of generic, ecoregion and species-specific parameters. Although many default values have been made available by the model developers and in past application studies, most parameters require calibration according to the biogeographical location of the target landscape and the tree species included in the simulations (McKenzie et al., 2019; Mina et al., 2021).

2.2.2 Study Area

The simulated area considered in this study is located in the southeastern part of Iberian Peninsula and it covers approximately 390,000 ha (37.2 °N, 3.1 °W, Figure 2.1). The topography is mostly mountainous, including three mountain ranges. In the southern part of the study area, Sierra Nevada spreads from east to west and contains the highest peak in the Iberian Peninsula, Mulhacén (3,478 m). In the northern part of the study area, Sierra de Arana is located in the west, while Sierra de Baza-Filabres is in the east. More than half of the study area is under protection, either as National or Natural Park, and therefore a variety of exploitation and management regimes can be found in the study area.

Several bioclimatic zones are found within the study area (REDIAM, 2018; Rivas Martínez, 1983). The supramediterranean zone (mean annual temperature 8–13 °C) is the one covering most of the area, at low altitudes of Sierra Nevada and connecting with Sierra de Arana. An important proportion of the Sierra de Baza surface is also represented by this bioclimatic zone. Supramediterranean ar-

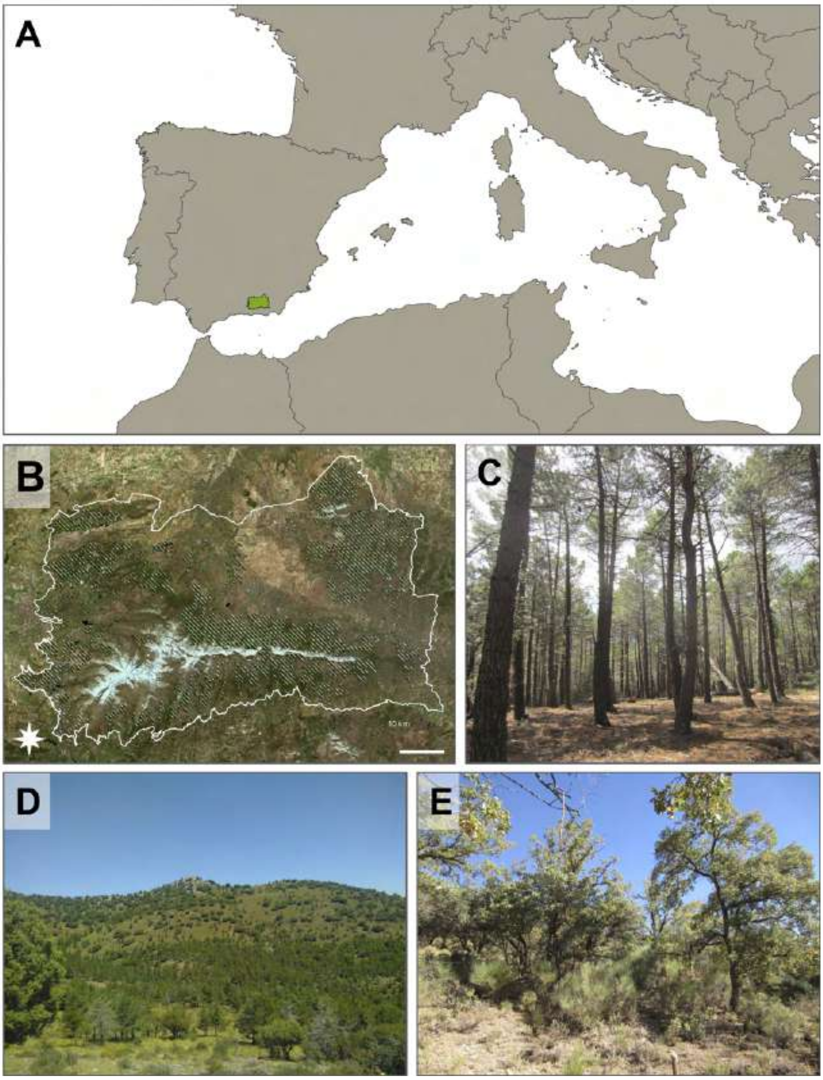

Figure 2.1: Study area location **(A)**, orthophoto of the study area **(B)** and pictures of representative forest types: pine plantations **(C)**, mixed open forest **(D)**, oak-dominated stand **(E)**. Shaded area in panel **(B)** delimitates pine plantations.

eas are mostly covered by a mosaic of conifer, mixed forests and sclerophyll shrubs. The highest areas represent the oromediterranean zone (mean annual temperature 4–8 °C) and are covered by conifers, shrubs and sparse vegetation, except for the very high altitudes in Sierra Nevada, which encompass the cryoromediterranean zone (i.e., alpine tundra, mean annual temperature <4 °C). These peaks are covered by scarce vegetation adapted to extreme climatic conditions. The rest of the study area, at altitudes commonly below 1,000 m, is mostly covered by mesomediterranean (mean annual temperature 13–17 °C) and thermomediterranean zones (mean annual temperature 17–19 °C). The precipitation follows a strong seasonal pattern, with dry summers and precipitation concentrated in a small number of events. Rainfall is the most common form of precipitation. Besides, snowfall at high altitudes is very important since slow melt down and subsequent infiltration into soil increases water availability for plants throughout the spring and summer season. Aspect also determines water availability due to different precipitation evapotranspiration patterns.

The study area is covered by diverse natural vegetation patches in combination with agriculture and *Pinus* forest plantations. Pine plantations are the dominant land use type, covering around 20 % of the study area, with a minor presence of natural pine forests. These plantations were mainly established between the 1950s and 1970s as means to halt soil erosion in recently abandoned agricultural areas. The main species are Maritime pine (*Pinus pinaster* Aiton), Aleppo pine (*Pinus halepensis* Miller.), black pine (*Pinus nigra* Arnold.) and Scotch pine (*Pinus sylvestris* L.) (Bonet García et al., 2009; Mesa Garrido, 2019; Pemán García et al., 2017). Pines were planted in high densities to drastically reduce soil loss. Afterwards, favourable climate conditions and lack of appropriate post-planting management have resulted in highly dense monospecific evenage stands. As a result, these forest plantations are nowadays under extreme risk by climate change and forest pests, which has resulted in decline and massive mortality processes (Sánchez-Salguero et al., 2010; Sánchez-Salguero et al., 2012a).

Almost 40 % of the study area is covered with shrublands and abandoned crops with sparse natural vegetation. Some of these areas host sparse trees (mainly *Quercus ilex* L.), which can be highly relevant seed sources at a local scale. Moreover, in a context of climate change and further abandonment of mountain agriculture activities, these sparsely vegetated systems can be highly important to understand the succession dynamics in pine plantations for two reasons:

1. Due to climate change, currently forested areas could suffer a decline and be replaced by shrublands as these areas become less suitable to sustain high levels of biomass; and

2. Tree species could expand to shrubland areas currently dedicated to marginal activities (mountain agriculture, livestock, fuelwood, and charcoal exploitation, etc.).

2.2.3 Model Initialization

In this section we describe the workflow followed to produce the necessary inputs required by LANDIS-II with PnET-Succession. We first focus on the generation of the initial vegetation conditions, followed by the methodological process to build biophysical inputs. The different sources of information used in this process are listed in Table 2.1.

Initial Vegetation Conditions

Most FLMs require estimates of initial conditions in the form of vegetation maps reporting the presence of tree species at the beginning of the simulations. Concretely, LANDIS-II requires a spatial representation of species cohorts by age classes (also called "initial communities"). To generate such vegetation maps, different information sources are often combined following a complex workflow that, if not exhaustively described, is often unreproducible. Even though such workflows can be modeland site-specific, three methodological steps can be defined:

Table 2.1: Information sources used in this study.

Information required	**Source**	**References**	**Spatial scale**
Plot-level vegetation information	Third Spanish National Forest Inventory (NFI)	Third Spanish National Forest Inventory (2007). Available as a Microsoft Access database at: at:https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datosnaturaleza/informacion-disponible/cartografia_informacion_disp.aspx Source: Ministerio para la Transición Ecológica y el Reto Demográfico	1:50.000

Polygon-level vegetation information	Spanish Forestry Map (FM)	Map resulting from photointerpretation. Accessible as vectorial file at: https://www.mapa.gob.es/es/cartografia-y-sig/ide/descargas/desarrollo-rural/mfe_andalucia.aspx Source: Ministerio de Agricultura, Pesca y Alimentación	1:50.000
	Andalusian Vegetation Map (VM)	Map resulting from photointerpretation and field sampling. Accessible as vectorial file at: https://descargasrediam.cica.es/repo/s/RUR Source: REDIAM, Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible	1:10.000
Climate data	Reference data	Annual precipitation, mean, minimum and maximum annual temperature for the period 1971–2000. Accessible as raster files at: https://descargasrediam.cica.es/repo/s/RUR Source: REDIAM, Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible	100 m resolution
	Climate series	Maximum and minimum temperatures and precipitation for the period 1950–2005. Network common data files published by Karger et al. (2020)	0.049 °resolution
		CO_2 concentrations times series for SSL station and period 1971–2018 published by Meinhardt and Centre (2020).	Point sampling: 47.9 °N, 7.9 °E
		Photosynthetically Active Radiation for the period 1950–2019. Network common data files published by Cornes et al. (2018) (Version 20.0).	0.25 °resolution
Soil data	Regional soil maps	Sand, clay and silt soil content and soil depth. Raster files published by Rodríguez (2008).	250 m resolution

1. Plot-level information (e.g., from national or regional inventories or permanent growth plots) is processed to extract tree measurements such as basal area, age or height;
2. Polygon-level information is processed to select stand-scale, spatially ex-

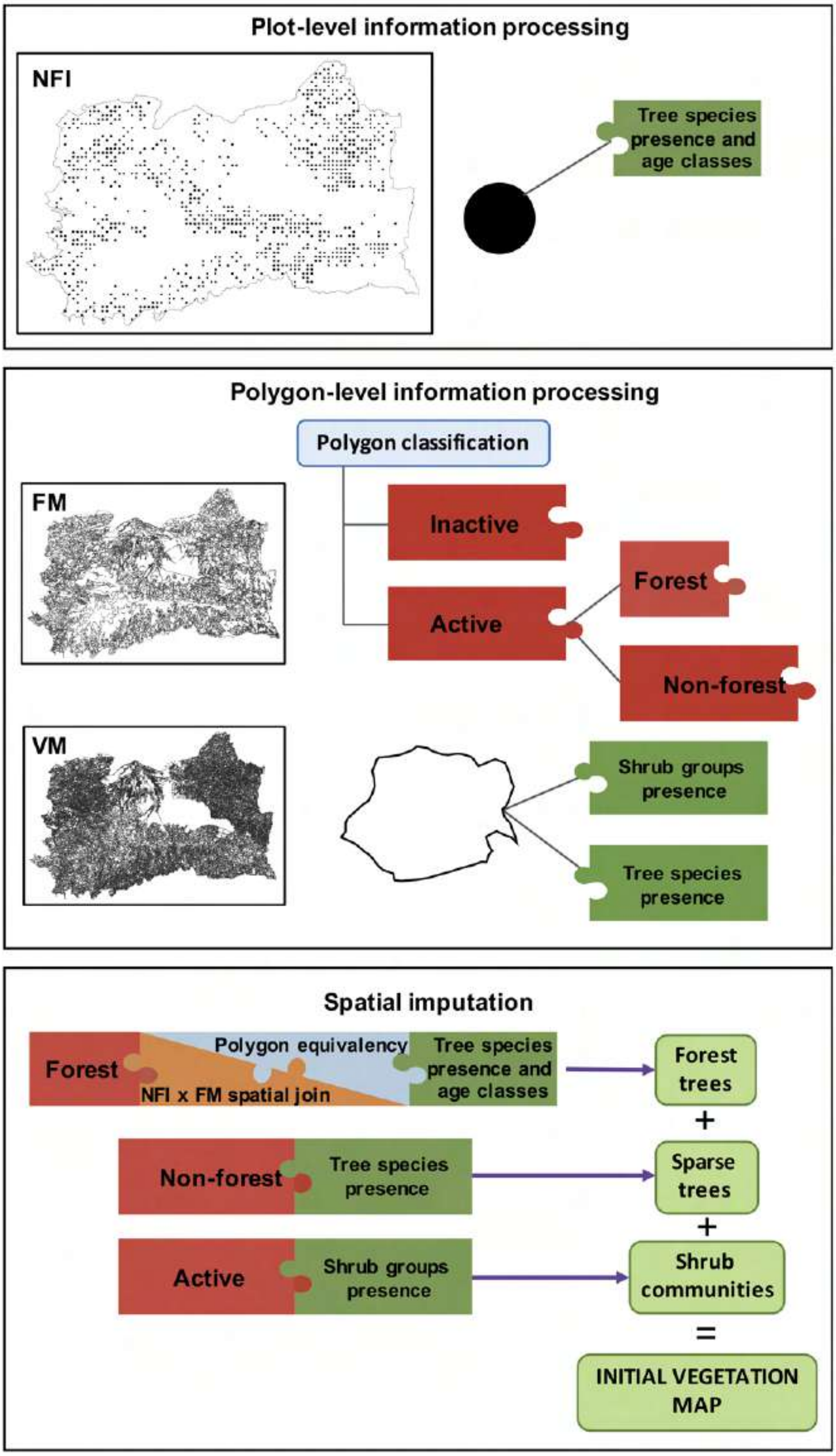
Plot-level information processing
NFI
Tree species presence and age classes
Polygon-level information processing
Polygon classification
FM
Inactive
Active
Forest
Non-forest
VM
Shrub groups presence
Tree species presence
Spatial imputation
Forest
Polygon equivalency
NFI x FM spatial join
Tree species presence and age classes
Forest trees
+
Non-forest
Tree species presence
Sparse trees
+
Active
Shrub groups presence
Shrub communities
=
INITIAL VEGETATION MAP

Figure 2.2: Schematic view describing the workflow of the initial vegetation map generation. Tree species presence and age were extracted from plots of the Third Spanish National Forest Inventory (NFI) during the plot-level information processing phase. During the polygon-level information processing, the Spanish Forestry Map (FM) was used to classify polygons as active/inactive and no forest/forest. The Andalusian Vegetation Map (VM) was used to extract the presence of shrub communities and sparse trees. At the spatial imputation phase, plot- and polygon-level information was combined to generate a continuous map of vegetation.

plicit variables which can be linked to plot-level information such as forest type, mean age, canopy cover, etc.;

3. A spatial imputation method is applied to produce a continuous map by assigning plot-level information to polygon-level information.

In the following sections, we describe the methodological details for each of the three methodological steps of the workflow, which is summarized in Figure 2.2.

Plot-level information processing Plot-level information is necessary to select the most common tree species and some of their demographic features in the area of interest. In our case, the Third Spanish National Forest Inventory (NFI) was used for this purpose (Table 2.1). The NFI contains homogeneous information about forest covers in Spain by reporting data collected in a systematic network of permanent sampling plots (Alberdi et al., 2017). The plots are evenly distributed on a 1 km^2 grid throughout the territory and contain plot- and tree-level information for each survey period. In addition to single-tree data (e.g., species, diameter, height, form, and health status), the plot is described in terms of the three most dominant tree species contributing to canopy cover. We selected the tree species to include in the model simulations based on the total coverage value of the species within the study area.

Tree age is often not available at single-tree level and its estimation is challenging as several factors influence growth rate of individual trees, leading to very different tree characteristics for the same age. Nevertheless, LANDIS-II uses cohort age-classes as a proxy for biomass, and therefore an estimated age is required for each species across the landscape. NFI provides estimated stand age for plots within even-aged stands. In our area, even-aged stands are composed by *Pinus* spp. Since these plots also have associated individual tree measurements (e.g., diameter, height), we calculated the average diameter per species and plot and joined it to the assigned stand age. In order to have as many observations as possible, we expanded the considered dataset to all plots within even-age stands from surrounding regions (provinces of Granada and Almeria). Since no estimated age was available for plots within uneven-age stands (mainly *Quercus* spp. and *Populus nigra*), a semi-quantitative method was applied. We used yield tables available from the literature (Teobaldelli et al., 2010). Then, we generated an age assignment table containing correspondence rules between tree age, diameter and height for each species under consideration. This table was validated based on expertise and observations in the study area. Finally, the age assignment table was used to attribute an age class to the species in each NFI plot (see Supplementary Table S.1 for more details).

Polygon-level information processing Many government and private forestry organizations utilize cartographic products to support forest management. Polygon-level information usually contains forest variables at a landscape scale such as forest type, coverage or stand development stage. Here, we used the Spanish Forestry Map (FM) and the Andalusian VegetationMap (VM) as the main source of spatially explicit landscape information Table 2.1. The FM is a vectorial file generated by photointerpretation. It contains a series of attributes describing the forest vegetation for each polygon: polygon identifiers and surface; province and region; forest and land use characteristics (vegetation type, structural type, land use categories); name, coverage and state of the three most dominant species in dominance order; and tree and total coverage fraction. Based on these attributes, polygons were classified as active (those containing or potentially containing vegetation units useful for our purpose) or inactive (those where natural succession is hampered by human activities: crops, infrastructures, firebreaks, etc.). Active polygons were in turn classified as forest and nonforest. Forest polygons have an average size of 51 ha and a maximum of 357 ha.

The VM is also a vectorial file that contains an extensive list of attributes (140) describing the presence and characteristics of the tree species, shrubs and pastures present in each polygon (e.g., vegetation community, canopy coverage) at a higher resolution than the FM. Due to the importance of sparse trees and shrublands in our study area (see section 2.2.2), we used the VM to consider the occurrence of sparse trees in non-forest polygons in the initial vegetation map. Moreover, since the VM also provides information about shrubs, grasslands and pastures, we used a variable termed "life form" attribute to analyse the presence of shrubs within the study area. The life form attribute is based on the classification proposed by Raunkiaer (1934) and subsequently revised by Ellenberg and Mueller-Dombois

(1967). According to this classification, plants can be: microphanerophytes (*"evergreen perennial plants that grow between 2 and 5 m, or whose shoots do not die back periodically to that height limit"*), nanophanerophytes (*"evergreen perennial plants that grow below 2 m tall, or whose shoots do not die back periodically to that height limit"*), chamaephytes (*"evergreen perennial plants whose mature branch or shoot system remains perennially within 25–50 cm above ground surface, or plants that grow taller than 25–50 cm, but whose shoots die back periodically to that height limit"*), hemicryptophytes (*"perennial plants with periodic shoot reduction to a remnant shoot system that lies relatively flat on the ground surface"*), geophytes (*"perennial plants with periodic reduction of the complete shoot system to storage organs that are imbedded in the soil"*), therophytes (*"annual plants whose shoot and root system dies after seed production and which complete their whole life cycle within 1 year"*). Shrub communities' size was extracted from this classification. Hemicryptophytes, geophytes and therophytes life forms were not considered for the analysis as they mostly refer to species with short life cycles. As a result, the presence of tall (2–5 m), medium (0.5–2 m), short (<0.5 m) shrub communities was extracted for each polygon in the study area. Each of these shrub communities was parameterized individually in PnET-Succession (see details below).

Spatial imputation Spatial imputation is applied to combine plot-level to polygon-level information. To generate the initial vegetation map suitable for LANDIS-II, we combined plot- and tree-level information (NFI) with polygon-level information (FM and VM). The final aim of this step is to produce a forest composition map containing the species-age assemblage (species and age of each cohort) in every cell within the study area (see Duveneck et al., 2015, for the description of a similar approach in North America).

First, we performed a spatial join between the forest polygons from the FM and the plots from the NFI (Figure 2.2). FM polygons containing one single NFI plot were assigned the species-age assemblage of the surveyed plot. FM polygons with more than one NFI plot were assigned the species-age assemblage which results from merging all plots species-age assemblages. This only occurred in a small proportion of cases: 80 out of 789 forest polygons had two NFI plots in them, 3 polygons had 3 NFI plots in them and one polygon had 4 plots in it.

Forestry Map polygons without NFI plots were analysed to identify an equivalent polygon among those which have one or more intersecting NFI plots. Polygon equivalency was analysed at three levels:

1. Full equivalency: polygons matching vegetation type, species dominance, species development state, and total coverage fraction;

2. Partial equivalency: polygons matching vegetation type, species dominance, and total coverage fraction; and
3. Species equivalency: polygons matching species dominance and total coverage fraction. FM polygons were assigned the species-age assemblage of their equivalent polygon.

If there were more than one equivalent polygon, the polygon was assigned the species-age assemblage resulting from the merge of all possible ones. FM polygons with no equivalent polygons were further analysed based on their species composition, without considering species dominance order. These polygons were assigned the species-age assemblage corresponding to the most common species-age assemblage containing the same species as the considered polygon in the whole study area. FM polygons containing species assemblages not occurring in the previously analysed polygons were assigned one cohort of each of the species present in it. The age of this cohort corresponded to the most common age for each species among all previously analysed polygons. This procedure resulted in the description of the forest trees within the study area.

Second, polygons labelled as non-forest by FM, were imputed to include sparse trees (Figure 2.2). We used VM to gather information for those polygons. Since VM does not report any variable describing the age of the species, VM polygons were imputed a species-age assemblage containing the reported species with the most common age for that species in the rest of the study area. By doing so, the description of the sparse trees within the study area was completed.

Third, we imputed shrub communities within the landscape by assigning the corresponding shrub community-age assemblage to each VM polygon (Figure 2.2). Shrubs were not allocated to different age classes but instead we arbitrarily assigned age 10 for all polygons. Since in LANDIS-II shrub biomass should not exceed tree biomass (see section 2.2.1), the role of shrubs in the model is mainly to compete for light and water in the understory (e.g., affecting establishment), thus we believe age class assignation for shrubs was not necessary.

Finally, we obtained the initial vegetation map by combining forest trees, sparse trees and shrubs communities. The map was rasterized at 100 m resolution (1 ha cells). Each cell was labelled with a code associated to a list of unique speciescohort assemblages.

Biophysical Inputs

The FLM LANDIS-II requires an input map of ecoregions as biophysical inputs. LANDIS-II ecoregions are continuous or discontinuous areas of the land-

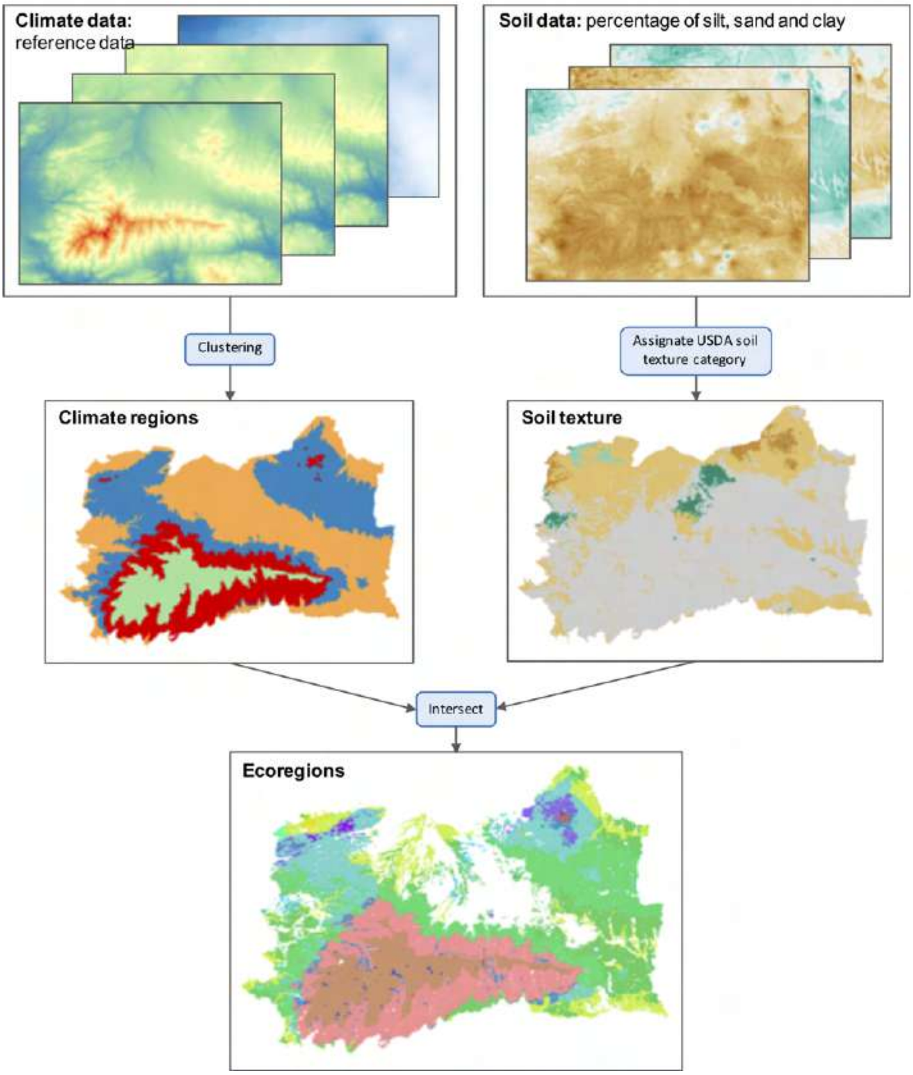

Figure 2.3: Schematic view of workflow followed to produce the ecoregions map. Reference climate data consist of annual precipitation, mean, minimum and maximum annual temperature for the period 1971–2000 at 100 m resolution. Clustering of climate data resulted in four climate regions. Soil data consist of a percentage of silt, sand and clay at 250 m resolution. The intersection of climate regions and soil textures resulted in 27 ecoregions.

scape which share climate conditions and soil texture (see section 2.2.1). To generate the map of ecoregions, we used a reference climate dataset and a regional soil map (Table 2.1). The reference climate dataset reports annual precipitation and mean, minimum and maximum temperature for the period 1971–2000 at a 100 m resolution. Firstly, an unsupervised k-means clustering was applied to the climate dataset to lump together cells with similar climate. MacQueen algorithm was used in this clustering (MacQueen, 1967). We evaluated different numbers of clusters and eventually ended up with four climate regions. The resulting ecoregions agree with our expectations considering topography and the bioclimatic zones found in the study area (Figure 2.3).

The resulting climate regions map was intersected with the soil texture map. The soil map reports the percentage of sand, silt and clay at a 250 m resolution. This map was derived by simply translating the percentages of sand, silt and clay to USDA soil texture categories. The final ecoregions map was therefore produced by overlapping the climate regions and the soil textures maps. This resulted in a total of 28 unique ecoregions defined by both a climate region and a soil type (Figure 2.3).

PnET-Succession also requires rooting depth for each ecoregion. Ecoregion rooting depth was calculated based on soil depth classes reported in the soil map (0–250 mm, 250–500 mm, 500–1,000 mm, 1,000–1,500 mm, >1,500 mm). The midpoint of each class was used to calculate the most frequent rooting depth for each ecoregion. Precipitation Loss Fraction and Leakage Fraction were given values of 0.6 and 1 for all ecoregions. All other PnET-Succession ecoregions parameters were given default values. A complete dataset containing model inputs is provided (see section "Data availability and reproducibility").

2.2.4 Calibration of Model Parameters

LANDIS-II and PnET-Succession require a set of parameter values for each species simulated in the landscape. Generic species parameters are required irrespective of the chosen succession extension (e.g., longevity, sexual maturity), while others are required by PnET-Succession (e.g., foliage nitrogen, foliage turnover, minimal, and optimal photosynthetic temperature). We firstly defined an initial set of parameter values from multiple sources. Then, we ran single-cell simulations to verify the species behaviour (e.g., growth, photosynthetic rates) under different conditions. On a single, empty 100 m cell, a single 10-years old cohort of each species was initialized and grown for 200 years preventing establishment of new cohorts. Five replicates were run for each simulation using static monthly averages of temperature, precipitation, PAR and CO_2 (Table 2.1 and Supplementary Figures S.11-S.14). Baseline climate conditions were used to avoid introducing variability due to fluctuating climate (Gustafson and Miranda, 2019).

The results of these simulations were compared with species biomass estimations for the study area and literature information. Biomass estimations were calculated for *P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *Q. ilex*, and *Q. pyrenaica* based on forest inventory data and allometric equations published in Montero et al. (2005). Simulated versus observed Relative Growth Rates in relation to species biomass were used for comparison as this metric is independent from age, which has a high uncertainty degree in NFI data.

Following calibration guidelines for PnET-Succession (De Bruijn et al., 2014; Gustafson and Miranda, 2019) and evidences from a sensitivity analysis with the same model (McKenzie et al., 2019), we adjusted the most influential species-specific parameter values in an iterative process until the species showed the expected behaviour based on authors' expertise and observations.

We also evaluated the response of competing assemblages of species typical of the different forest types included in our landscape. These multi-species simulations allow the calibration in relative terms, as well-known competition effects can be assessed and species parameters can be adjusted accordingly. In these simulations, species are established in the cell at the same time and no new establishment is allowed, which is often not the case in natural ecosystems. Thus, the observed species development is the result of their growth traits and their different performance under competition and not due to different establishment strategies or other advantages.

2.2.5 Landscape Simulation

We simulated forest dynamics at the landscape scale incorporating the effect of spatial processes such as dispersal and climate and soil heterogeneity. We initialized the model with the biophysical inputs described above and with the parameters calibrated in the previous step. To verify the influence of shrub communities on simulated forest dynamics, we initialized LANDIS-II with two different vegetation datasets: (1) with shrub communities and (2) without shrub communities. Since the aim of this study was to initialize the landscape for further experiments with LANDIS-II and PnET-Succession, neither natural nor human-driven disturbances (i.e., fire, harvest) were included in the experiment. We ran five model replicates using baseline climate for 200 years (Table 2.1 and Supplementary Figures S.11-S.14). We analysed model outputs in terms of temporal patterns of average biomass for each species. Moreover, we mapped and compared total aboveground biomass for selected simulation years across the landscape. All analyses were performed in R version 3.5.3 (R Core Team, 2020) and QGIS 3.10 (QGIS Association, 2020).

2.3 Results

2.3.1 Spatial Imputation and Initial Vegetation Map

The analysis of 981 NFI plots falling within the study area resulted in eight species having a coverage value higher than 1 %: *Quercus ilex* (25 %), *Pinus sylvestris* (18 %), *Pinus pinaster* (16 %), *Pinus nigra* (16 %), *Pinus halepensis* (16 %), *Quercus pyrenaica* (2 %), *Populus nigra* (1 %), and *Juniperus oxycedrus* (1 %). These species were selected to be included in the study. Besides, two extra species —*Quercus faginea* and *Juniperus communis*—were also included due to their importance in specific environments. *J. communis* covers vast areas above the tree line (cushion shape shrubs) (García, 2001) and *Q. faginea* is also locally abundant.

The analysis of the FM resulted in a classification of active versus inactive cells within the study area. Inactive areas cover 19 % of the study area and mainly refer to crops and firebreaks (17.3 %). Moreover, active cells were classified as forest and non-forest, which represent 41 and 40 % of the study area, respectively.

The intersection of NFI plots and FM polygons defined the species-age assemblage of a total of 789 polygons within the study area. Out of 3,113 polygons with no NFI plot in them, 84 % of them were imputed based on equivalent polygons (55 % full equivalent, 22 % partial equivalent and 7 % species equivalent). The remaining 16 % of polygons were imputed the species assemblage reported in the FM and the most common age for each of the species.

The use of the VM allowed a more detailed description of active non-forest areas. The analysis of sparse trees in non-forest polygons increased by 4 % the surface of the study area where tree species are present. Even though it may seem as a small portion of the landscape, these sparse trees can represent important seed sources when long-term forest dynamics are simulated. Moreover, the VM analysis allowed the inclusion of shrub communities in the landscape's cells, which can affect the shade conditions as well as water availability.

Figure 2.4 shows the initial vegetation map as a result of combining the presence of forest trees, sparse trees and shrubs communities. Several portions of the landscape are covered by shrublands and *Juniperus* spp., surrounded by a mosaic of *Pinus* spp., *Quercus* spp. and mixed *Pinus-Quercus* forests, with a minor presence of *Populus nigra*.

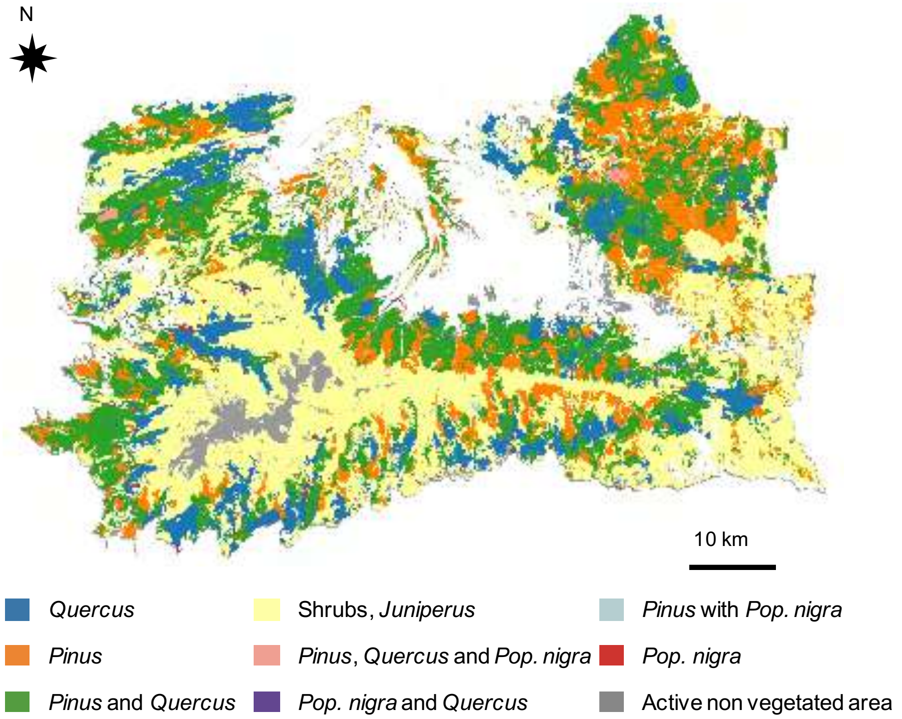

Figure 2.4: Map of initial vegetation conditions including shrub communities. Each category represents a community dominated by one or more tree species, where shrubs and *Juniperus* spp. may also be present.

2.3.2 Calibration of Model Parameters by Means of Site-Level Simulations

Estimating species parameter values was a complex task due to the amount of information sources required to cover all of them. Table 2.2 reports the most important parameters required by LANDIS-II and PnET-Succession. A detailed explanation of all parameter values, sources and rationales for their adoption is provided in Supplementary Table S.2.

Biomass estimations for *P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *Q. ilex*, and *Q. pyrenaica* were compared with results from single-cell simulations

Table 2.2: Species parameter values for LANDIS-II and PnET-Succession. [1]Montoya Oliver and Mesón García (2004), Serrada et al. (2008), and Valladares Conde (2005). [2]Kattge et al. (2020). [3]Niinemets and Valladares (2006) and Pausas et al. (2004). FolN: Nitrogen foliar content; SLWmax: Maximum specific leaf weight at the top of canopy; Tofol: foliage turnover; HalfSat: Photosynthesis half saturation light level; H3, H4: Water stress parameters according to Feddes et al. (1978); PsnTMin, PsnTOpt: photosynthesis minimum and optimum average daytime temperature (Gustafson and Miranda, 2019).

Species	**Long.[1] (years)**	**FolN[2] (%)**	**SLW max** ($\mathrm{g\,m^{-2}}$)	**TOfol[2]** ($prop.\ year^{-1}$)	**HalfSat[3]** (μmol $\mathrm{m^{-2}\,s^{-1}}$)	**H3[3] (m)**	**H4[3] (m)**	**PsnT Min[1] (°C)**	**PsnT Opt[1] (°C)**
J. communis	600	0.85	200	0.50	264.5	115	155	3	21
J. oxycedrus	600	0.85	200	0.66	264.5	115	155	3	21
P. halepensis	150	1.19	240	0.34	282.5	118	160	3	26
P. nigra	400	1.02	240	0.26	245.0	115	155	2	23
P. pinaster	200	1.00	240	0.24	245.0	115	155	3	25
P. sylvestris	300	1.33	240	0.36	266.5	110	150	1	20
Pop. nigra	90	2.50	85	1.00	227.0	105	145	2	31
Q. faginea	300	1.92	110	1.00	224.5	115	155	3	26
Q. ilex	600	1.42	150	0.52	199.0	118	160	2	28
Q. pyrenaica	300	1.85	80	1.00	224.5	110	150	1	22
short shrubs	50	0.70	100	0.75	170.0	118	160	2	27
medium shrubs	50	0.75	100	0.75	175.0	118	160	2	27
tall shrubs	50	0.80	100	0.75	180.0	118	160	2	27

initialized with individual species. Results of biomass and photosynthetic rates of species simulated individually on a single cell are reported in the Supplementary Figures S.8-S.10. Simulated results are within the range of estimations, although estimations are highly variable among plots.

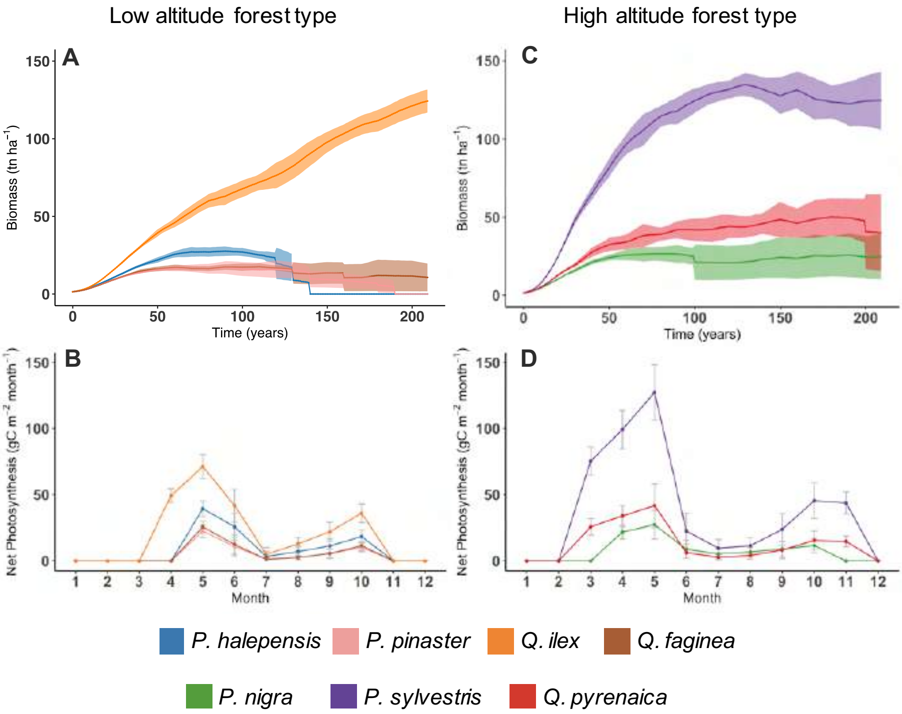

Figure 2.5: Mean simulated annual total biomass (wood, roots and foliage) **(A, C)** and monthly net photosynthesis **(B, D)** for the two chosen forest types. Shaded area refers to standard deviation. Values of net photosynthesis are averages between years 50–75, with error bars indicating standard deviation. Note that lines connecting the points serve for illustrative purposes only, since PnET-Succession simulates photosynthesis at monthly time scale (not daily).

Among the more than 70 of single-cell simulations that were performed, we chose to show here two representing typical species assemblages of low and high altitude forest types (Figure 2.5). In the low altitude forest type, composed of two pine and two oak species, our results indicated a dominance of *Q. ilex* over *Q. faginea*, *P. halepensis*, and *P. pinaster* (Figure 2.5A). Cohorts of the two latter species were simulated to die by year 140 and 190, respectively, since they approached their longevity (pink and blue lines). *Q. ilex* clearly dominated *Q. fagi-*

nea but it did not fully outcompete it. The advantage of *Q. ilex* in this forest community seems to be related to its capacity to start photosynthesizing earlier in spring than the other species (Figure 2.5B).

In the high altitude forest type, *P. sylvestris*, *P. nigra*, and *Q. pyrenaica* coexisted along the simulation, although *P. sylvestris* built higher biomass compared to the other two species (Figure 2.5C). The advantage of *P. sylvestris* was related to its higher photosynthetic rate from the beginning of the season, while *Q. pyrenaica*, being a deciduous species, increased its photosynthesis more gradually after having built foliage biomass (Figure 2.5D). Generally, we found that PnET-Succession reproduced reasonably well the bimodal growth patterns of Mediterranean tree species, mostly occurring during spring and fall instead of summer which is characterized by a lack of precipitations.

2.3.3 Landscape-Level Simulation

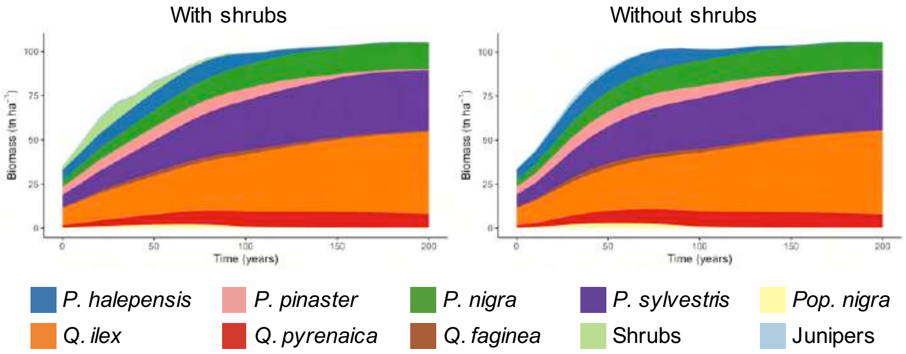

Figure 2.6: Average biomass of species through time for the whole landscape. Note that Junipers (*J. communis* and *J. oxycedrus*) and shrub communities (short, medium, and tall) have been grouped together.

Both simulations with and without shrubs showed a trend to increase the average biomass of all tree species during the first years of the simulation and stabilization afterwards (Figure 2.6). In the simulation including shrubs, this increase was slower than in the simulation without shrubs, with a faster increase in the first 50 years. In both simulations the total average biomass at stabilization was around 100 tn ha^{-1}.

We found differences among species in terms of simulated biomass growth. Among pine species, *P. sylvestris* and *P. nigra* were those with a higher increase of average biomass in both simulations. Biomass of *P. halepensis* and *P. pinaster* increased during the first 50 years, followed by a decline and disappearance from the landscape toward the last decades of the simulation. Among oaks, biomass of *Q. ilex* increased notably, while *Q. pyrenaica* increased at lower rates and stabilized after about 100 years. Biomass of *Q. faginea* and *Pop. nigra* had similar trends, increasing slightly in the early years and declining afterwards, but still maintaining presence at low levels of biomass. Junipers slightly increased their biomass during the first 30 years and then strongly declined. These species show similar patterns in both simulations, but under the simulation without shrubs we observe a steeper increase of biomass during the first years. Shrub communities increased their average biomass during the first 40 years and declined afterwards.

Initial total landscape biomass (time 0) was similar in both simulations since shrub communities accounted for low levels of biomass (5.1 % of total biomass). At time 50, the area with high biomass is wider in the simulation without shrubs (Figure 2.7). This pattern was observed at time 100 too, although the difference between the two simulations was smaller (see total biomass at each time step in Figure 2.7). At time 150 and 200, both simulations showed a similar quantity and distribution of the biomass across the landscape, with slightly higher values of biomass in the simulation without shrubs than in the one with shrubs. The biomass distribution within the study area followed the altitudinal gradient, with higher biomass found at medium elevations, specially at time step 150. At the beginning of the simulation, areas at high elevation (above c.a 2,000 m a.s.l.) show the smallest values of biomass relatively to the rest of the study area. This pattern remained by the end of the simulation in both cases.

2.4 Discussion

We provide detailed step-by-step example to initialize, calibrate and set up a forest landscape model. Our work could help other potential users to better understand what is required to start applying such models. Thus, our fully documented methodological process represents a step forward toward the transparent application of forest landscape models in regions without prior application. We also made available a high-resolution map of vegetation conditions and calibration details for a large mountainous landscape in the European Mediterranean area, together with the input data and scripts used in the process. Our landscape level simulations reveal distinct dynamics among species according to their competitive potential and simulated intra-annual growth. These results also indicate

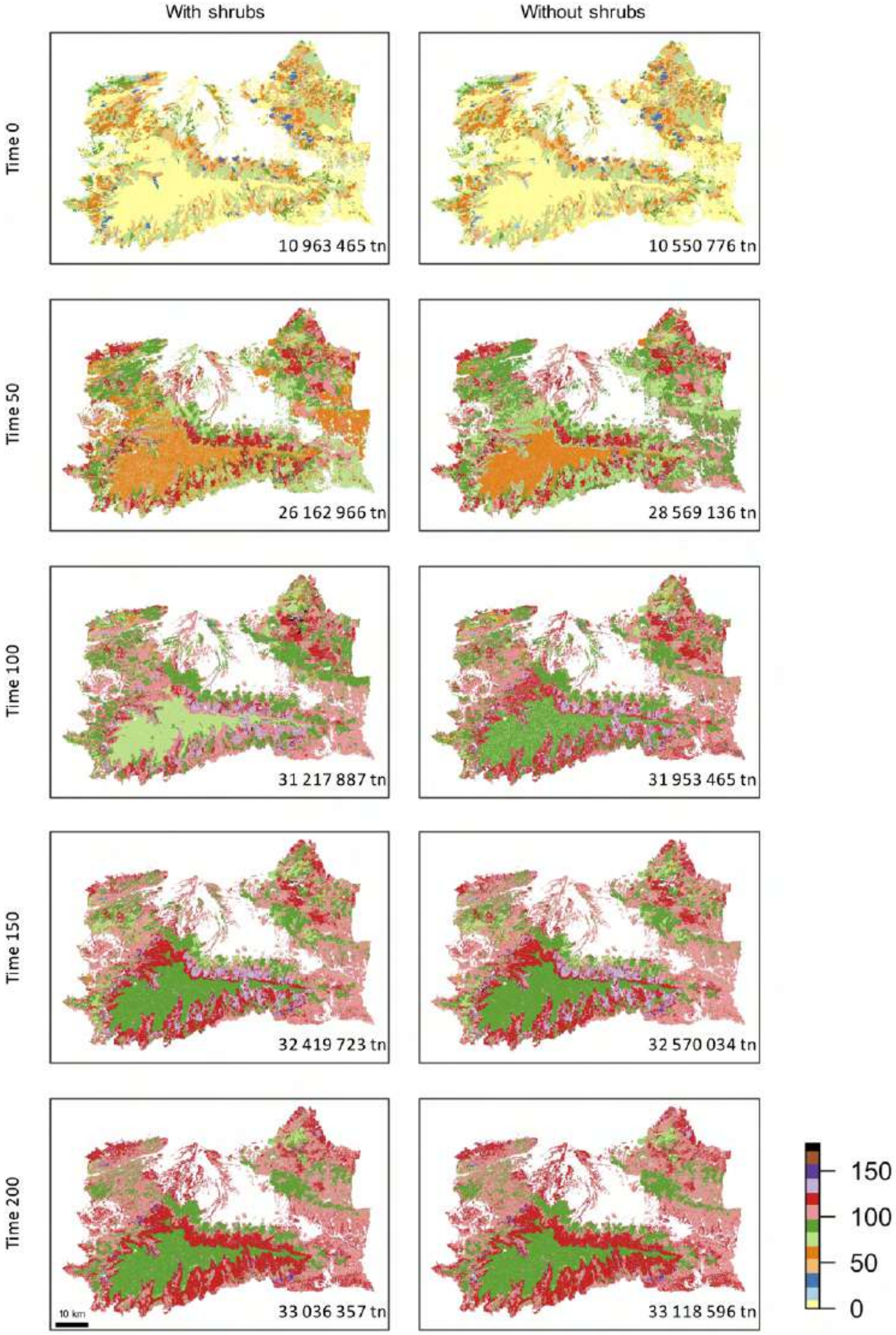
With shrubs
Without shrubs
Time 0
10 963 465 tn
10 550 776 tn
Time 50
26 162 966 tn
28 569 136 tn
Time 100
31 217 887 tn
31 953 465 tn
Time 150
32 419 723 tn
32 570 034 tn
Time 200
33 036 357 tn
33 118 596 tn
10 km
150
100
50
0

Figure 2.7: Total aboveground biomass ($\mathrm{tn\,ha^{-1}}$) at years 0, 50, 100, 150, and 200 for the two simulations, as indicated in the scale bar on the right. Number in each panel indicates the total aboveground biomass (Tg) for the whole landscape at each time step.

that shrub communities shall be considered in forest landscape models as they have the potential to influence forest dynamics by delaying growth and expansion of tree species in Mediterranean ecosystems.

2.4.1 Spatial Imputation and Initial Vegetation Conditions

The selection of species to be included in modelling studies is typically done by analysing data from terrestrial plot measurements such as forest inventories (e.g. Wang et al., 2019). However, for certain ecosystems, limiting this inspection to forest inventories has some disadvantages. Forest inventory data commonly report information on tree species, neglecting important functional groups (in our case, *J. communis* and shrubs communities). Moreover, selection is usually based on variables such as basal area or stand coverage. This selection may result in the exclusion of species that may not be abundant at the landscape level but whose presence is crucial at the local scale. For example, *Q. faginea* would have been initially excluded from our study since its coverage falls below the 1 % of the study area (0.03 %). However, this species is found at high abundance in some locations and has a higher susceptibility to summer drought than *Q. ilex*. Therefore, the dynamics and distribution of *Q. faginea* are expected to be highly affected by climate change (Quero et al., 2006). Similarly, *J. communis* was included due to its importance in areas above the treeline. In these areas, *J. communis* is susceptible to interact with tree species under climate change conditions by limiting or facilitating uphill migration of tree species. Therefore, even though forest inventory data are important resources for generating inputs for FLMs, we recommend combining such datasets with other information sources (e.g., vegetation maps, local studies) according to the forest ecosystem under consideration and study focus —in our case, climate change applications—. Considering factors such as relevance in specific habitats or cultural importance (e.g. Lucash et al., 2019) may result in inclusion or exclusion of some species.

Our method, which combined multiple information sources allows the inclusion of fine-coarse information such as the presence of sparse trees and shrub communities. The inclusion of sparse trees in the initial vegetation map is important in the Mediterranean mountains, since we simulate succession in pine plantations, artificially created stands where regeneration is highly affected by seed dispersal from adjacent patches of native vegetation (González-Moreno et al., 2011; Navarro-González et al., 2013). Although shrubs' biomass is generally low, they can shade the forest floor and therefore influence simulated light and soil water dynamics, as well as affect establishment (further discussion below). Moreover, shrubs play a key role in other processes such as fire dynamics due to their role as fuel in forest fires (Syphard et al., 2006).

In this study, we have used a categorical methodology for the spatial imputation, contrary to commonly used methods based on geographic or data space distance (e.g. Duveneck et al., 2015; Ohmann et al., 2014; Wilson et al., 2012). Our study area is a highly anthropized mosaic of different land uses and management regimes, and therefore imputation based solely on distance might not have been an appropriate criterion, as indicated by Duveneck et al. (2015). For example, the most common forest type in our landscape, pine plantations, are the result of past forestry policies which were applied almost simultaneously all over the region. Therefore, a high similarity is expected between stands, regardless of the physical distance between them. This is a common situation in other Mediterranean ecosystems (EEA, 2016), and therefore this approach could also be used in such cases.

The uncertainties of this methodology are inherently related to the uncertainties of the information sources. Besides, an additional source of uncertainty in the initial vegetation conditions map is related to the assignation of age to cohorts. Tree age data is rarely available at single-tree level in forest datasets, as reliable tree age estimations are resource-consuming and often invasive (Fazan et al., 2012; Rohner et al., 2013). Thus, modellers are commonly forced to assign each tree (or cohort) to an age class inferring it from available measurements (e.g., diameter, height, average stand age; Abrams (1985) and Rozas (2003). In the case of LANDIS-II, a cohort's age determines simulated biomass, which in turn influences light and water availability at cell-level. Therefore, assumptions in the age assignation process may not be so relevant as long as the relative difference between species reflects real conditions. Considering this, we created correspondence rules between tree age and diameter and height for each of the simulated species and age classes. Thus, the growth pattern assigned to each of the species is relative to the other species, reflecting the differential access to water and light by each species-age. This methodology could be further improved by considering additional local yield tables and observations. Nevertheless, by documenting such correspondence rules the model inputs generation is significantly more transparent and reproducible than other LANDIS-II studies (e.g. Mina et al., 2021).

Our goal was to increase the reproducibility of model input generation by ensuring high transparency and detail in the process description. The methodology presented in this study does not necessarily introduce new methods compared to previous studies (e.g. He et al., 1998) but rather it highlights all aspects of the process, which we believe could be of great benefit for beginner modellers to set up applications in new landscapes. Firstly, considering multiple information sources at plot- and polygon-level may be necessary. In our case, multiple vegetation maps were required to consider forested areas, dispersed trees and shrub communities. Secondly, the collected information likely requires processing and transformation, which may introduce assumptions (e.g., age assignation). Thirdly, the selection of the appropriate spatial imputation method should consider the study area characteristics (e.g., coetaneous patches of pine plantations) and available information.

2.4.2 Calibration of Model Parameters and Site-Level Simulations

Calibration of model parameters was performed by running simulations and testing long-term species dynamics and competitive interactions at site-level. The obtained results were iteratively assessed to adjust parameter values until the species showed their expected growing patterns. Experiments at site scale using landscape models have also been used before to analyse the influence of different factors on model outputs by avoiding the high complexity resulting from large landscapes simulations (Gustafson et al., 2017; Gustafson et al., 2018).

During the calibration phase, species parameters were adjusted to ensure that the model simulates realistic species biomass estimations. Species biomass data derived from field observations (e.g., growth-and-yield sites, inventories and permanent plots) are usually highly variable as they differ depending on multiple factors (e.g., location, stand development, site index). Moreover, biomass values often have a high degree of uncertainty, since they are commonly estimated based on general allometric equations from other measured variables (e.g., diameter, height, wood density) (Forrester et al., 2017). Therefore, such comparisons should be interpreted with caution. In this study we used such estimations to ensure that the simulated biomass falls within realistic ranges rather than adjusting parameter values to match the exact values (see Supplementary Figure S.10). With this approach, we calibrated the most relevant species for this study (*P. halepensis*, *P. nigra*, *P. pinaster*, *P. sylvestris*, *Q. ilex*, and *Q. pyrenaica*).

Besides, we review here other studies which provide biomass estimations for some of our species. The dynamics of *Q. pyrenaica* stands have been studied by Santa Regina (2000), who estimated its biomass in four plots in northwestern Spain. Our simulations have a high degree of agreement for foliage biomass, while certain overestimation remains for wood biomass. This difference, nevertheless, can be justified as in the plots studied by Santa Regina (2000) the presence of shrubs could be reducing *Q. pyrenaica* productivity. Río and Sterba (2009) studied the productivity of mixed stands of *P. sylvestris* and *Q. pyrenaica*. They found that although *P. sylvestris* is less productive when growing in mixed stands, the reduction in productivity is smaller than the reduction in occupied area. Accordingly, our simulations show a decrease in productivity of *P. sylvestris* when growing together with other species such as *Q. pyrenaica*, but it remains as a highly productive species.

Other methodologies have been applied for model calibration (e.g. Cassell et al., 2019; Duveneck et al., 2017; Mina et al., 2021). As an example, Duveneck et al. (2017) used data from flux towers within New England (United States) to calibrate PnET parameters. The application of some methodologies over others usually responds to the availability of data for the simulated area. In this sense, the lack of available biomass accumulation curves limited the application of more exhaustive calibration methodologies. Our calibration could therefore be improved if additional data sets become available, such as high-resolution biomass measurements or growth rates based on flux towers measurements.

Our results clearly show that PnET-Succession reproduces the characteristic bimodal growth observed in Mediterranean species (Larcher, 2000). This growth pattern is the result of dry summer conditions, which impose a limitation for growth to numerous species. Thus, Mediterranean species often show two peaks of productivity through the year, in late spring and fall (Camarero et al., 2010; Gutiérrez et al., 2011). *Q. ilex* bimodal growth has been studied in detail by Gutiérrez et al. (2011). They report asymmetrical radial increment peaks in May and September for a coastal location in northeastern Spain, with high plasticity dependent on climatic conditions and most of the growth occurring during the first growing phase. The simulated growth of *Q. ilex* reproduces this pattern both when the species is simulated growing alone or in association with other species. Modelling such growth interannual variability remains a challenge for forest models, for which improvements are proposed to include such processes (Mina et al., 2016). In the case of PnET-Succession, the high temporal resolution (monthly scale) and mechanistic approach allows reproducing such patterns and therefore makes this model highly suitable for applications in Mediterranean systems.

Distinct dynamics were observed according to the species competitive potential and simulated intra-annual growth. Species leaf habits is one of the factors influencing species competitiveness. Among the simulated species considered in this study, only *Q. faginea*, *Q. pyrenaica*, and *Pop. nigra* are deciduous while all other species are evergreen. Deciduous species have a higher potential for net photosynthesis in PnET-Succession (De Bruijn et al., 2014) but they are generally less shade and drought tolerant and need to spend more energy in building foliage biomass than evergreen species. The trade-off between benefits and losses caused by different leaf habits explains the coexistence of species with different strategies (Escudero et al., 2017), as it is clearly observed in the growth patterns of *Q. ilex* and *Q. faginea*.

The calibration of non-tree species —junipers and shrubs—was particularly challenging. Although we believe including both junipers (*J. communis* and *J. oxycedrus*) in the initial vegetation map was important in our target ecosystem, the lack of information and reliable data on these species limited a finer calibration. As a result, both species were assigned with very similar parameter values, their simulated behaviour was almost identical and thus they were grouped together. In the case of shrub communities, since they represent functional groups rather than single species, calibration was achieved mostly by extrapolation, comparison with similar studies (e.g. Cassell et al., 2019) and tuning according to expected simulated behaviour relatively to tree species. Their ecological role, for the sake of this study, was mainly as shade providers and competitors for establishment, and therefore our main objective in this sense has been oriented to ensure survival and growth beneath the tree canopy. For further applications where the role of non-tree species is more relevant (e.g., fire dynamics, facilitation), their parameterization shall be improved to better reflect differences between shrubs species or functional types.

2.4.3 Landscape-Level Simulation

Our results show that the shrub communities influence the forest dynamics by delaying the growth and expansion of tree species. In our simulations, we found that shrubs reduce tree species establishment. However, shrubs are known to serve as nurse plants, favouring tree seedling growth by amelioration of adverse dry conditions and protection against herbivory (Castro et al., 2004; Gómez-Aparicio et al., 2005; Prévosto et al., 2020).

Modelling the role of understory in forest succession has also been investigated by Thrippleton et al. (2016) with the LandClim model. Similarly to our results, they found delayed establishment of trees when herbaceous understory was abundant. Moreover, both Thrippleton et al. (2016) and our results show that shrubs are unable to establish under dense canopies, eventually declining and even disappearing from the landscape. This agrees with field observations: weak regeneration of shrubs and tree species under dense canopies biomass even when the sapling bank is present (Mendoza Sagrera, 2008). Also, the decline of shrubs in our simulations was likely not realistic, since small-scale perturbations creating patches where light availability increases and shrub communities thrive (e.g., due to fire, Leverkus et al., 2014) were not included in our experiment. However, the interactions occurring between trees and non-trees species and abiotic factors such as fire justify the need to include these communities in these kinds of applications (e.g. Loudermilk et al., 2013).

The increase of forest biomass observed in our simulations at landscape level was somewhat expected, since we did not include harvesting or natural perturbations (e.g., fire, pest outbreaks). Additionally, simulations were run with the same climate inputs used for calibration (baseline climate), thus potential impacts of changing climate (e.g., higher temperatures, extended drought, CO_2 fertilization) were not considered. At medium altitudes, where most forest stands are found, the growing tendency in biomass was likely a result of pine plantations being relatively young at the beginning of our simulations. Pine plantations in Sierra Nevada and Sierra de Baza have been showing in latest years signs of decay as a result of increasing drought stress and intense interspecific competition (e.g. Sánchez-Salguero et al., 2010; Sánchez-Salguero et al., 2012a; Sánchez-Salguero et al., 2012b). These mortality events could not be observed in our study since increasing drought was not considered in our climate inputs.

Even though there was a general growing trend in biomass, the dynamics among species differed. *P. halepensis* and *P. pinaster* biomass declined as they approached longevity and seemed unable to regenerate beneath the canopy, while *Q. ilex* kept growing. *P. sylvestris* and *P. nigra*, however, were able to coexist with *Q. pyrenaica*, and therefore they remained present in the landscape and even increased their biomass through time. Factors influencing the establishment of pines and oaks in Sierra Nevada and Sierra de Baza have been profusely studied (e.g. Gómez-Aparicio et al., 2009; Herrero Méndez, 2012; Mendoza et al., 2009a; Mendoza et al., 2009b), showing limitations to recruitment mainly due to high post-dispersal seed predation rates and dry summer conditions. Our simulations also reflect poor establishment of some species, probably related to dry summer conditions and species shade tolerances being higher than in reality. In the case of junipers, they are probably limited by a short growing season due to their minimum and optimal photosynthesis temperatures and low biomass levels which prevents them from accessing light and water.

2.4.4 Modelling Aspects, Limitations and Future Research

The selection of the model used in this study was based on the flexibility and potentiality of this model. LANDIS-II is a well-documented model supported by an active scientific community, which ensures help and support for new modellers. Moreover, several model extensions are available for a wide variety of future applications (e.g., harvest, fire, wind, biological agents). To simulate forest dynamics, we specifically chose PnET-Succession as it simulates ecological succession with a more mechanistic approach than past extensions. As mentioned above, by simulating growth at monthly resolution, intra-annual growth variability can be properly captured, which is of crucial importance for simulations under climate change and applications in the Mediterranean area.

However, the model is still limited in some aspects which could be further improved. First, the need to provide cohort age certainly adds uncertainty to the initial conditions. Given that PnET-Succession uses age to determine initial cohorts' biomass, other variables such as diameter, basal area or height —often available from field observations—could be used instead, reducing uncertainty. Even though latest PnET-Succession version allows providing initial biomass, this variable often needs to be estimated with allometric equations. Besides, since cohort's biomass is highly dependent on tree density, tree density could also be incorporated into the model in some way to improve model representation of competition effects (but see Wang et al., 2014a). This would be especially relevant in ecosystems such as pine plantations, where extremely high tree densities cause inter- and intraspecific competition to be an important factor explaining vegetation dynamics.

The grouping of cells into homogeneous climatic conditions (ecoregions) prevents a fine-coarse capturing of topographic influence on climate, which is a relevant issue in mountainous areas. The definition of such ecoregions is commonly done by clustering average climate information to define homogeneous climate regions. These homogeneous regions are assigned with climate time series typically obtained as the average among all cells within the ecoregion. By doing so, the influence of topography on climate is not well captured and extreme conditions, such as the ones found in the mountain peaks, are smoothed down. In our case, the increase in biomass at high altitudes was probably due to the fact that temperature was not limiting enough the establishment of species beyond their natural treeline. In a large model comparison study, Petter et al. (2020) also found that no clear treeline emerged from LANDIS-II simulations, in which the area above vegetation was binned into a single ecoregion, compared to other models in which each cell has its own climatic condition. The use of continuous maps for climate conditions (i.e., each cell assigned its own environmental and climate condition) could improve how PnET-Succession simulates the effect of topography on climate and thus on vegetation changes. Other forest landscape models developed for mountain environments already make use of continuous maps explicitly accounting for topography (e.g. LandClim; Schumacher et al., 2004). This feature is currently under development for LANDIS-II, which was initially designed to efficiently simulate large landscapes (more than 1 million interacting cells).

Even considering the above-mentioned limitations, the model showed a great potential for a wide range of applications in the Mediterranean area. The transparent initialization of the model and the documented calibration can serve as a guide for new users, encouraging the application of forest landscape models. Besides, testing different initialization data has allowed us to confirm the importance of shrub communities in the forest dynamics within the study region. Further experiments will analyse the vegetation dynamics under natural perturbations such as fire or defoliators. Moreover, the inclusion of climate change and silviculture will allow us to explore future forest dynamics, and, by doing so, deliver management recommendations to promote ecosystems adaptation to global change.

Chapter 3

Forest management scenarios drive future dynamics of Mediterranean planted pine forests under climate change

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Manuscript

Key words Mediterranean forests, planted pine forests, diversification, climate change, management scenarios, LANDIS-II, forest type change

Resumen

Las plantaciones de pinos son comunidades muy abundantes en la cuenca mediterránea como resultado de reforestaciones pasadas. Estos bosques muestran una alta homogeneidad específica y estructural. A fin de promover la adaptación al cambio climático y aumentar su resiliencia, se recomienda su diversificación hacia bosques mixtos. Este estudio pretende evaluar el desarrollo futuro de estos bosques de pinos como resultado de los impactos combinados del clima y la gestión forestal. Mediante la aplicación de un modelo de paisaje forestal (Forest Landscape Model, LANDIS-II) para simular diferentes escenarios climáticos y diversas estrategias de gestión, diseñadas en colaboración con gestores forestales, se evalúan sus efectos sobre el funcionamiento de las plantaciones de pinos y los cambios en términos de composición. Los escenarios de cambio climático causaron una alteración en la fenología de estos bosques, reduciendo el crecimiento estival y aumentando la productividad fotosintética en primavera y otoño, particularmente bajo escenarios de altas emisiones. La biomasa aumentó a lo largo del tiempo y de forma más acusada ante escenarios de cambio climático, pero este incremento varió según la especie, resultando en cambios en la tipología de bosque que encontramos en el paisaje inicialmente ocupado por plantaciones de pinar. Nuestros resultados muestran a la sucesión natural como el principal impulsor de cambio, aunque la gestión intensa favorece este proceso limitando el crecimiento de los pinos y favoreciendo el de las quercíneas. Además constatamos la importancia de la gestión activa de las plantaciones de pinar de cara a favorecer el establecimiento de bosques mixtos y adaptados al cambio climático más rápidamente que únicamente mediante sucesión natural. Además, nuestra aproximación espacialmente explícita nos ha ayudado a identificar áreas donde la dispersión de semillas o la exclusión competitiva limitan la diversificación del bosque, obteniendo así recomendaciones útiles para la gestión.

Abstract

Planted pine forests are highly abundant communities in the Mediterranean Basin. Being the result of past reforestation, these forests show high species and structural homogeneity; therefore, a diversification to mixed forests is recommended to promote adaptation and increase their resilience to climate change. This study aims at evaluating how these pine forests will develop in the future as a result of the combined impacts of management and climate. We applied a forest landscape model (LANDIS-II) to simulate different climate scenarios and management strategies designed in cooperation with forest managers to assess their effects on the performance of planted pine forests and their change in terms of forest composition. Climate change scenarios caused a shift in the phenological growth pattern of planted pine forests by reducing forest growth during summer and increasing photosynthetic productivity in spring and fall, particularly under high emission scenarios. Biomass increased through time and more strongly under climate change, but this increase differs among species, resulting in changes of forest types across the landscape. Our results portray natural succession as the main driver of forest change, but intensive management enforced this process by limiting pine growth and promoting oaks growth. We highlight the importance of active management on planted pine forests to favour mixed and climate-adapted ecosystems in shorter time scales than offered by succession alone. Moreover, our spatially explicit modelling approach helps to identify areas where lack of seed dispersal or competitive exclusion prevents diversification, providing useful recommendations for interventions.

3.1 Introduction

Monospecific and even-age forests constitute the most abundant forest types in Europe as a result of intensive anthropogenic management over the last centuries (EEA, 2016). These ecosystems have been created or promoted for purposes such as timber production, soil erosion protection or hydrological management (Pemán García et al., 2009). In Mediterranean areas, such forest communities are usually originated by plantation after disturbance (e.g., fire, logging) and often composed of pine species (*Pinus* spp). These pine forests frequently present high densities, low structural heterogeneity and low tree species diversity, which make them vulnerable to perturbations (Senf and Seidl, 2022). Moreover, climate change has emerged as a new driver. Under future projected climate, Mediterranean forests are expected to suffer forest dieback as a result of increased competition under water shortage (Navarro-Cerrillo et al., 2019; Peñuelas and Sardans, 2021).

On the contrary, mixed forests, and concretely conifer-broadleaved mixtures, show better capacities to face drought events and higher resilience to climate change in dry areas (Pardos et al., 2021). Thus, diversification of pure stands to mixed forests is recommended as a suitable strategy to promote adaptation to climate change (De-Dios-García et al., 2015), increase resilience to disturbances (Messier et al., 2022) and ensure ecosystem services provision in the long term.

Due to the low levels of structural and compositional tree species diversity of planted pine forests, there is a general consensus on the need to manage them through silvicultural practices to increase their species diversity (Oettel and Lapin, 2021). However, how to implement it strategically across large and complex forest landscapes remains a challenge. Under these circumstances, there is an urgent need to better understand how these forests might develop under future and uncertain climate regimes, and to evaluate adaptive management scenarios to increase their potential resilience to climate change. Mediterranean pine forests constitute a good example to study the effects of management, since they are located in highly climate-sensitive areas to climate change, cover large surfaces (Rubio-Cuadrado et al., 2018), and present a variety of conditions in terms of dominant species and climate, which allows observing the influence of different factors.

Focusing on a 390,000 ha, forested landscape in southeastern Spain, our overarching goal was to evaluate how planted pine forests might change through time as a result of the combined impacts of management and climate scenarios. We assessed different trajectories of these forests using a forest landscape model that incorporates climate and management effects on forest dynamics. Management scenarios were co-designed with foresters to reproduce realistic management strategies. With this work we aim to answer the following questions:

- How will future climate and management affect the performance (i.e., photosynthesis and biomass) of planted pine forests?
- How will different climate and management scenarios affect the forest composition change of these pine dominated systems?
- What management regime is better suited to drive these forests towards a more mixed and, therefore, climate-adapted forest ecosystem?

3.2 Methodology

3.2.1 Study area

The study area is located in southeastern Spain (Figure 3.1). It includes Sierra Nevada, Sierra de Arana and Sierra de Baza-Filabres mountain ranges, resulting in a complex landscape ranging from 400 to 3,479 m a.s.l. Planted pine forests (hereafter pine forests) represent 17 % of the surface and are located at intermediate elevations (1578±358 m a.s.l.). Dominant pine species vary with elevation, from *Pinus halepensis* Miller. (Aleppo pine) and *Pinus pinaster* Aiton (Maritime pine) at the lowest elevations, to *Pinus nigra* Arnold. (Black pine) and *Pinus sylvestris* L. (Scots pine) at higher elevations (Mesa Garrido, 2019). These forests were originally established to reduce soil erosion and have received limited management, which has resulted in highly dense monospecific even-age stands. Oak forests are also dominant, with *Quercus ilex* L. (Holm oak), *Q. pyrenaica* Willd. (Pyrenean oak), and *Q. faginea* Lam. (Portuguese oak) all dominant in the region. Apart from pines and oaks, large areas are covered by sclerophyll shrublands in lowlands and sparse alpine vegetation at the high altitudes. Climate is highly seasonal, with dry hot summers and mild winters typical of the Mediterranean climate. The pine forests considered in this study are mainly located at the intermediate bioclimatic belt (mean annual temperature 8–13 °C), with some patches at warmer and colder belts (13–17 °C and 4–8 °C, respectively) (Rivas Martínez, 1983).

3.2.2 Modelling approach

LANDIS-II is a widely-applied forest landscape model created to simulate forest growth and disturbance across large landscapes (Scheller et al., 2007). The spatially-explicit structure allows simulating forest succession and seed dispersal

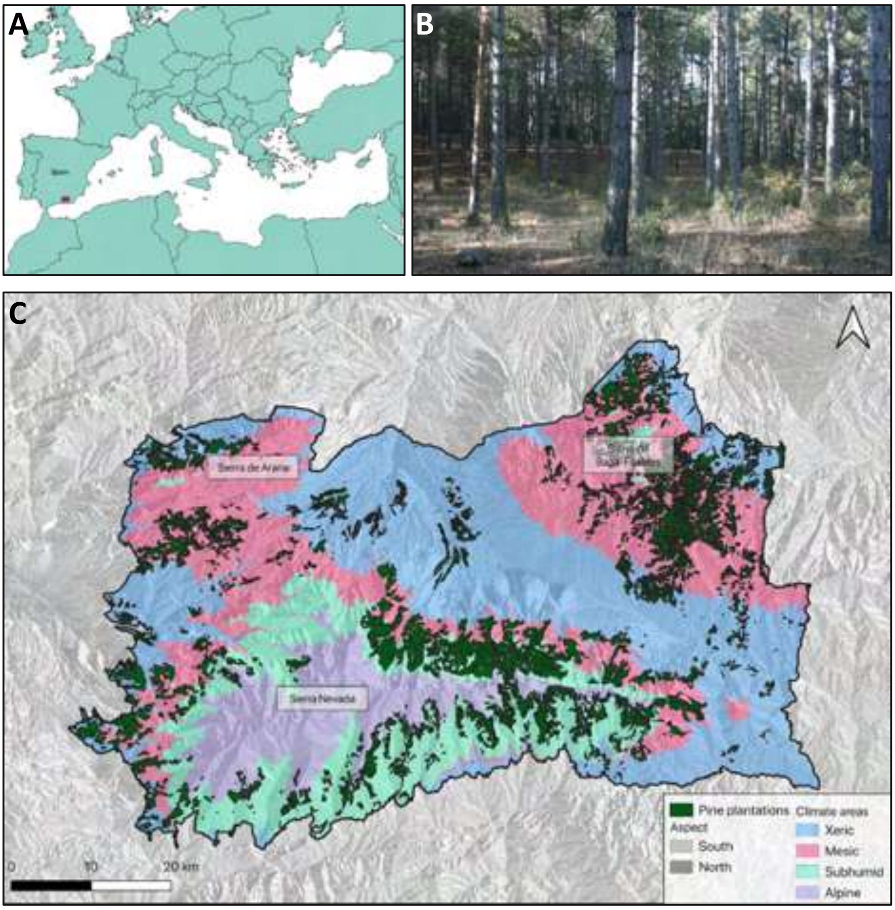


Figure 3.1: Schematic view of the study area: **(A)** location; **(B)** planted pine forests; **(C)** details of study area, with colours referring to climate regions and pine forests overlapped and highlighted in dark green.

among interconnected grid-cells at decadal to multi-century time scales, as well as the potential influence of natural disturbances (e.g., fire, insects, wind), management interventions and land use changes. Trees are grouped into species- and age-specific cohorts in each cell. LANDIS-II is built on a core module interacting with multiple model extensions handling ecological processes such as succession or disturbances at various levels of complexity.

Model initialization

The methodology and data sources for generating 1-ha resolution initial vegetation conditions and biophysical inputs are extensively described in Suárez-Muñoz et al. (2021). Within initial vegetation conditions —i.e., current species presence and age representing the starting point for the simulations—shrub species groups were also included as they are an abundant land cover in the study area as well as important elements affecting forest dynamics in drought-prone Mediterranean areas (Cassell et al., 2019). Biophysical inputs were obtained by combining homogeneous climatic regions, derived from historical climate maps, with maps of soil texture.

Forest growth and succession

To simulate future succession, we used the LANDIS-II PnET-Succession extension v4.1 (De Bruijn et al., 2014). PnET-Succession simulates cohorts' competition for light and water, so that photosynthetic processes are explicitly linked to changing environmental drivers such as temperature, precipitation and CO_2 (De Bruijn et al., 2014). A mechanistic process-based approach is used to simulate forest dynamics, which is being considered better suited for long-term projections under unprecedented environmental conditions (Gustafson et al., 2015). PnET-Succession simulates species-cohort growth integrating competition with other cohorts and the effect of changing climate. Gross photosynthesis is calculated as a function of foliar nitrogen multiplied by a series of reduction factors, which control how water availability, temperature, age or light limit potential photosynthesis. Species-specific parameters and monthly climate series are considered in the calculation of these reduction factors. We calibrated PnET-Succession parameters by running single-cell simulations with different species combinations and compared outcomes with empirical biomass values derived from silvicultural schemes proposed by Campos and Díaz-Balteiro (2015). Further details on calibration of species parameters are given in Suárez-Muñoz et al. (2021) and Supplementary Material S3.1.

Climate change

We considered three climate scenarios: contemporary climate (current), moderate emissions (RCP4.5) and high emission (RCP8.5). Climatic series for LANDIS-II simulations were obtained from the MIROC5 global circulation model and precipitation data were further bias-corrected based on meteorological stations data in the study area. Monthly precipitation and temperature data were obtained from CHELSA (Karger et al., 2020). This dataset contains historical series (1950-2005) as well as future projections (2006-2100) downscaled to ~5 km spatial resolution. Photosynthetically active radiation (PAR) data were obtained from Cornes et al. (2018) version 20.0e and CO_2 concentrations were obtained from Mina et al. (2021). Future projections showed a clear increasing gradient in temperatures and CO_2 from current to RCP8.5 scenario, while trends for precipitation were less divergent between emission scenarios, despite showing a slight decreasing gradient under climate change (Figure 3.2 and Figure S.37). More details on the data sources, the generation of climate scenarios and the precipitation bias correction are provided in Supplementary Material S3.2.

Forest management

Management scenarios were designed in close collaboration with local managers and forest experts. They represent divergent viewpoints towards the management of pine forests in our study area, as well as an intensity gradient in terms of amount of biomass harvested and proportion of landscape affected (Figure 3.3). Overall, we considered four forest management scenarios: non-management, conservative, proactive and proactive-plus. 'Non-management' represents a common situation in large portions of the territory, as a result of limited budget allocated to forest management. The 'conservative' scenario is driven by the precautionary principle: managers often attempt to prevent post harvesting mortality due to windstorms or snowfalls in weakened stands. Thus, 'conservative scenario' is based on low thinning intensities to avoid the risk of losing pine canopy cover, while lightly promoting *Quercus* spp. growth. By contrast, the 'proactive' scenario is derived from the idea that over-precautionary management causes little or no effect on pine forests, and therefore it is not sufficient to trigger changes in species composition. Under this scenario, higher amounts of biomass are removed within stands while the proportion of area harvested is comparable with the conservative scenario. Finally, the proactive-plus scenario represents a situation where the amount of biomass removed within stands is the same as in proactive scenario, but more resources are allocated to forest management and therefore

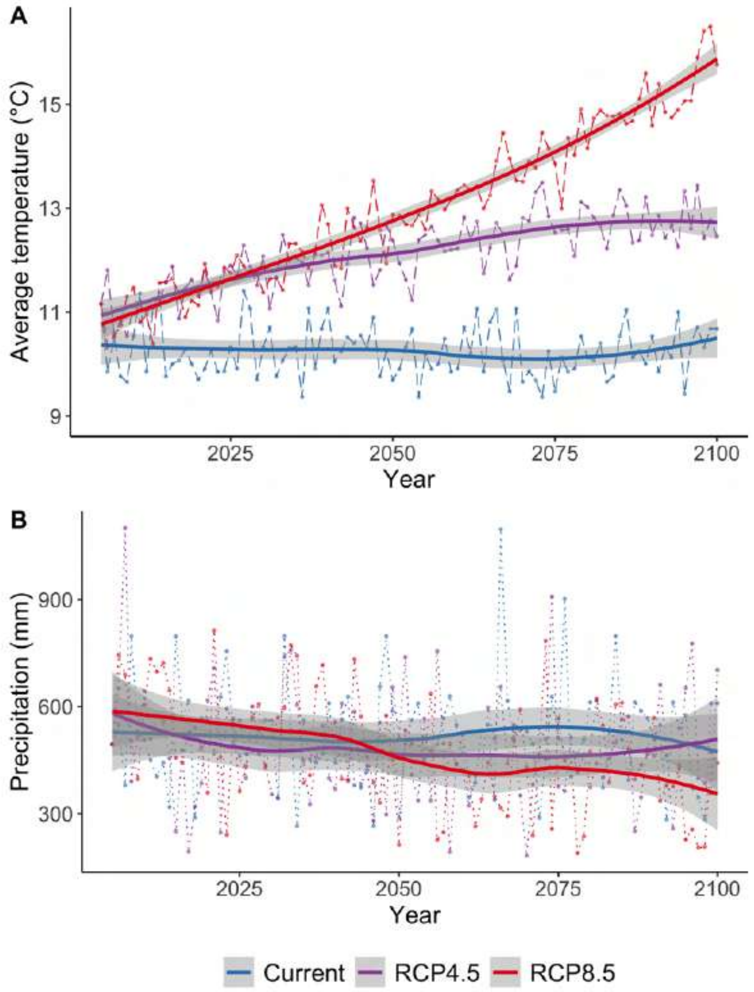


Figure 3.2: Annual average temperature **(A)** and precipitation **(B)** under current, RCP4.5 and RCP8.5 climate scenarios. Data refer to climate region 3, where the highest proportion of pine forests is found. Trend line and shaded area indicate smoothed conditional mean and confidence intervals based on loess method. Monthly average temperatures are shown in Figures S.31-S.33.

broader areas of the landscape are treated.

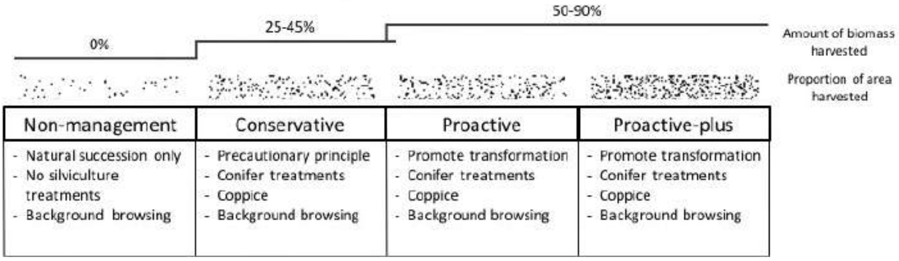


Figure 3.3: Schematic description of management scenarios: non-management, conservative, proactive and proactive-plus. Amount of biomass harvested refers to the percent removed intensity at each harvest event. The proportion of area harvested refers to the proportional area treated every 10 years.

Forest management was implemented with the Biomass Harvest extension v4.4 (Gustafson et al., 2000), which reproduces silvicultural activities by harvesting biomass from the landscape based on user-defined rules. Prescriptions define which cells, species and age ranges are targeted and which proportion of biomass is removed from each cohort. The study area was divided into forest stands (Supplementary Figure S.36) grouped into management units (Supplementary Figure S.37), each with its own set of silvicultural prescriptions and harvest treatment frequency. Management units were based on land property (public/private) and conservation use (reserve/non-reserve). Non-reserve public areas, where most of the planted pine forests are located (81 % of the surface), were managed more intensively than private ones, and reserve areas were not managed under any scenario, reflecting what is commonly occurring in the territory (Junta de Andalucía, 2004b; Junta de Andalucía, 2011). Further details on the implementation of management scenarios and silvicultural prescriptions are provided in the Supplementary Material S3.3.

3.2.3 Experimental design and analysis

A combination of climate and management scenarios was simulated in this study for the period 2005-2100, for a total of 60 simulations (3 climate scenarios x 4 management scenarios x 5 replicates). Model outputs were analysed by extracting variables for the area covered by the pine forests according to the Andalusian Map of Vegetation Land Cover (REDIAM, 2006) (Figure 3.1). Thus, we refer to the results at landscape level as the aggregated values of all cells within pine forests and to cell level when data for each cell were analysed independently, allowing to evaluate the existence and changes in spatial patterns.

Model outputs were assessed by analysing changes in average monthly net photosynthesis (hereafter photosynthesis) and above ground biomass (hereafter biomass). We compared photosynthesis at the beginning and at the end of the simulation period. Biomass was analysed both at cell- and landscape-level. The temporal trend in cell-level biomass was analysed by applying the non-parametric Mann-Kendall trend test (Mann, 1945). This test evaluates the significant trend of a variable over time based on the Kendall rank correlation, which measures the strength of a monotonic association between two variables. Kendall's tau statistic ranges from -1 and 1, and indicates a negative and a positive, respectively, trend in the analysed variable through time. Landscape-level biomass was evaluated by analysing species-specific biomass densities through time.

We also evaluated changes in overall forest composition by computing the difference in forest types coverage between the initial and final years of the simulation. We reclassified species biomass into pure (>90 % of the biomass in a cell composed of only pines, oaks, or shrubs), mixed (no specific group has more than 90 % of the biomass) and empty forest types (no biomass). Mixed stands were further categorised into pine-dominated or oak-dominated if a group accounted for more than 50 % of the biomass. All analyses were performed using the software R v4.1.1 (R Core Team, 2022).

3.3 Results

3.3.1 Net photosynthesis changes

Our results indicate a seasonal growth pattern in concordance with tree species growing in the Mediterranean climate (e.g., two active growing periods and summer growth stagnation, Figure 3.4). Monthly climate clearly influenced such intra-annual growth pattern while changes caused by management interventions did not alter the photosynthetic pattern of pine forests at landscape level (Supplementary Figure S.41). Under current climate, the intra-annual growth pattern was similar at the beginning and at the end of the simulation, with maximum photosynthesis in May. Changes due to forest succession caused a slight decrease in photosynthesis during early summer and a slight increase in autumn, resulting in a small net decrease between the beginning and the end of the simulation (-17.87 $\mathrm{g\,m^{-2}}$).

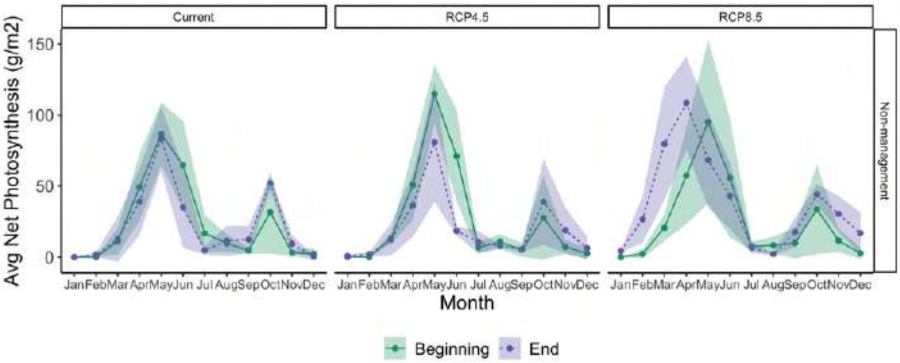


Figure 3.4: Average monthly net photosynthesis of the area covered by planted pine forests (elevation 1578±358 m a.s.l.) across climate scenarios. Since differences between management scenarios were minimal, results are shown for non-management. See Supplementary Figure S.41 for all scenarios. Beginning and End periods correspond to the average among the first and the last three simulation timesteps, respectively (years 2005, 2010 and 2015 and years 2090, 2095 and 2100). Ribbon represents the standard deviation among timesteps from the mean values of five replicates.

Compared to current climate, climate change increased intra-annual photosynthesis both at the beginning and at end of the simulation. Under RCP4.5, spring growth increased at the beginning of the simulation (max 114.72±20.57 $\mathrm{g\,m^{-2}}$ in May), while at the end the summer stagnation started earlier and was more pronounced, but the autumn growing period lasted longer than under current climate. Overall, annual photosynthetic productivity under RCP4.5 decreased through time like the current climate scenario (-71.36 $\mathrm{g\,m^{-2}}$ between the beginning and the end of the simulation). Under RCP8.5, the spring growing period reached similar levels than under current conditions at the beginning of the simulation (95.34±57.69 $\mathrm{g\,m^{-2}}$ in May), but summer stagnation was more pronounced in comparison to the other climate scenarios. At the end of the simulation, however, we found the RCP8.5 scenario resulted in much earlier spring growth and much later autumn growth. Specifically, spring growing phase started in February, reaching its maximum in April (108.42±32.77 $\mathrm{g\,m^{-2}}$), while growth continued during late autumn until December. This resulted in an overall increased increment of annual photosynthesis between the beginning and the end of the simulation under RCP8.5 (+142.80 $\mathrm{g\,m^{-2}}$).

3.3.2 Biomass trends

We found a significantly increasing trend in total biomass in large areas of the landscape under all simulated scenarios, especially under RCP8.5 climate (Table 3.1). Under current climate, only mesic and subhumid areas showed increasing trends in total biomass while xeric areas showed decreasing trends (Supplementary Figure S.42). Management modulated the increase in biomass by limiting its increase under more intense management scenarios. As such, the increasing trend in biomass was stronger under non-management than under the more intense management. For example, 63 % of the area shows a significantly increasing trend and 12 % a no significant trend under the conservative RCP4.5 scenario, while under the proactive-plus RCP4.5 scenario 47 % of the area shows a significantly increasing trend and 18 % of the area shows no significant trend.

Table 3.1: Percentage of cells within planted pine forests which show significant values of Mann-Kendall trend (tau) for total above ground biomass through time. Trend calculated over the average total biomass maps among replicates for each timestep. Total column refers to the percentage of area for which the trend is significant.

Harvest scenarios	**Climate scenarios**	**Negative trend** ($tau < -0.5$)	**No trend** ($-0.5 \leq tau \leq 0.5$)	**Positive trend** ($tau > 0.5$)	**Total**
Non-manag.	Current	1.1 %	25.4 %	41.5 %	68.0 %
Conservative	Current	1.5 %	23.1 %	37.2 %	61.8 %
Proactive	Current	2.3 %	22.9 %	36.0 %	61.2 %
Proactive-plus	Current	4.1 %	21.8 %	29.5 %	55.4 %
Non-manag.	RCP4.5	0.5 %	10.6 %	69.6 %	80.7 %
Conservative	RCP4.5	0.5 %	12.6 %	63.2 %	76.3 %
Proactive	RCP4.5	0.7 %	14.2 %	56.6 %	71.6 %
Proactive-plus	RCP4.5	1.1 %	18.2 %	47.9 %	67.2 %
Non-manag.	RCP8.5	0.2 %	5.6 %	87.4 %	93.2 %
Conservative	RCP8.5	0.2 %	5.9 %	87.5 %	93.5 %
Proactive	RCP8.5	0.2 %	8.1 %	84.6 %	92.8 %
Proactive-plus	RCP8.5	0.3 %	10.3 %	78.9 %	89.5 %

For individual species, we observed differences across simulated scenarios (Figure 3.5). Pines remained the most abundant species group at landscape level throughout the entire simulation under all climate and management scenarios.

Biomass of *Pinus nigra* increased under all climate scenarios but its biomass accrue was limited by intensified management interventions. On the other hand, biomass of *P. halepensis* decreased towards the end of the simulation and this decrease was more pronounced under RCP8.5. *P. sylvestris* and *P. pinaster*, however, remained quite stable through the simulation under all scenarios, although *P. pinaster* was limited by intensive management and seemed to be benefited under RCP8.5 climate. Among oaks, *Quercus ilex* —and less clearly *Q. pyrenaica*— increased in biomass during the last 50 years of the simulation under all climate and management scenarios, but more strongly under more intense management and more rapidly under RCP8.5.

Species composition varied across the landscape (Figure 3.6). Pine biomass decreased in xeric areas under all management and climate scenarios, but more clearly under more intense management and the current and RCP4.5 climate. On the other hand, oak biomass declined at mesic and subhumid areas under current and RCP4.5 climate scenarios and more so under non-management and conservative management scenarios.

3.3.3 Forest composition change under climate and management scenarios

The opposing trends in the biomass of oaks and pines resulted in changes of forest types for some areas. Pine forests, initially pure or mixed pine-dominated stands, partially developed into oaklands by the end of the century. Our results show a reduction in the area initially covered by pure pine and mixed pine-dominated stands, and an increase of pure oak and mixed oak-dominated stands (Figure 3.7). This pattern was consistent among all management and climate scenarios but was promoted by more intense management. Under the proactive-plus scenario the highest increase in oak stands and the highest reduction in pure pine stands was achieved, followed by the proactive scenario. Conservative and non-management scenarios showed similar increase in oak stands, but the decrease in pure pine stands was more pronounced under the conservative scenario.

Climate interacted with management by amplifying the above-mentioned effects. The increase in oak stands and the decrease in pure pine stands under each management scenario were generally more pronounced under RCP8.5 scenario, followed by RCP4.5 compared to current climate. Only under current climate and non-management we observed a slight increase in pure pine stands, likely due to a shift from mixed pine-dominated to pure pine stands.

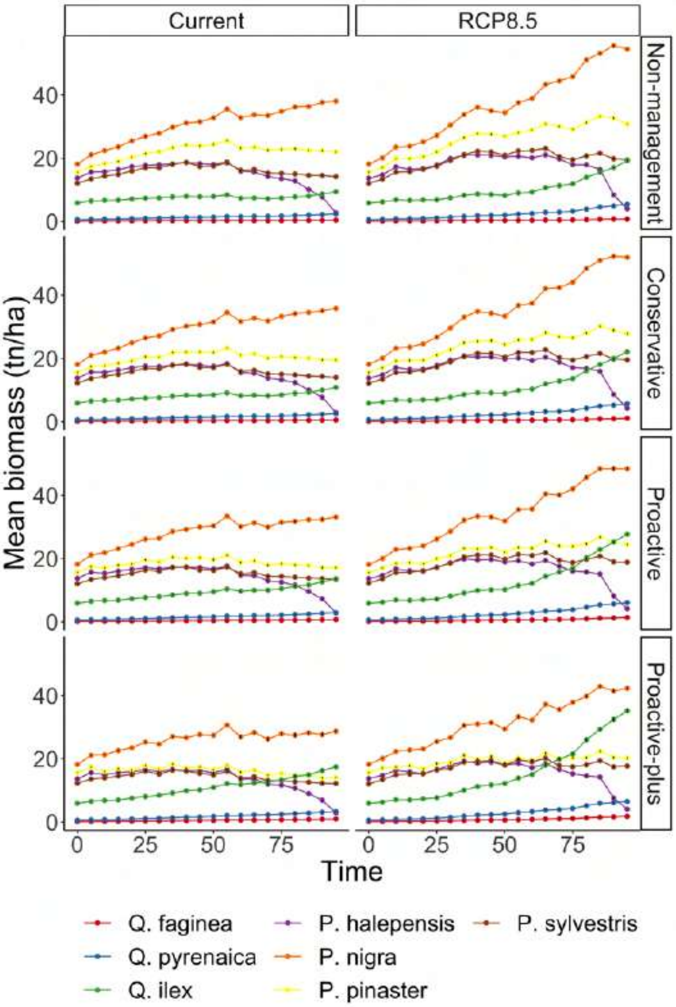


Figure 3.5: Above ground biomass of pines and oaks through time at landscape level (the region initially covered by planted pine forests) for all management scenarios under Current and RCP8.5 climate scenarios. Values correspond to mean across 5 replicates and error bars, when visible, represent standard deviation.

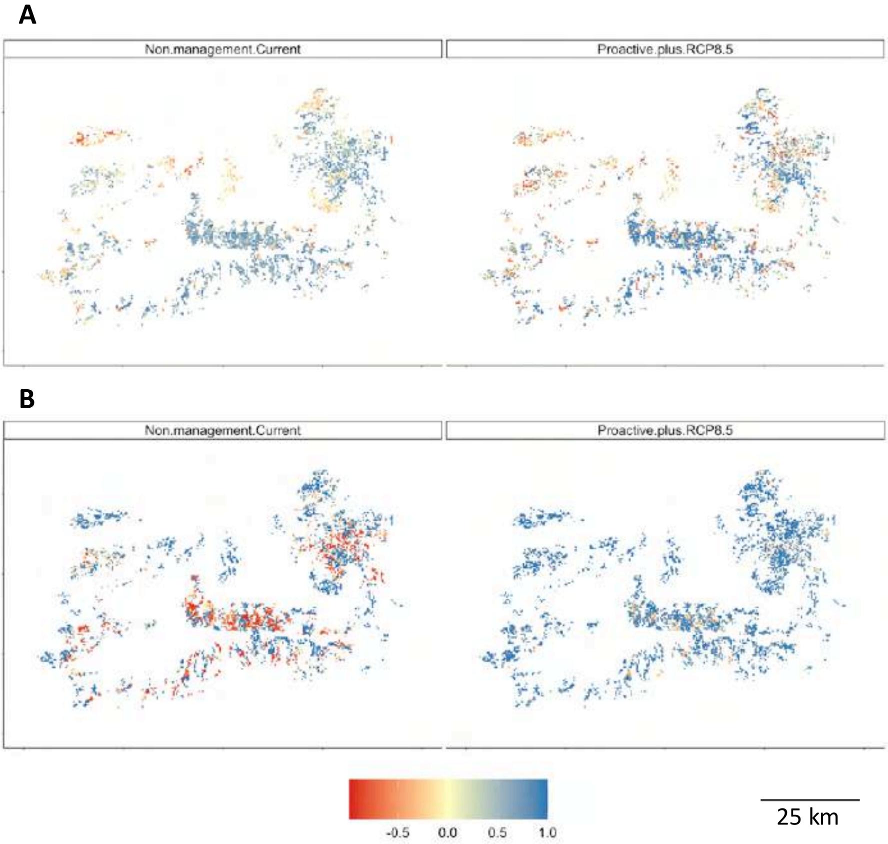


Figure 3.6: Pines **(A)** and oaks **(B)** above ground biomass trend through time as Kendall's *tau* statistic (colour gradient) for non-management, proactive-plus, current and RCP8.5 scenarios. Trend calculated over the average total biomass among replicates for each timestep. All scenarios combinations and significance levels (p-values) can be found in Figures S.43-S.46.

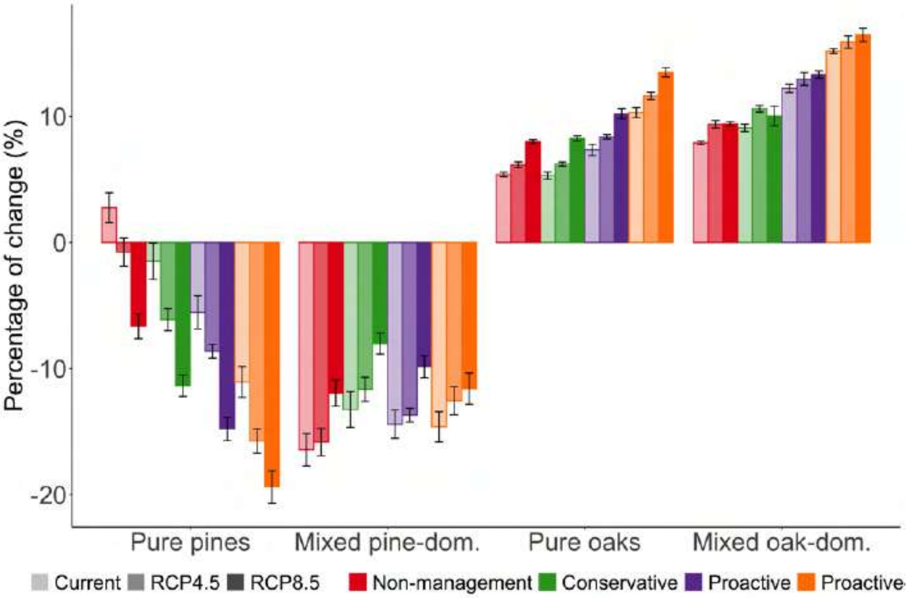


Figure 3.7: Change in percentage of the most abundant forest type area between initial and final year of the simulation (2005 and 2100, respectively). Error bars depict the standard deviation among the five replicates. See Table S.11 for the minor forest types.

The change in forest types shows a characteristic spatial pattern (Figure 3.8). Pine stands which were transformed into oak stands were mainly located in xeric areas, while pine stands in mesic and subhumind areas remained so by the end of the century. As an example, there was a clear transformation from pine stands to oak stands in the northwestern area (Sierra de Arana in Figure 3.1) while the large east-to-west patch of pine stands found in the centre of the study area (Sierra Nevada) mainly remained as pine stands (Figure 3.8).

3.4 Discussion

3.4.1 Climate controls biomass accruing in the landscape while management determines forest composition

Our analysis revealed that climate change had a large impact on the seasonal photosynthetic pattern of Mediterranean pine forests. Climate change generally

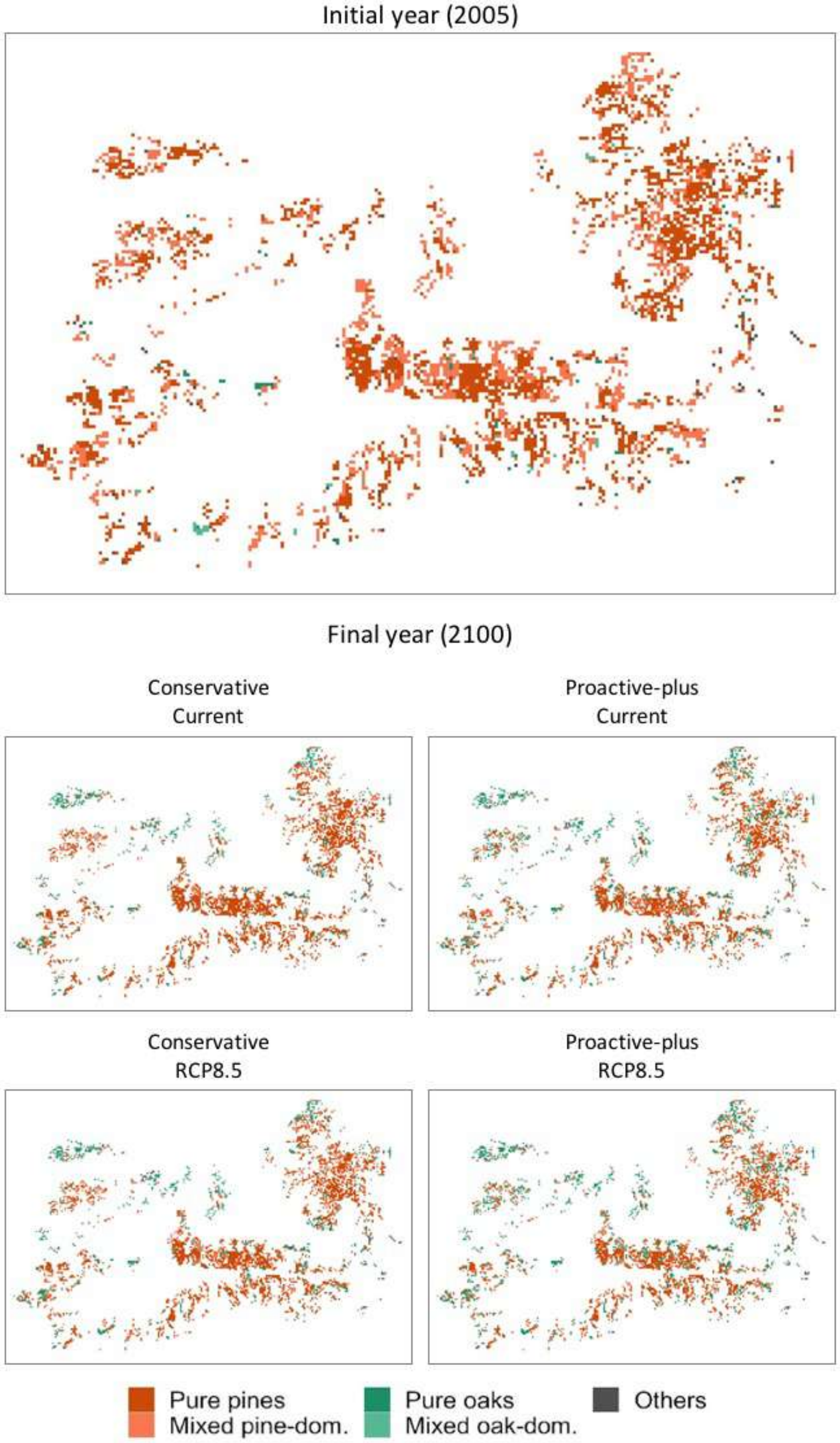

Initial year (2005)
Final year (2100)
Conservative
Current
Proactive-plus
Current
Conservative
RCP8.5
Proactive-plus
RCP8.5
Pure pines
Mixed pine-dom.
Pure oaks
Mixed oak-dom.
Others

Figure 3.8: Map of forest types at initial and final year of the simulation (2005 and 2100, respectively) for conservative and proactive-plus management scenarios under current and RCP8.5 climate. Maps are displayed for one model replicate. Pure shrubs, mixed shrub-dominated, mixed no dominance and empty cells, only sporadic within pine forests, were grouped in category Others.

increased annual growth, causing a higher net annual productivity by the end of the century under extreme climate change (RCP8.5). The differences between climate change scenarios were due to the fact that growth would no longer be limited during winter under extreme climate change (Figure 3.2) (e.g., see Di Filippo et al., 2021, for *P. halepensis* forests), compensating additional growth losses due to more pronounced summer droughts. Our findings corroborate other studies showing enhanced growth due to climate change on Mediterranean forests. For instance, Madrigal-González et al. (2018) reported net positive effects of climate change on *P. pinaster* growth over the last decades in the central part of the Iberian Peninsula, while Gea-Izquierdo et al. (2011) found that cold *Q. ilex* stands in the Iberian Peninsula may be benefited under climate change by analysing tree-rings over the last 100 years. Nevertheless, increased tree vulnerability due to climate change —and related increase in disturbances herewith not considered (see below)—remains a complex topic (Allen et al., 2015).

In the Mediterranean area, weather extremes (e.g., drought events) are expected to become more frequent together with the reduction in annual precipitation (Zittis et al., 2021). Since precipitation is the main driver of Mediterranean forest growth (Durante et al., 2009), an increment in drought-induced mortality is expected under climate change (Peñuelas and Sardans, 2021). Thus, the underestimation of extreme weather events incidence (see Fischer et al., 2013) and the lack of a clear decreasing trend in accumulated precipitation in the climate projections could be another reason for the low mortality observed under extreme climate change (García-Duro et al., 2021). This is especially relevant since PnET-Succession considers drought mortality only due to carbon starvation and not hydraulic-related mortality —a process rarely integrated in simulation models (Bugmann et al., 2019)—. Model comparisons could deliver crucial insights on uncertainties behind simulated processes, and therefore provide managers with more robust recommendations to support decision-making (Boulanger et al., 2021).

Our results showed that pine forests will likely accrue biomass through time in mesic and subhumid areas. Meanwhile, in xeric areas the increasing trend of biomass was only observed under extreme climate change, when higher projected temperatures allowed the continuation of growth for most part of the winter. An overall increase in biomass under RCP8.5 scenario was also simulated by García-Duro et al. (2021) in the Southern Carpathian temperate forests. García-Duro et al. (2021) and other authors (Wergifosse et al., 2022) have suggested that this simulated growth increment could be an effect of increased CO_2 concentrations stimulating higher carbon uptakes and primary productivity, as well as the effect of milder temperatures lengthening the growing season (Ueyama et al., 2020).

An increasing trend in biomass was observed not only under extreme climate change but also under current conditions and moderate climate change. This was likely due to the natural ageing of these pine forests, initially composed of relatively young stands. However, we acknowledge that our results apply in the lack of potential disturbances (e.g. pest outbreaks, fires). Disturbance events whose incidence is expected to increase under climate change (Seidl, 2017), could subtract important amounts of biomass from the landscape (Fyllas and Troumbis, 2009, fires), (Pureswaran et al., 2018, *Thaumetopoea pityocampa*). Therefore, further research should focus on the interaction between disturbances, climate and management, since disturbances could disrupt potential beneficial effects of climate warming (Walker et al., 2019).

Our study also showed that the effects of climate on total biomass were modulated by management. The co-design of management scenarios represents a gradient of intervention intensity limiting the growth of pines and therefore favouring oak expansion. This strategy resulted in different patterns depending on the climate area. In xeric areas, the decreasing pine biomass trend probably responded to a combination of management impact and mortality of *P. halepensis* due to its longevity. In mesic and subhumid areas, overcompetition of pines and limited capacity of oaks to establish and developed diluted the effects of management. Nevertheless, intensive management could be causing a positive effect in all areas as it reduces competition, which could help these forests avoid the drought stress caused by climate change (Navarro-Cerrillo et al., 2019).

3.4.2 The transformation of planted pine forests is driven by forest succession and enforced by intensive management

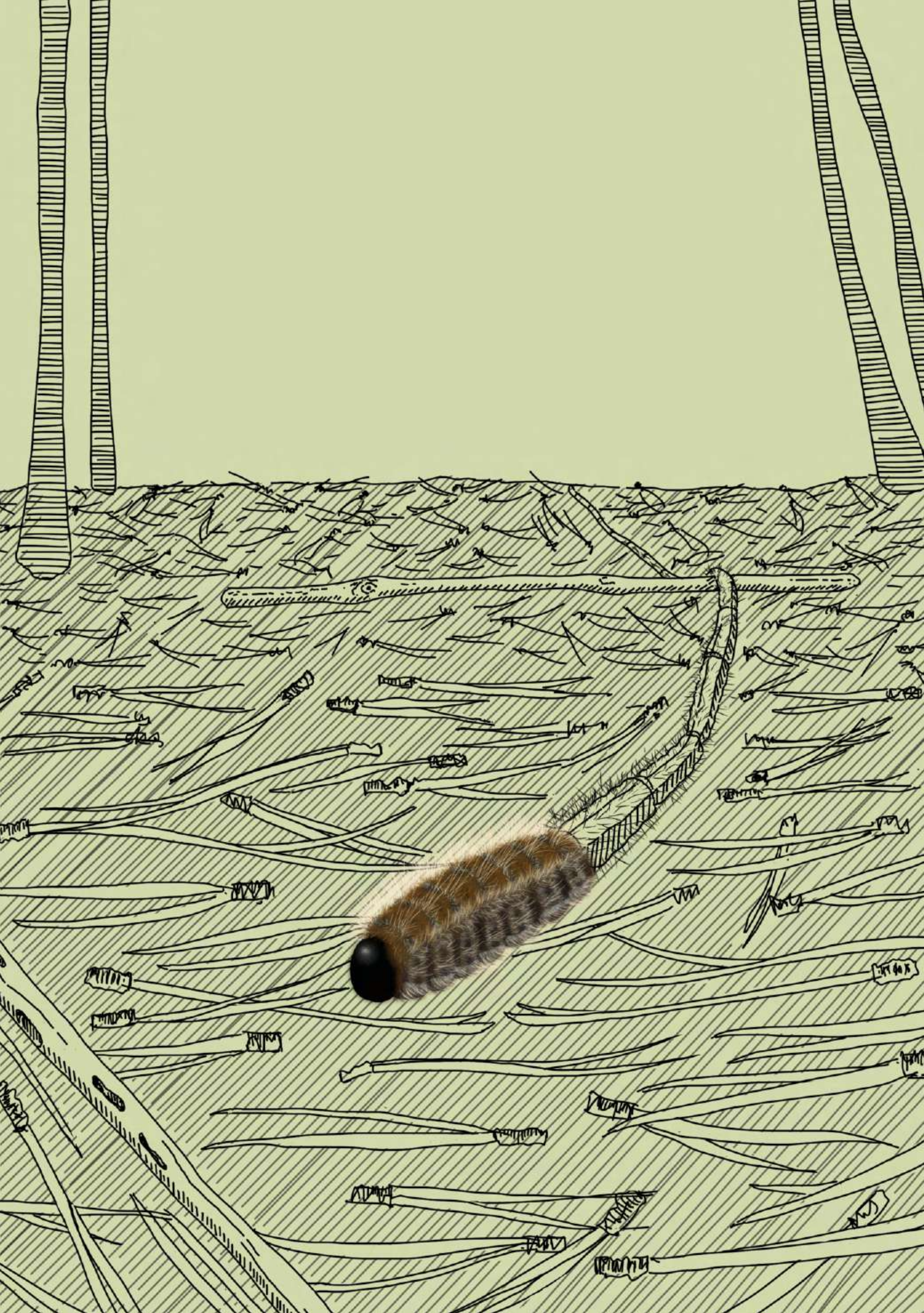
Changes in forest types arose as an emergent process from the above-described dynamics in photosynthesis and biomass of pine forests. Other studies suggested that natural succession is causing a slow transformation of pine forests into oaklands (Dios et al., 2019). The marginal presence of oaks with the ability to resprout, the capacity of *Q. ilex* to colonise pine stands and the limited regeneration capacity of pines under dense canopies could explain this pattern (Gómez-Aparicio et al., 2009). Moreover, as pines reach their longevity limits, windows of opportunity appear for new species to become dominant. Longer simulation experiments could give insights into this process, although these would require making arbitrary assumptions on climatic conditions beyond 2100, which is the typical end-point of climate projections.

Our findings suggest that climatic patterns across space can play an important role in the transformation of pine forests. For instance, xeric areas showed clear transformation dynamics while in mesic and subhumid areas this alteration was less pronounced (see climate regions in Figure 3.1). Xeric areas have shown to be more affected by recent climate change than milder areas (Peñuelas and Sardans, 2021), which would explain the decreasing trend in biomass and the change in forest types under current and moderate climate change. Moreover, due to the increased growth rates under extreme climate change, the highest rate of transformation occurred under this scenario. However, the uncertainty associated with the projection of extreme weather events —herewith not considered—calls for precaution in driving optimistic conclusions about extreme climate change scenarios. In addition to climatic effects, intense management practices can enforce the conversion of xeric pine forests towards oaklands. Although no management scenario caused a full transformation from pine-dominated to mixed stands, scenarios with more intense management interventions promoted a higher rate of transformation than less intensive scenarios. This confirms that targeting management actions on forests that are more vulnerable to climate change can proactively facilitate transition to better-adapted forest ecosystems in shorter time scales than by natural succession (Millar and Stephenson, 2015). Moreover, our results support previous findings showing that management practices have stronger impacts on forest structure and composition than the direct effects of climate change (Mina et al., 2017).

3.5 Conclusions and implications for management

This work aimed to deepen our understanding on how Mediterranean planted pine forests might evolve under different management and climate scenarios. Climate change is likely to induce a shift in the phenological growth pattern of these forests by reducing growth during summer but anticipating the spring growing phase. Forest biomass will increase through time as stands mature and are further promoted by a longer growing season under climate change. However, this increase is different among species groups, resulting in a future landscape that will be made of different forest types. Moreover, despite multiple possible alternatives, management will have a strong influence on future forest dynamics, likely promoting a shift from pine forests to oaklands, especially in xeric areas under more intense management scenarios.

The management alternatives considered in this study represent forest managers' viewpoints that constitute a gradient of intervention intensity in the landscape. Although our outcomes portray natural succession as an important driver of change, they also confirm that choices in management regimes can enforce changes in future landscape trajectories. In large, diverse and complex landscapes, however, such transformations do not occur homogeneously across spaces, such as in our mountain regions where changes will likely be more pronounced in xeric areas and small patches in subhumid and mesic areas. Our spatially-explicit modelling analysis allows a prioritisation of areas to intervene, which could save precious resources by avoiding unnecessary interventions in areas where natural succession is already occurring. Instead, management should focus on those areas where such processes are inhibited to promote more climate-adaptive ecosystems. In such areas, where lack of seed dispersal or excess of competition prevents natural diversification, small-scale highly intense interventions could be considered.



Part III

Defoliators dynamics

Chapter 4

INSTAR: An Agent-Based Model that integrates existing knowledge to simulate the population dynamics of a forest pest

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Key words *Thaumetopoea pityocampa*, Agent-Based model (ABM), Forest pest, Population dynamics, Pattern-oriented

Resumen

Los pinares de repoblación, muy comunes en la cuenca mediterránea, están afectados de forma recurrente por plagas forestales debido a sus características intrínsecas (alta densidad, baja heterogeneidad espacial) y a factores externos (tendencia hacia un clima más cálido y seco). *INSTAR* es un modelo de agentes que pretende simular las dinámicas poblacionales de la plaga *Thaumetopoea pityocampa*. El modelo ha sido diseñado usando una aproximación modular: diversos módulos interconectados (submodelos) facilitan la incorporación de nuevo conocimiento sobre la biología de esta plaga y pueden servir como patrón para el diseño de otros modelos similares. El modelo es espacial y temporalmente explícito y permite su implementación bajo distintos escenarios de clima y uso del suelo. En este manuscrito, *INSTAR* está descrito en detalle usando el protocolo estándar ODD (Overview, Design concepts and Details).

La temperatura es uno de los factores principales que modulan las dinámicas poblacionales de *T. pityocampa*. Por lo tanto, para ser coherente y estructuralmente realista, *INSTAR* debe reproducir fielmente el efecto de este factor en la fenología de la especie. Este requisito ha sido probado a través de un test de consistencia de los submodelos responsables del desarrollo de la especie. Esta evaluación se compone de una calibración de la fenología de la especie y un test de estrés realizado mediante la exposición del modelo a escenarios climáticos extremos. Como resultado de la calibración, el modelo reproduce con éxito la fenología de la especie en el área de estudio. Además, el test de estrés confirma que el modelo se comporta según lo esperado cuando se expone a valores climáticos extremos. Los resultados presentados en este manuscrito constituyen una primera validación de los submodelos de desarrollo. Tras esto, *INSTAR* está preparado para análisis más profundos sobre su sensibilidad e incertidumbre.

Abstract

Pine plantations, very common in the Mediterranean basin, are recurrently affected by forest pests due to intrinsic characteristics (high density, low spatial heterogeneity) and external factors (consistent trend towards a warmer and drier climate). *INSTAR* is an Agent-Based Model aiming to simulate the population dynamics of the *Thaumetopoea pityocampa* forest pest. The model has been designed using a modular approach: several interconnected modules (submodels) facilitate the incorporation of new knowledge about the pest biology and can serve as template for the design of other similar models. The model is spatially and temporally explicit and allows its implementation under different climate and land use scenarios. *INSTAR* is described in detail in this manuscript using the standardized ODD (Overview, Design concepts and Details) protocol.

Temperature is known to be one of the main factors modulating the population dynamics of *T. pityocampa*. In order to be coherent and structurally realistic, *INSTAR* should faithfully reproduce the effect of this factor on the species' phenology. This requirement has been assessed here through a consistency test of the submodules responsible for species development. This assessment is constituted by a calibration analysis of the pest phenology and a stress test performed by exposing the model to extreme climate inputs. As a result of calibration, the model successfully reproduces the phenology of the species in the simulated study area. Moreover, the stress test confirmed that the model behaves as expected when exposed to extreme input values. The results presented in this manuscript constitute a first internal validation of the development submodels. After this, *INSTAR* is ready for a deeper analysis consisting on a sensitivity and uncertainty analysis.

4.1 Introduction

Pine plantations are very common in the Mediterranean basin, where they were used in the early decades of the 20th century as management tools to halt soil loss. In Spain alone, 2.5 million hectares were planted between 1940 and 1980 (PFA, 2002). Currently, their intrinsic characteristics (mainly low diversity and high stand density), together with external factors (i.e. climate change) cause pests to be a recurrent problem within these forests.

Forest pests receive great attention due to their relevance in ecosystems functioning and the economic impacts they cause on managed forests (see Wingfield et al., 2015). Numerous articles are published every year providing insights on species physiology, reporting outbreaks and first records of species and showing up-to-date occurrences (Higham et al., 2017; Tanase et al., 2018; Valenta et al., 2017; Zanetti et al., 2017). Researchers also highlight the potential impacts of forest pests under climate change scenarios, which are expected to be more acute in coniferous forests and the boreal biome (Seidl et al., 2017). In this regard, current knowledge confirms the lower resistance and thus higher vulnerability of single species forests to disturbances such as forest pests, among others (Fares et al., 2015).

The lack of integrative and synthetic knowledge makes it difficult to forecast pest behaviour under specific abiotic scenarios and landscape configurations. Although experiments are possible on a small scale (individuals, small areas), obvious restrictions exist when the goal is to understand the dynamics of large-scale systems, such as extensive plantations and/or long time periods. This situation reveals an important drawback when trying to design more effective and feasible management strategies that use up-to-date knowledge. Therefore, there is a need to generate tools that can help foresters to avoid or minimise pest damage and ensure sustainability among forests masses (Fares et al., 2015).

Modelling has demonstrated its usefulness when carrying out *in silico* experiments (Chowdhury and Stauffer, 2005) and synthesising information from different scales, thus helping with acquiring more comprehensive and holistic knowledge. Our aim is to improve the general understanding of forest pest dynamics by studying specific cases, as suggested by Fares et al. (2015). Thus, our approach is to create a model which explicitly simulates the concatenated linkages between the abiotic configuration of the landscape (topography, climate, meteorology, etc.) and the performance of the ecosystem components (pine plantations and forest pests) in a global change scenario. The pine processionary moth (*Thaumetopoea pityocampa*) is especially suited for modelling purposes for several reasons:

- The pine processionary moth lifecycle allows for simplification without neglecting crucial processes: its characteristic gregarious behaviour allows modelling into groups of individuals that behave as fully functional units which constitutes an advantage in terms of computing power needs. Nevertheless, the lifecycle of this species is influenced by interacting abiotic and biotic factors, and therefore modelling such a complex system constitutes an interesting challenge. Winter temperature and habitat (Démolin, 1969b; Hódar et al., 2002; Masutti and Battisti, 1990) are among the most important abiotic factors influencing these pest dynamics, while biotic factors such as parasitism or amount and quality of available pine biomass also play a key role in modulating *T. pityocampa* populations (Battisti, 1988; Charbonnier et al., 2014; Hódar et al., 2002; Hódar et al., 2004; Torres Muros, 2015).
- The pine processionary moth lifecycle is representative of many forest pests: long defoliating larval stage followed by pupation and short non-feeding moth stage (Barbosa et al., 2012; Dajoz, 2000; Netherer and Schopf, 2010), thus simulating its population dynamics can serve as inspiration to model the behaviour of other forest pests. Similar to other species, *T. pityocampa* is experiencing an expansion process fostered by the spread of the abovementioned pine plantations in which it feeds as well as climate change (Battisti et al., 2005; Hódar and Zamora, 2004; Petrucco Toffolo et al., 2006). Modelling the population dynamics of this species can help in understanding the potential impact of global change on the functioning of pine plantations in the Mediterranean area. This is of high importance given the extent of such forests and their potential growth decline due to the interaction between defoliation and drought stress (Linares et al., 2014; Sangüesa-Barreda et al., 2014). Besides, modelling the population dynamics of this species will also allow the study of the interaction between pests and land uses, therefore helping to improve management strategies in the long term (Castagneyrol et al., 2014b; Régolini et al., 2014).
- The pine processionary moth constitutes a forestry, ecological and public health problem nowadays since affected trees reduce their growth and are more sensitive to other pests (Arnaldo et al., 2010; Jacquet et al., 2012; Kanat et al., 2005; Markalas, 1998). It also causes stinging and allergic reactions to humans and animals due to its urticating hairs (Battisti et al., 2017; Rebollo et al., 2002; Vega et al., 2003). Thus, simulating the population dynamics of *T. pityocampa* could help manage its outbreaks to minimise health and ecological impacts.

Some authors have modelled the distribution of *T. pityocampa* by means of equations-based models (Robinet et al., 2014) or statistical analysis (Régolini et al., 2014; Seixas Arnaldo and Monteiro Torres, 2005). Most authors interested in this species highlight the importance of climate on the impact of the pest, and some have even attempted to model the effects of climate change on it (Robinet et al., 2007; Robinet et al., 2015; Robinet et al., 2014; Seixas Arnaldo et al., 2011). However, no Agent-Based Model (ABM) model is available for *T. pityocampa*.

In this article, a spatial and temporally explicit ABM called *INSTAR* is presented. *INSTAR* has been designed to simulate the population dynamics of *Thaumetopoea pityocampa*. This manuscript firstly provides an overview about the ecological background of the target species. The structure and functioning of *INSTAR* are then described in detail according to the ODD protocol ("Overview, Design concepts and Details") proposed by Grimm et al. (2010). Finally, we present a consistency test of the submodules responsible for species development, constituted by a calibration analysis of the pest phenology and a stress test exploring the influence of extreme temperatures on the model.

4.2 Ecological background of the species

T. pityocampa is present in the entire Mediterranean Basin, from North Africa to the South of Europe and from the Atlantic Coast to the western part of Turkey, and it is especially present in afforested areas. It is a univoltine oligophagous species feeding on *Pinus* spp., and more rarely on *Cedrus* spp. and planted *Pseudotsuga* spp. (Battisti et al., 2015). A complete outline on the biology of *Thaumetopoea* species in general, and of *T. pityocampa* in particular, can be found in Roques (2015). However, the detailed features of the *T. pityocampa* cycle widely vary between sites and between years.

The biological cycle of *T. pityocampa* is shown in Figure 4.1. After mating, female moths lay between 150–350 eggs around pine needles or, more rarely, twigs. Eggs are exposed to predation and parasitism mainly caused by *Ooencyrtus pitocampae* and *Baryscapus servadeii*. Parasites are temperature-limited, and therefore the parasitism rate shows an altitude gradient: the higher the altitude, the lower the parasitism rate (Torres Muros, 2015). Hatching occurs in early summer in northern (and higher) locations and late summer in southern (lower) ones, thus avoiding high temperatures which are lethal for the larvae (Démolin, 1969a; Seixas Arnaldo et al., 2011).

Larvae are mainly characterised by their gregarious behaviour. Just after hatch-

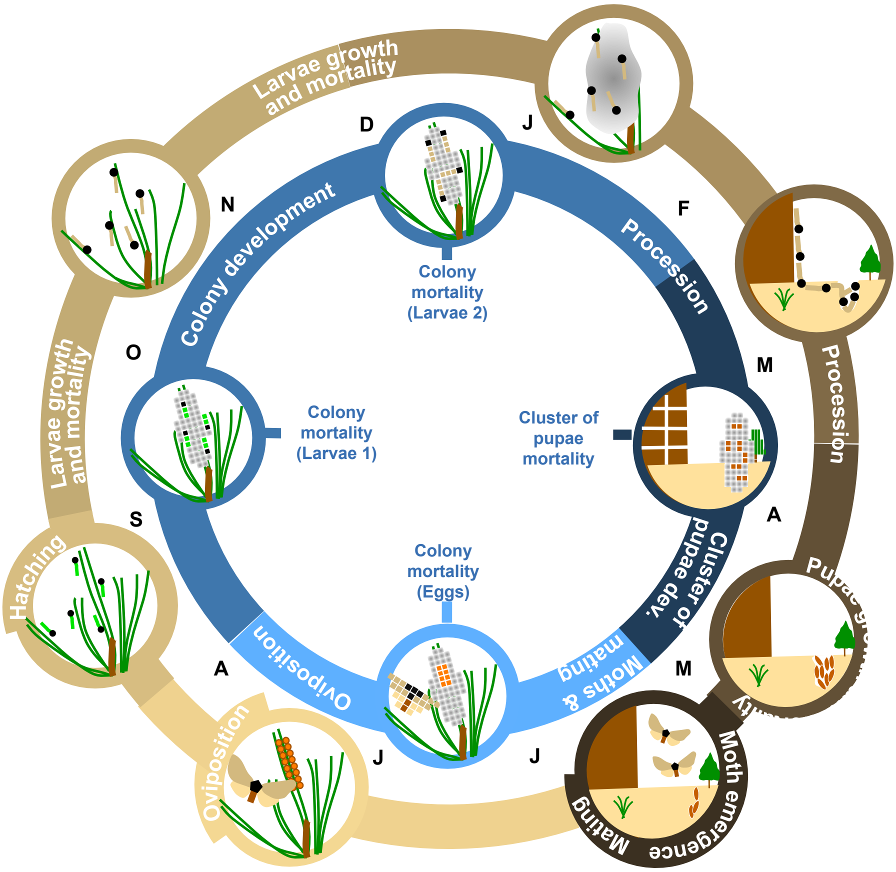


Figure 4.1: Diagram showing the simplified version of the cycle implemented in *INSTAR* (inner circle), as well as the biological cycle of the processionary moth (outer circle). The modelled entities are shown in blue, while the real entities are shown brown. The biological cycle of the species is simulated in *INSTAR* by three types of submodels: development (colony, pupae and host development), mortality (colony and pupae mortality) and movement (procession, mating and oviposition).

ing, larvae build silk nests or colonies, as protection against low temperatures and predators. Since *T. pityocampa* is a poikilothermic species, air temperature plays a key role during larval development (Démolin, 1969a; Hoch et al., 2009; Huchon and Demolin, 1970; Robinet et al., 2007), as well as in later stages. Moderately high temperatures (below 30 °C according to Démolin, 1969a) accelerate larval growth, while cold temperatures delay development and can cause mortality due to freezing or starvation. Thus, *T. pityocampa* has a higher affinity for trees situated at the edge of the stands or around clear areas, since nests there receive more light and therefore are in a more advantageous situation in terms of temperature (Démolin, 1969a). Moreover, larvae colonies can move within the tree to find the most exposed areas of the pines at each moment (Démolin, 1969a; Hoch et al., 2009; Pimentel et al., 2011). Normally, larvae feed during the night and digest during the day inside their nests. In contrast to other defoliator species, the larval phase of *T. pityocampa* takes place during winter. Therefore, increasing winter temperatures due to climate change are expected to favour this species (Battisti et al., 2005; Netherer and Schopf, 2010).

Larval development requires five larval stages or "instars". Growth and survival of early development stages depend on food quality (Hódar et al., 2002) and higher survival rates are observed for pine trees not affected by defoliation during previous years (Hódar et al., 2004). On the other hand, late stages are more limited by the amount of food available (Démolin, 1969a; Hoch et al., 2009; Hódar et al., 2002; Huchon and Demolin, 1970; Robinet et al., 2007). Full larval development cannot last less than 4 months under optimal conditions. For all larval stages, it is reported that optimal daily temperature is between 20–25 °C and mortality quickly reaches 100 % at 32 °C (Démolin, 1969a). Apart from temperature, larval survival is also affected by predators (Barbaro and Battisti, 2011) and parasites (Battisti et al., 2015), with the incidence of these factors being quite variable among studies.

When larvae complete their development, usually at the end of winter or beginning of spring, they constitute the characteristic processions and search for a place to bury (Figure 4.1). Once the leading larva chooses a suitable spot, the whole group buries and pupal development starts. Pupation success rate depends on shading and parasitism and therefore optimal burial spots are characterised by high radiation and reduced vegetation cover (Dulaurent et al., 2011; Dulaurent et al., 2012; Robredo, 1963; Torres-Muros et al., 2017). Moths select trees on the edge of the stand when laying their eggs. These behaviours generate a characteristic spatial pattern: the pest concentrates in low density stands or stand edges, and pupae are especially present in clear areas between trees.

Like all other *Thaumetopoea* spp., *T. pityocampa* is a univoltine species, but pupae can engage in extended diapause. In Mediterranean environments only 2.5 % of pupae show extended diapause (i.e. more than two years, Torres-Muros et al., 2017), but in other environments the proportion of latent pupal population can be much higher (Aimi et al., 2006). The conditions inducing extended diapause are still uncertain (but see Salman et al., 2019). When pupation process ends, moths emerge and live between 1 and 2 days, during which time they mate and lay their eggs on a nearby pine (Zhang and Paiva, 1998) ("Mating" and "Oviposition" in Figure 4.1).

4.3 Model description

According to Gertseva and Gertseva (2004), *INSTAR* can be classified as a homomorphic (all components of the model have analogous components in reality, but not *vice versa*), time-dependent, continuous (it represents continuous changes of an object over time) and deterministic Agent-Based Model (ABM). ABM has been chosen as the modelling technique, since this approach allows an easy integration of multiscale information, which is specially abundant in the case of *T. pityocampa*: physiological data based on observations of individuals under laboratory conditions (Berardi et al., 2015; Hoch et al., 2009), influence of environmental factors based on observations of populations and field experiments (Castagneyrol et al., 2014a; Cayuela et al., 2014; Démolin, 1969b; Linares et al., 2014; Samalens and Rossi, 2011; Torres-Muros et al., 2017), and population history based on observations of outbreaks on a regional scale (Hódar et al., 2012; Li et al., 2015). The following sections describe *INSTAR* according to the "Overview, Design Concepts, and Details" (ODD) protocol proposed by Grimm et al. (2010), which is a very useful tool to characterise ABMs using a standard structure.

4.3.1 Overview

Purpose

The overarching purpose of *INSTAR* is to simulate the population dynamics of *Thaumetopoea pityocampa*. Specifically, it simulates the phenology and spatial distribution of the pine processionary moth. *INSTAR* will help us to test whether our current knowledge on the species biology, distribution and individuals' behaviour explains the population dynamics patterns observed in selected forests. Thus, in the short term, it aims to identify caveats and gaps in our knowledge about such dynamics, and promote research aiming to fill these gaps. The first steps in this process are presented in this study. It consists in the construction, documentation and initial testing of the model.

More specifically, and following Jakeman et al. (2006), the context of *INSTAR* refers to the following topics which help clarify our purpose. Firstly, it addresses questions such as: How well can *INSTAR* simulate the dynamics of the processionary moth forest pest in a spatially and temporally explicit way? Is it possible to obtain landscape level metrics (defoliation rate per year and watershed) modelling the behaviour of individual agents? Is *INSTAR* able to reproduce natural patterns of the *T. pityocampa* cycle such as density-dependent restrictions? Moreover, *INSTAR* has been designed to satisfy the needs of scientists interested in simulating ecological processes and, specifically, *T. pityocampa* population dynamics, who would find in *INSTAR* a modular tool to conduct *in silico* experiments.

Entities, state variables and scales

An overview of entities and state variables can be found in Table 4.1. *INSTAR* contains a simplified version of the biological cycle of *T. pityocampa*, represented by three entities: egg and larval colonies, clusters of pupae and moths; the pine trees on which larvae feed are represented by the entity hosts; and the environment is constituted by cells.

Each colony represents all surviving individuals from the same egg laying and its stage defines the phase of the lifecycle in which the colony is, namely: “egg”, larvae 1 (L1, representing the first two instars: I and II) or larvae 2 (L2, representing the last three instars: III, IV and V). This entity is also defined by the state variables number of individuals (i.e. the number of eggs, larvae 1 or larvae 2 contained in the colony), days as egg, days as L1 and days as L2 (days remaining for the stage to be completed), and host (colonies develop on pine crowns, and therefore their location within the environment is described by the host they are linked to). Except for the host they are linked to, all colony variables values change throughout the simulation, i.e. they are dynamic state variables.

Table 4.1: Summary of entities and state variables within *INSTAR*.

Entity	State variable	Description	Values (units)
Colony	stage	Indicates in which phase the colony is.	"Egg", L1, L2
	number of individuals	Number of individuals within the colony.	0-~200 (ind.)
	days as egg	Number of days remaining before the colony in instar "Egg" will change to instar L1.	0-30 (days)
	days as L1	Number of days remaining before the colony in instar L1 will change to instar L2.	0-30 (days)
	days as L2	Number of days remaining before the colony in instar L2 will transform into a cluster of pupae.	0-90 (days)
	host	Pine on which the colony is located, to which it is linked.	Host ID
Cluster of pupae	number of individuals	Number of individuals within each cluster.	0-~200 (ind.)
	days as pupae	Number of days remaining before the cluster of pupae will become moths.	0-215 (days)
	location	Cell where it is located.	Cell coordinates
Moth	sex	Sex of the moth.	Female, Male
	mated	Describes whether the moth is mated or not.	Boolean (true/false)
	location	Cell where it is located.	Cell coordinates
Host	height	Pine height.	1-20 (m)
	quantity	Relative amount of available biomass for larvae: 0 % corresponds to a completely defoliated tree while 100 % corresponds to a tree in the best possible conditions.	0-100 (%)
	quality	Indicates whether a tree was defoliated the previous year or not.	defoliated, not defoliated
	location	Position of the host in the world.	x and y coordinates
Cells	elevation	Elevation above sea level.	0-8000 (m a.s.l.)

probability of emergence	Probability of emergence which defines the number of individuals from a cluster of pupae those survive and become moths. It is calculated based on the number of hosts per cell (see sections 4.3.3 and 4.3.3.	0-12 (%)
maximum temperature	Maximum air temperature each day.	−50-+50 (℃)
minimum temperature	Minimum air temperature each day.	−50-+50 (℃)

The entity cluster of pupae refers to all individuals from an egg laying that have reached the end of the larval stage and have successfully buried in the soil on a given cell. This entity is used to model the development of pupae and is defined by similar state variables as the colonies: number of individuals, days as pupae and the static variable location.

Finally, the entity moth represents an individual moth in the real world. It has a static assigned sex and can be mated or not. Thus, in the transformation from cluster of pupae into moths there is an individualisation process, which is explained in detail in section 4.3.3.

Host entity represents trees (*Pinus* spp.) on which the larvae develop. Hosts are characterised by their static variables location and height (as surrogate of tree size), which defines its carrying capacity, i.e. how many colonies can feed on it before it gets defoliated. Moreover, they also have the dynamic state variables quantity of available biomass, and quality, which indicates if the tree was defoliated in the previous season or not. *T. pityocampa* is an oligophagous species feeding on different *Pinus* spp., with variable susceptibility depending on tree species and study site. In SE Spain *T. pityocampa* is found and thrive on *P. sylvestris*, *P. nigra*, *P. pinaster* and *P. halepensis*, as well as some others less frequent species. Thus, we assume that parameters from different host species are straightforward to use on *INSTAR* and that *INSTAR* can be applied to any *Pinus* spp. affected by *T. pityocampa*. Nevertheless, differences in development according to host species cannot be ignored and surely *INSTAR* performance can be improved by parameterising the state variables and submodels according to each species (see section 4.3.3).

INSTAR works with a 30 m spatial resolution at a temporal resolution of 1 day. The world in the model is constituted by cells, which represent 30×30 m, and have elevation associated as a static variable. Cells also have dynamic state variables referring to weather conditions, which change in every time step (1 day). These are the minimum and the maximum temperature. Moreover, cells also have an assigned integrated temperature, an internal variable referring to the temperature of a colony which is exposed to the cell air temperature and the number of insolation hours per day, according to Démolin (1969a). This variable is calculated as:

$$integratedtemperature = \\ maximumtemperature + (1.5 \times insolationhours)$$

Process overview and scheduling

Figure 4.1 depicts a schematic overview of the submodels that take place in each time step as well as the entities which perform them. After initialisation (see section 4.3.3), every time step consists of:

- Environment reading: cells minimum and maximum temperature are updated to the current date and integrated temperature is calculated.
- Colonies update: number of individuals is updated following the "colony mortality" submodel and stage is updated following the "colony development". Then, "procession" submodel is applied to colonies which have completed their development and will become a cluster of pupae.
- Clusters of pupae update: number of individuals is updated following the "pupae mortality" and the length of this phase is adjusted through the "pupae development" submodel. Once a cluster completes its development it results in a number of moths.
- Moths update: moths become mated following the "mating" submodel and choose a host on which to lay their eggs through the "oviposition" submodel.
- Hosts update: the available biomass, quantity, is updated every day based on growth and larvae consumption through the "host development" submodel.

These submodels are explained in detail in section 4.3.3. Besides that, from the observer perspective, in each time step several state variables values are stored. For a detailed explanation of how model outputs are structured see details regarding observation in the following section.

4.3.2 Design concepts

This section explains how some important concepts are implemented in *INSTAR*. These basic concepts describe characteristics of ABMs that are not common in other modelling approaches. Describing these concepts in a standard structured format can help transmit the key aspects of the model to others, either ABM experts or those not familiar with this approach (Railsback and Grimm, 2011).

The basic principle of *INSTAR* model is that *T. pityocampa* population dynamics are strongly influenced by the environmental (mainly climate) conditions and therefore these define the impact of the forest pest, the timing of its outbreaks and the areas where it has the highest incidence.

The spatial distribution of the pest as well as the forest state (amount and quality of available biomass) emerges from the simulation as a result of an individual's behaviour. On the one hand, the selection of burial spots and the pines on which moths lay their eggs define the spatial location of the newly created agents, and thus their impact on the pines. On the other hand, timing and scale of the pest outbreaks is regulated through mortality and development. Literature shows a higher incidence of the pest on areas with low pine density (Régolini et al., 2014) and shifts in phenology due to climate changes (Hódar and Zamora, 2004).

Colonies in stage L2 adapt to increase their success probability by selecting the burial site considering the number of hosts on the cells around them and choosing the one which optimises the probability of survival.

T. pityocampa development is dependent on environmental conditions and adjusts its biological cycle to keep it univoltine (Berardi et al., 2015; Démolin, 1969a). *INSTAR* implements this by indirect objective-seeking, constraining the total duration of the biological cycle to one year by shortening and lengthening the colony and cluster of pupae phases depending on the environmental conditions.

INSTAR entities are able to use information from their surroundings and themselves to define their behaviour, i.e. they *sense* (Railsback and Grimm, 2011). Colonies can sense the state variables of their host and the cell where they are located. Moreover, colonies are also able to sense the number of hosts within a certain radius to select a spot where to bury (see "procession" submodel in section 4.3.3). Similarly to colonies, the clusters of pupae can also sense the state variables of the cells where they are, since it affects their mortality. Finally, at the end of the cycle, female moths can sense if there is a male moth within a certain distance and where the surrounding pines are (see "mating" and "oviposition" submodels in section 4.3.3). No prediction or learning mechanisms are implemented in *INSTAR*.

Agents interact with each other in an indirect way. Colonies within the same host compete with each other for their food. When the number of colonies on a host equals its carrying capacity, the biomass consumption will slowly lead to complete defoliation of the tree, and therefore to the death of larvae present on it (see "colony mortality" submodel in section 4.3.3). Moreover, there are intra- and intergenerational interactions. The intragenerational interaction appears when colonies turn into clusters of pupae and these into moths as development takes place, inheriting state variables values. The number of individuals of the cluster of pupae is inherited from the number of individuals of the colony it comes from, and the number of moths that emerge from the burial site is defined by the number of individuals within the parent cluster of pupae. Moreover, the location of each agent is defined based on the location of its predecessor. On the other hand, the intergenerational interaction comes from the defoliation of one season defining the quality state of the host in the coming season and thus affecting the probability of survival of the coming generation of larvae.

To simulate the intrinsic variability of natural processes, several stochastic processes are included during *INSTAR* initialisation: assigning quantity to hosts; assigning number of individuals to colonies; assigning days as egg to colonies; and selecting which are the initial infected hosts. Moreover, pseudorandom numbers are also used during the model running to: assign moth sex (1:1 ratio); decide whether a female moth becomes mated or not once it finds a male moth and choose the hosts where moths lay their eggs, following a weighted random selection based on distance to the moth. These functions are explained in details in the corresponding submodels descriptions (section 4.3.3).

The representation of *T. pityocampa* biological cycle in three agent types, responds to a necessity to simulate the behaviour and characteristics of each development phase. Colonies and clusters of pupae are, in a way, collectives since they represent a group of individuals. This assumption does not constitute an oversimplification of the real system considering the characteristic gregarious behaviour of this species, where colonies behave as fully functional units (Démolin, 1969a). Besides, defining them as collectives is an advantage since it reduces computing power needs, thus allowing the simulation of larger areas.

To observe the pest dynamics and hosts state, *INSTAR* provides several outputs. At system-level, average hosts quantity, percentage of infected pines and number of individuals of *T. pityocampa* at each life stage are stored for each day. Moreover, monthly averages of all these state variables are also stored at cell level.

This allows the evaluation of the forest pest development over time for a whole landscape unit (i.e. a specific forest, a basin, etc.) as well as within the simulated area (stand edges, distribution and movement of each phase, most affected hosts, etc.).

4.3.3 Details

ABMs often require a high number of parameters and detailed information is needed to fully parameterise the model (Kelly (Letcher) et al., 2013). Thus, as any other ABM, *INSTAR* parameterisation requires an exhaustive review of literature as well as testing. During last 20 years we produced and recorded data on *T. pityocampa* in Sierra Nevada and surrounding areas (SE Spain) regarding phenology, relationship with altitude, egg parasitoidism, or tree species selection, and therefore the model is based on these local data whenever possible. When unavailable, data were taken from scientific literature elsewhere. The parameters used by *INSTAR* are listed in Table 4.2 and decisions for parameter estimation are fully explained in Supplementary Material S4.1. In any case, *INSTAR* was built as a customisable model in which parameter values can be changed to fit biological information to local conditions as well as to incorporate new information when it becomes available, constituting one of its potential.

Some of *INSTAR* parameter values are well referenced pest traits (CS_{mean}, CS_{sd}, $Procession_{max-distance}$, $Mating_{prob}$) or have been based on best available knowledge considering certain assumptions (Egg_{min}, $L1_{min}$, $L2_{min}$, $Pupae_{max}$, NPP, $Ql_{threshold}$, see section 4.3.3 and Supplementary Material S4.1). Other parameters require calibration for each study area ($T_{egg-devel}$, $T_{larvae-devel-high}$, $T_{larvae-devel-internal}$, $T_{larvae-devel-low}$, as presented in this manuscript). Finally, another set of parameters are required for model functioning and can serve in the future for purposes such as scenario setting (Qt_{mean}, Qt_{sd}, $L1_{mort}$, $L2_{mort}$, $L2_{mort-threshold}$) or pest expansion experiments ($Mating_{max-distance}$, $Flight_{max-distance}$, $T_{lethal-max}$, $T_{lethal-min}$).

Table 4.2: *INSTAR* parameters. *Parameter values before calibration analysis presented in section 4.4.

Parameter	**Value (units)**	**Description and references**	**Model details in**
Qt_{mean}, Qt_{sd}	50, 20 (%)	Mean and standard deviation used to assign initial values of quantity to the hosts, following a normal distribution with such parameters. Reference: This study, assuming an intermediate health state of the simulated pine stand.	4.3.3
CS_{mean}, CS_{sd}	193.2, 4.5 (ind.)	Mean and standard deviation used to assign initial values of number of individuals to the colonies, following a normal distribution with such parameters. Reference: Torres Muros (2015).	4.3.3
$Ql_{threshold}$	57.16 (%)	Threshold used to define the quality of the host based on their quantity at the end of the defoliating season. Reference: Muukkonen (2005a).	4.3.3
Egg_{min}	30 (days)	Minimum time needed for colonies at stage “egg” to become L1. Reference: Démolin (1969a).	4.3.3
$L1_{min}$	30 (days)	Minimum time needed for colonies at stage L1 to become L2. Reference: Démolin (1969a).	4.3.3
$L2_{min}$	90 (days)	Minimum time needed for colonies at stage L2 to become cluster of pupae. Reference: Démolin (1969a).	4.3.3
$L1_{mort}$	10 (%)	Percentage of individuals which die in a colony at stage L1 if its host was defoliated the previous season. Reference: This study, to be parameterised with real data when available.	4.3.3
$L2_{mort}$	2 (%)	Percentage of individuals which die daily in a colony at stage L2 if its host has a quantity below $L2_{mort-threshold}$. Reference: This study, to be parameterised with real data when available.	4.3.3

$L2_{mort-threshold}$	20 (%)	Threshold defining the quantity of hosts below which individuals of colonies at stage L2 die due to food scarcity. Reference: This study, to be parameterised with real data when available.	4.3.3
$T_{lethal-max}$	32 °C	Maximum temperature above which colonies die. Reference: Démolin (1969a).	4.3.3
$T_{lethal-min}$	−12 °C	Minimum temperature below which colony die. Reference: Démolin (1969a).	4.3.3
NPP	28 (%)	Net Primary Production rate defining the daily increase of quantity in the hosts during the growing season. Reference: self-defined based on $Ql_{threshold}$, assuming constant growth rate and according to the growing season described by Alcaraz-Segura et al. (2016).	4.3.3
$T_{egg-devel}$	20 °C*	Maximum temperature above which colonies at stage "egg" develop. Reference: based on Démolin (1969a).	4.3.3
$T_{larvae-devel-high}$	25 °C*	Maximum temperature below which colonies at stage L1 or L2 develop. This parameter is used in combination with $T_{larvae-devel-internal}$ and $T_{larvae-devel-low}$. Reference: based on Démolin (1969a).	4.3.3
$T_{larvae-devel-internal}$	20 °C*	Minimum integrated temperature above which colonies at stage L1 or L2 develop. This parameter is used in combination with $T_{larvae-devel-high}$ and $T_{larvae-devel-low}$. Reference: based on Démolin (1969a).	4.3.3
$T_{larvae-devel-low}$	−10 °C*	Minimum temperature below which colonies at stage L1 or L2 stop their activity. This parameter is used in combination with $T_{larvae-devel-high}$ and $T_{larvae-devel-internal}$. Reference: based on Démolin (1969a).	4.3.3
$Pupae_{max}$	215 (days)	Maximum time needed for cluster of pupae to become moths. Reference: Démolin (1969a).	4.3.3

$Procession_{max-distance}$	1.23 (cells)	Maximum distance that colonies can processionate to find a suitable place to bury. Reference: Robredo (1963).	4.3.3
$Mating_{max-distance}$	3 (cells)	Maximum distance that moths can fly to find a suitable partner to mate. Reference: This study, see Supplementary Material S4.1 for a detailed explanation.	4.3.3
$Mating_{prob}$	95 (%)	Probability for a female moth to become mated when a male moth is found within $Mating_{max-distance}$. Reference: Rhainds (2010).	4.3.3
$Flight_{max-distance}$	3 (cells)	Maximum distance that mated moths can fly to find a suitable host to lay their eggs. Reference: This study, see Supplementary Material S4.1 for a detailed explanation.	4.3.3

Initialisation

INSTAR is initialised by creating cells and hosts and assigning their state variables values for the simulated area. Elevation, host location and height are loaded as input data (see section 4.3.3). Moth probability of emergence is then calculated for each cell based on number of hosts on it as follows:

$$probabilityofemergence = \begin{cases} 0.12 & \text{if } h_i < 3 \\ 0.1636 - 0.0169 \times h_i & \text{if } 3 \leq h_i \leq 10 \\ 0 & \text{if } h_i > 10 \end{cases}$$

where h_i is the number of hosts in cell i. This function assumes that the number of hosts per cell is a good surrogate of shaded surface, which affects soil moisture and temperature. These seem to be the main factors explaining the cluster of pupae emergence rate according to Torres-Muros et al. (2017), who reported mortality and emergence rates of cluster of pupae based on vegetation cover and soil moisture. Above 10 hosts per cell, full coverage was assumed and therefore cause the probability of emergence to be 0. Below 3 hosts per cell, no effect on surface coverage was considered, and therefore maximum probability of emergence was assigned, following data from Torres-Muros et al. (2017). A linear relationship was assumed between these two values, resulting in the above-mentioned function.

After this, quantity and quality values of hosts are assigned. The quantity assigned to each host is based on a normal distribution with mean Qt_{mean} and standard deviation Qt_{sd}, therefore allowing the user to setup the initial state of the pine stand. Quality is defined as defoliated or not defoliated according to a threshold value $Ql_{threshold}$. Three extra internal variables are calculated for hosts:

- The carrying capacity (cc) of each host: the number of colonies that a pine can host. It is calculated based on observations relating the number of colonies on highly defoliated trees and tree height. Briefly, the number of winter colonies in trees suffering a severe (~90 %) defoliation was related to the height of the tree for 20 pines of a pine plantation near Sierra Nevada Protected Area (unpublished data from J.A. Hódar, see Supplementary Material S4.1 for details). In this way, estimate of how many colonies are needed to completely defoliate a tree depending on its size (height) is obtained:

$$cc = 11.63 \times \ln \text{height} - 4.60$$
$$R^2 = 0.65$$

- The daily consumption per colony (consumption): the relative amount of biomass consumed per day by one colony in L2 stage, given the carrying capacity (cc) of the host on which it is feeding. It is calculated by assuming that all colonies consume the same amount of biomass per day, regardless of the number of individuals in it; it also assumes that colonies feed during the minimum number of days needed for a colony in L2 stage to develop into a cluster of pupae (i.e. 90 days) and considering full consumption a defoliation of 90 %, in agreement with observations used for the carrying capacity calculations which are as follows:

$$consumption = \frac{90}{90cc} = \frac{1}{cc}$$

- and moth suitableness (mu) of each host, which is calculated as:

$$mu = \sum (count \times coefficient)_i$$

Where i corresponds to the cardinal and intercardinal directions (i.e. north, northeast, east, etc.), the count is the number of trees in each direction i at a radius of 1 cell (30 m) and each coefficient provides a weighting (see Supplementary

Material S4.2) for the influence on each direction of the suitableness of a tree for the moth. This weighting creates an initial distribution of colonies in which there are more colonies on more exposed trees, which is what happens in the real world since burials occur in clear spots and moths choose a host based on the distance to their emergence point.

Afterwards, colonies are initialised. The number of colonies to be created is defined by the percentage of infected pines, which can be set by the user as a model input. In this study, real data from a defoliation monitoring programme within the Andalusia region (southern Spain) are used. This programme assigns a defoliation value from 0 (no defoliation) to 5 (complete defoliation) to each forest plot at the end of every defoliating season. These data are used to define the percentage of infected pines and thus the number of colonies present in the landscape. Colonies are then distributed among the hosts by weighted random selection based on moth suitableness: the higher the moth suitableness, the less probability for the host to be infected (i.e. to have colonies on it). Colonies are initialised as "egg" stage with days as egg corresponding to a random number between 0 and Egg_{min}.

Input data

INSTAR uses a set of input data as follows:

- Map of elevation for the simulated area, obtained from the Andalusian Network of Environmental Information (REDIAM) in a raster format and 30×30 m resolution.
- Daily maps of meteorological variables (maximum and minimum temperature) for the simulated area and period. These maps are raster files generated by a hydrometeorological model interpolating data from weather stations at 30×30m resolution (Herrero et al. (2007), see Supplementary Material S4.3 for more details). In this study, the meteorological dataset corresponds to years 2008–2013 (see section 4.4 for more details).
- Map of the pines present in the simulated forest. This map is a vector file derived from Airborne Laser Scanning data, which contains the location and height of trees (more details about this processing in Supplementary Material S4.4). All identified trees are considered to be pines (i.e. hosts).
- Initial percentage of infested pines. In this study, this percentage was based on defoliation data from Andalusian defoliation monitoring programme. This dataset provides an infestation rate based on observed defoliation for

each plot within the region, on a 0–5 scale. The initial percentage of infested pines is calculated based on the defoliation assigned by the monitoring programme to the plot where the simulated area is located. This dataset is fully documented by Ros-Candeira et al. (2019).

Submodels

INSTAR uses a series of submodels to simulate the development of the pest, as well as its interactions with the hosts and the cells (Figure 4.1). These submodels make use of best available current knowledge about *T. pityocampa*, but have been built in such a way that will allow an easy integration of new information as knowledge on this pest increases. As an example, if new information on pupae distribution is found, the "procession" submodel could be adjusted to follow such distribution by including a kernel function. These submodels can be classified into three types: mortality, development and movement.

Mortality submodels Mortality submodels simulate the death of organisms due to abiotic or biotic conditions. Since some of *INSTAR* agents represent groups of organisms, some mortality factors apply to the agent as a whole (i.e. they cause the death of a whole colony), while others apply to a portion of the individuals that the agent represents (i.e. they cause the reduction in the number of individuals of a colony). *INSTAR* applies mortality submodels to colonies and clusters of pupae, while moth mortality is already included in pupae mortality and hosts do not have an associated mortality submodel since *T. pityocampa* rarely causes pine death.

The submodel "colony mortality" can reduce the number of individuals of the colonies or kill whole colonies to simulate mortality rates due to different abiotic and biotic factors. Such mortality rates differ between each stage. At the beginning of stage "egg", when the colony is created, a mortality factor due to parasitism is applied. Mortality is calculated based on Torres Muros (2015). It considers elevation to be a proxy for egg parasitism and causes the original number of individuals to be reduced as follows:

$$numberofindividuals_{aftermortality} = \\ numberofindividuals_{original} \times p_i$$

where

$$p_i = \frac{e^{n_i}}{1 + e^{n_i}}$$

and

$$n_i = 0.2082 + (0.0006 \times elevation)$$

where p_i is the percentage of individuals which survive at a cell i.

At stage L1, two mortality factors are applied. The first one is related to quality of the host and is applied at the beginning of this stage, when "eggs" become L1. If quality is defoliated, number of individuals is reduced by a certain percentage $L1_{mort}$. The second factor is due to lethal temperatures and is applied every day: the whole colony dies if maximum temperature is higher than $T_{lethal-max}$ or minimum temperature is below $T_{lethal-min}$.

At stage L2, two mortality factors are also applied every day. The first one is related to scarcity of food: if quantity of the host is below a certain threshold $L2_{mort-threshold}$, number of individuals is reduced by a certain percentage $L2_{mort}$. The second factor is the same as for stage L1: the whole colony dies if maximum temperature is higher than $T_{lethal-max}$ or minimum temperature is below $T_{lethal-min}$.

The submodel "pupae mortality" affects the variable number of individuals of the cluster of pupae to simulate mortality rates due to shading (Torres-Muros et al., 2017), which is assumed to be related to the number of hosts on a cell. A mortality factor is applied at the beginning of this phase, when colonies in stage L2 become a cluster of pupae. The state variable probability of emergence defines the percentage of number of individuals which survive and result in the number of moths which are created (see "pupae development" submodel, section 4.3.3):

$$numberofindividuals_{aftermortality} = numberofindividuals_{original} \times probabilityofemergence$$

No mortality submodel is applied to moth agents, since it has been included in the probability of emergence of "pupae mortality" submodel.

Development submodels Development submodels are used to simulate how an organism increases its biomass over time or how it changes to the next stage of its life-cycle. These submodels are depicted in Figure 4.1. In *INSTAR*, hosts, colonies and clusters of pupae have an associated development submodel, while a moths' development submodel is not required based on the assumption that all moths live one day.

The submodel "hosts development" defines how quantity and quality state variables change over time. The quantity of a host on a given day is defined as:

$$quantity_t = quantity_{t-1} - consumption + growth$$

where

$consumption =$

daily consumption per colony × number of L2 colonies on the host

$$growth = \begin{cases} \text{NPP between April and August} \\ 0\ \%\ \text{the rest of the year} \end{cases}$$

Regarding quality, this variable is assessed before the growing season starts (i.e. on the 31st March). Quality will be defined as defoliated if quantity at that moment is below $Ql_{threshold}$, and not defoliated otherwise.

The submodel “colonies development” sets the time that is needed for a colony to change its stage and eventually become a cluster of pupae through “procession submodel”. Each colony stage has a counter as state variable (days as egg, days as L1 and days as L2, respectively), which defines the length of each stage in number of days. When the counter of each stage reaches 0, the following stage starts (from “egg” to L1 and from L1 to L2). Finally, colonies in stage L2 will perform the “procession” submodel when days as L2 become 0. These counters are initially set to the minimum length of each phase based on literature (Egg_{min}, $L1_{min}$, $L2_{min}$) but they will be extended under certain conditions:

- If maximum temperature is below $T_{egg-devel}$, “egg” stage will be extended by one day, i.e. *INSTAR* halts the development of eggs on those days where temperature is lower than the threshold ($T_{egg-devel}$).
- If maximum temperature is above $T_{larvae-devel-high}$ and the integrated temperature is below $T_{larvae-devel-internal}$, L1 stage will be extended by one day. Moreover, if minimum temperature is below $T_{larvae-devel-low}$, L1 stage will be further extended by one day. Same rules apply to L2 stage. In other words, *INSTAR* halts larval development when temperatures are not high enough for larvae to digest the biomass they have ingested, but, in addition, also when temperatures a too low for larvae to leave their nests to feed.

Extension in colony stages causes the following pupae phase to decrease in the same length (see "pupae development" submodel, section 4.3.3), in order to maintain a univoltine cycle as literature refers (Berardi et al., 2015).

The submodel “pupae development” sets the length of the phase cluster of pupae within the lifecycle of the processionary by adjusting the days as pupae state variable, similar to "colony development" submodel. Days as pupae are decreased by 1 in every time step. When it becomes 0, the cluster of pupae disappears and becomes a certain number of moths. The number of moths which are then created is defined by number of individuals. For the sake of simplicity, *INSTAR* does not consider extended diapause, as our study area is located in the Mediterranean area, where *T. pityocampa* rarely engage in extended diapause (see section 4.2). Nevertheless, a submodel implementing this phenomenon could be easily integrated.

Movement submodels Movement submodels are used to describe processes where an agent selects a place to move to based on information from its surroundings. Three movement submodels are defined in *INSTAR*: "procession", which simulates the search for a burial spot, performed by colonies in L2 stage; "mating", which simulates the search of a male moth, performed by female moths; and "oviposition", which simulates the selection of a host to lay the eggs on (i.e. creation of a new colony), and is performed by mated female moths.

The "procession" submodel defines the place where colonies at stage L2 and days as L2 equal to 0 become a cluster of pupae. Agents performing this submodel search among the surrounding cells within $Procession_{max-distance}$ and select the ones with the lowest pine density (i.e. number of pines in cell). If several cells have the smallest pine density, they choose the closest one among them. A cluster of pupae is created in that cell and the colony disappears. The state variables of the newly created cluster of pupae are inherited from the parent colony: number of individuals corresponds to the number of individuals of the parent colony and days as pupae equals $Pupae_{max}$ minus the number of days that the parent colony was extended (see "colony development" submodel description).

The "mating" submodel defines which moths will become mated and where they will be located after mating. Female moths become mated with a probability $Mating_{prob}$ if there is at least one male moth within $Mating_{max-distance}$. When this happens, mated moths move halfway towards their partner.

The submodel "oviposition" selects the host on which a new colony will be created (i.e. the host to which the new colony will be linked to). After "mating", mated moths choose a host to lay their eggs within $Flight_{max-distance}$. Weighted random selection is used to define which will be the selected host. This selection gives a higher probability of being chosen the closer the host is to the moth. If no host is found, no colony is created. The state variables of the newly created colony are defined as: number of individuals corresponds to a random number within a normal distribution with mean CS_{mean} and standard deviation CS_{sd}, stage is "egg" and days as egg equals Egg_{min}. The other state variables are set to 0.

4.4 Model consistency test

INSTAR has been written in NetLogo language (Wilensky, 1999) and reviewed in an iterative process by a multidisciplinary team consisting of computer scientists, modellers and ecologists. An independent implementation of each individual submodel has been used to check that the model agrees with the conceptual model initially proposed by Torres Muros (2015) or, in other words, for model verification in the sense of Findeisen et al. (1978). The last *INSTAR* stable version can be freely downloaded from GitHub (http://sl.ugr.es/github_instar) and run under a NetLogo free licence (https://ccl.northwestern.edu/netlogo). Besides this, a demo execution of *INSTAR* can be run at https://vlab.geodab.eu, a virtual laboratory promoted by ECOPOTENTIAL project (https://ecopotential-project.eu).

4.4.1 Methodology

Pattern-oriented modelling led *INSTAR* design and helped to decide which processes should be included in the model, as recommended by Wiegand et al. (2003). The most important pattern regarding pine processionary population dynamics corresponds to phenology, which is mainly driven by temperature. Thus, in order to be coherent and structurally realistic, *INSTAR* should faithfully reproduce the effect of this factor on the species' phenology. The submodels involved in this process are development submodels (section 4.3.3) and therefore, a calibration of the parameters involved in these submodels has been performed. Besides this, a stress test was simulated by defining extreme climate scenarios as input data. Stress tests often help to identify unexpected behaviours which cannot be detected when the model is run under normal conditions and therefore extreme unrealistic inputs are used in these tests (Railsback and Grimm, 2011). These experiments constitute a first internal validation of the development submodels (Figure 4.2), since they can help with confirming hypothesis and observing unexpected model behaviours. After these tests, parameterisation and sensitivity analysis are needed before the model can be fully applied.

A virtual experimental area was created for this analysis by using a combination of real and built-in datasets (see Supplementary Material S4.5 for more details).

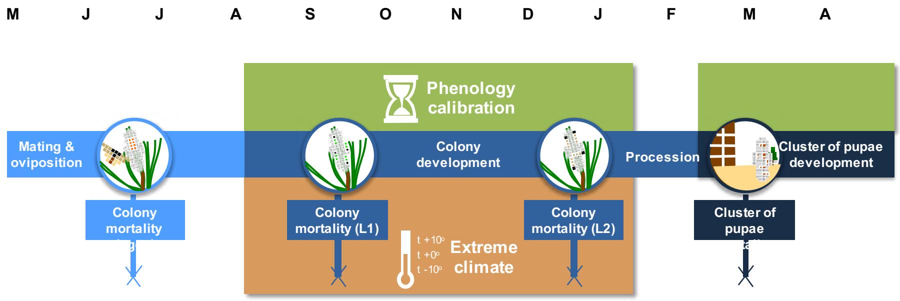


Figure 4.2: Diagram showing the submodels within *INSTAR* that are analysed in the consistency tests. Green box corresponds to phenology calibration experiment, while orange box refers to extreme climate experiment.

This virtual area is 15 × 12 cells large, covering an area of 450 × 360 m^2 (16.2 ha). The location is real: Sierra Nevada Protected Area (south-eastern Spain) at an elevation of 1706±34 m a.s.l. and contains 1128 pine trees, which have been extracted using an existing LiDAR dataset (see section 4.3.3). Finally, the climatic data needed to conduct the consistency analysis were generated by WiMMED hydrological model (see section 4.3.3) and correspond to years 2008–2013.

Phenology calibration

Each phase in *T. pityocampa*'s life-cycle shows a characteristic phenology, which shifts each year within certain limits depending on climate conditions. Thus, testing whether *INSTAR* reproduces a realistic phenology constitute one of the first steps to validate the model. In order to test whether the phenology of the model reproduces field observations, a calibration of the "colonies development" submodel was performed. The parameters involved in this submodel are the temperature thresholds regulating the length of each phase and the minimum lengths of each stage (see Table 4.2). This calibration analysis aims to find the values of the parameters $T_{egg-devel}$, $T_{larvae-devel-high}$, $T_{larvae-devel-low}$ and $T_{larvae-devel-internal}$ that best reproduce the species phenology in the study area.

INSTAR results were calibrated against field observations provided by the Sierra Nevada Global Change Observatory (Bollullos and Aspizua, 2014). The observations consist on a dataset reporting hatching, procession and egg laying dates recorded for several plots within the Sierra Nevada mountain range during years 2009, 2010 and 2011. A summary of this dataset can be observed in Table 4.3.

Calibration was performed following a stepwise approach: egg development

Table 4.3: Average, earliest and latest hatching, procession and egg laying dates for *Thaumetopoea pityocampa* observed in Sierra Nevada during years 2009, 2010 and 2011. Data from Sierra Nevada Global Change Observatory (Bollullos and Aspizua, 2014). [a]Note the year difference: earliest procession date occurred in 2009.

	Hatching date			**Procession date**			**Laying date**		
	Earliest	Avg ± SD	Latest	Earliest	Avg ± SD	Latest	Earliest	Avg ± SD	Latest
2009	23rd Jul.	12th Aug. ± 10 days	4th Sep.	4th Mar.	26th Mar. ± 13 days	12th May	22nd Jun.	27th Jul. ± 20 days	31st Aug.
2010	28th Jul.	22nd Aug. ± 11 days	28th Sep.	28th Nov. 2009[a]	8th Feb. ± 47 days	19th May	2nd Jul.	3rd Aug. ± 20 days	23rd Sep.
2011	28th Jul.	21st Aug. ± 10 days	12th Sep.	24th Jan.	23rd Mar. ± 25 days	19th May	9th Apr.	28th Jul. ± 22 days	12th Sep.

calibration followed by larvae development calibration. In the first step, the parameter $T_{egg-devel}$, which modulates how long the stage "egg" takes by adjusting days as egg, was calibrated in order to obtain simulated hatching dates within the range of the above-mentioned observations. For this analysis, a systematic execution of the model was performed with values of $T_{egg-devel}$ ranging from 15 to 25 °C in 1 °C steps. Every simulation was run in triplicate, lasted 4 months and was initialised at Julian day 210 of the corresponding year (2009, 2010 and 2011). For each simulation, the hatching date of each colony was recorded and the difference between observed and simulated average hatching date was calculated as a metric of model fit.

Once the parameter $T_{egg-devel}$ was calibrated, the second step of the calibration took place. The parameters $T_{larvae-devel-high}$, $T_{larvae-devel-low}$ and $T_{larvae-devel-internal}$ were calibrated to obtain procession dates within the range of the above-mentioned observations. These parameters affect how long the stages L1 and L2 take by adjusting days as L1 and days as L2 (see section 4.3.3). For this analysis, a new systematic execution of the model was performed. A range of values for each parameter was tested: 20-30 °C for $T_{larvae-devel-high}$, 15-25 °C for $T_{larvae-devel-internal}$ and -15 to -5 °C for $T_{larvae-devel-low}$, in 1 °C step, resulting in 1331 combinations of parameter values. Simulations were initialised with colonies at stage L1, to avoid noise coming from the previous stage. Each simulation was started on Julian day 226 of the corresponding year and lasted 9 months, therefore extending to the beginning of next year. Thus, input datasets correspond to years 2008/2009, 2009/2010 and 2010/2011. The initialisation date corresponds to the average hatching date derived from the previous experiment. For each combination of parameter values and input dataset, five replicates were run. Finally, to avoid noise coming from other submodels, mortality submodels based on host quality and quantity were disabled and the procession submodel was unconstrained (colonies could bury in all cells around them). In this case, the procession date of each colony was recorded in each simulation and the difference between observed and simulated average procession date was calculated as a measure of model fit.

The above described stepwise calibration was based on hatching and procession dates within 1-cycle runs. Once the involved parameters are calibrated, it becomes necessary to test whether the selected parameter values reproduce the phenology pattern over the years. To test these criteria, *INSTAR* was run for the period 2008–2011 using the selected values for parameters $T_{egg-devel}$, $T_{larvae-devel-high}$, $T_{larvae-devel-internal}$ and $T_{larvae-devel-low}$.

Extreme climate stress test

By exposing the model to extreme climate, we aim to test the model consistency in relation to temperature influence on pest development. As mentioned at the beginning of this section, extreme unrealistic inputs are used in these tests in order to observe divergent behaviours in the model against normal input data. Thus, three input scenarios were used in this experiment: NORMAL, corresponding to the daily maps obtained from measured temperatures, MINUS10 and PLUS10. Scenarios MINUS10 and PLUS10 were generated by respectively subtracting and adding an offset (10 °C) to the measured temperatures, in order to reach lethal temperatures for the processionary moth and test whether *INSTAR* simulates development and mortality due to extreme temperatures as expected. The offset was applied equally to maximum and minimum temperatures, therefore maintaining the thermal range. Simulations were run in triplicate for the period 2008–2013. Considering these scenarios, larval development is expected to be accelerated when temperatures are high and delayed when they are low. Moreover, larvae mortality rates are expected to increase, even causing pest annihilation, due to the higher occurrence of extreme temperatures above or below the species survivability thresholds.

4.4.2 Results

Phenology calibration

Results from the egg development calibration can be observed in Figure 4.3, which shows the difference between observed and simulated average hatching date for each year along the $T_{egg-devel}$ tested gradient. The line indicates the mean of the difference among all three years. Data from year 2009 show differences of less than 2 days between simulated and observed mean hatching date for $T_{egg-devel}$ values 15–22 °C. Data from years 2010 and 2011 show higher differences, above 5 days for $T_{egg-devel}$ values 15–22 °C. For $T_{egg-devel}$ values 23–25 °C, the trend changes and all differences range between 3.5 and 7.5 days. When the mean difference among all years is analysed, small fluctuations are observed. The minimum value is found for 4.8 days, corresponding to $T_{egg-devel}$ equal to 22 °C and the maximum value, 6.0 days, is reached for $T_{egg-devel}$ equal to 25 °C. Considering these results, the selected value for $T_{egg-devel}$ corresponds to 22 °C.

Once the egg phase was calibrated, larvae development calibration was carried out. Difference in average procession date between observations and simu-

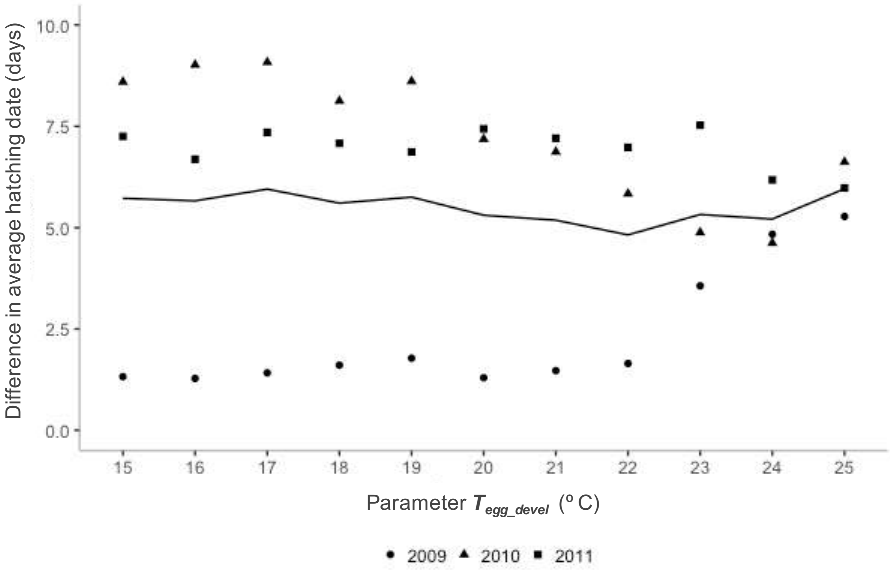


Figure 4.3: Difference in observed and simulated average hatching date for years 2009, 2010 and 2011 along $T_{egg-devel}$ tested values. Line shows the mean among years.

lations, which has been considered as the calibration metric for larvae development phase, was calculated for each combination of parameter values and seasons. The minimum difference across years corresponds to 2.5 days and is found for $T_{larvae-devel-high}$ equal to 27 ℃, $T_{larvae-devel-internal}$ equal to 25 ℃, and $T_{larvae-devel-low}$ equal to -8 ℃, followed by all other $T_{larvae-devel-low}$ tested values except for -5 ℃ (data not shown). Figure 4.4 shows the mean difference for the three years along the tested values for parameters $T_{larvae-devel-high}$ and $T_{larvae-devel-internal}$ ($T_{larvae-devel-low}$ fixed to -8 ℃). A local minimum can also be observed for $T_{larvae-devel-high}$ equal to 22 ℃ $T_{larvae-devel-internal}$ equal to 23 ℃. This local minimum, however, is not so clearly observed for data regarding each year separately (see Figures S.52-S.54 in Supplementary Material S4.6).

The influence of parameter $T_{larvae-devel-low}$ can be observed in Figure 4.5. Differences generally remain below 10 days for all years and parameter values. Small differences are obtained for year 2008/2009 for most parameter values, except for $T_{larvae-devel-low}$ equal to -5 ℃. Year 2009/2010 shows the highest differences for values below -9 ℃, while year 2010/2011 shows fluctuating differences. If the mean across years is considered, a consistent increase can be noticed for values -7 ℃ to -5 ℃. As mentioned above, the minimum difference

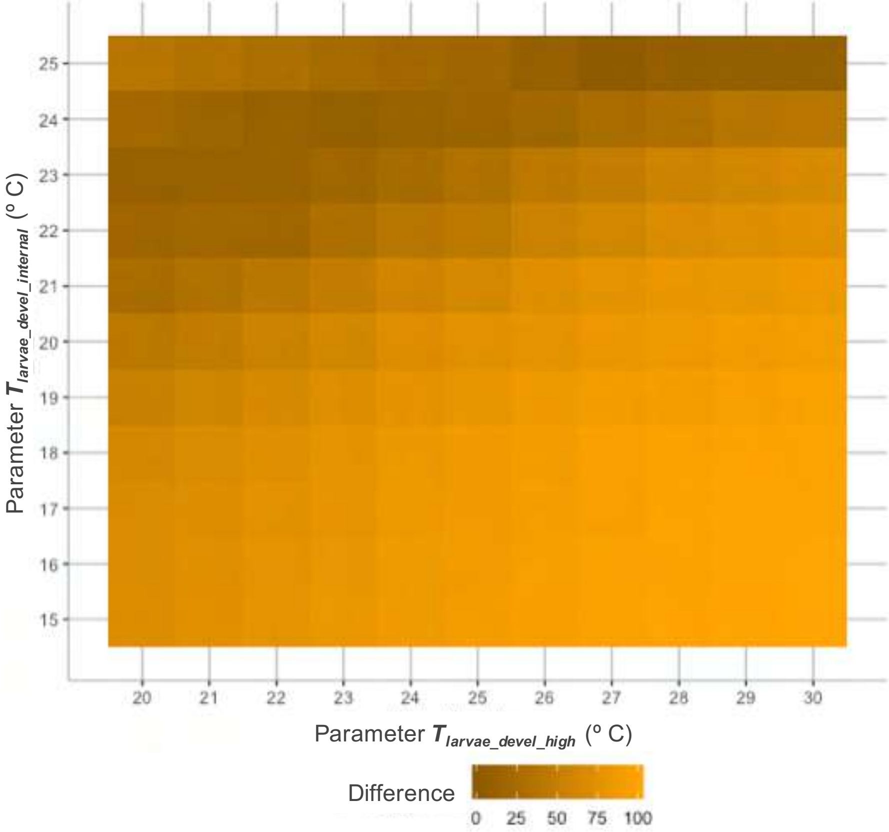


Figure 4.4: Difference between observed and simulated average procession date, in number of days. Data refer to the mean across years 2008/2009, 2009/2010 and 2010/2011 for each combination of parameters $T_{larvae-devel-high}$ and $T_{larvae-devel-internal}$. The value for parameter $T_{larvae-devel-low}$ is fixed to -8 ℃.

is found at -8 ℃. The influence of parameter $T_{larvae-devel-low}$ when the local minima of $T_{larvae-devel-high}$ equals 22 ℃ and $T_{larvae-devel-internal}$ equals 23 ℃ can be observed in Figure S.55 in the Supplementary Material S4.6, resulting in higher differences for most values and years. It should be noted that parameter $T_{larvae-devel-low}$ is evaluated only when maximum daily temperature is above $T_{larvae-devel-high}$ and / or integrated daily temperature is below $T_{larvae-devel-internal}$ (see section 4.3.3), which could explain the seemly erratic behaviour of this parameter.

Once the above described parameters were calibrated, results of the simulation regarding species phenology using the selected values for parameters $T_{egg-devel}$, $T_{larvae-devel-high}$, $T_{larvae-devel-internal}$ and $T_{larvae-devel-low}$ (22 ℃, 27 ℃, 25

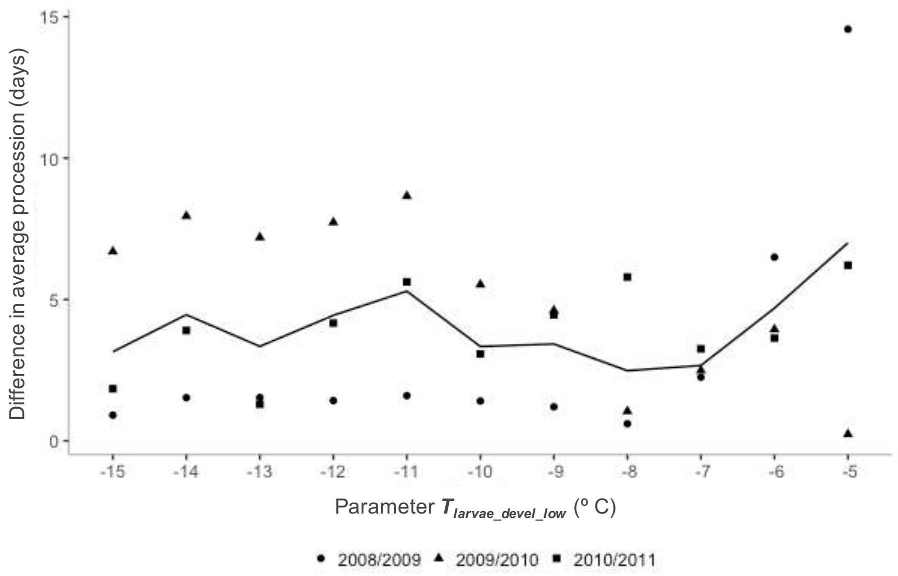


Figure 4.5: Difference between observed and simulated average procession date, in number of days along $T_{larvae-devel-low}$ gradient. Data for each year (points) and across years (line) for parameter $T_{larvae-devel-high}$ fixed to 27 °C and parameter $T_{larvae-devel-internal}$ fixed to 25 °C.

°C and -8 °C, respectively), are shown in Figure 4.6, which also shows the observed phenology. Egg layings fall within the observed ranges for years 2009 and 2011, but tend towards earlier dates for year 2010 in comparison to observations. Hatchings and processions occur within the observed range for all three years.

Extreme climate stress test

Pest dynamics for each scenario are shown in Figure 4.7. As expected, high larvae mortality rates resulted in a reduced number of individuals in both MINUS10 and PLUS10 scenarios compared to the NORMAL scenario. In the MINUS10 scenario, the population was greatly limited (Figure 4.7A). Under the PLUS10 scenario, however, larvae mortality due to high temperatures was as high as to cause full annihilation of the pest before the first cycle was completed (Figure 4.7B).

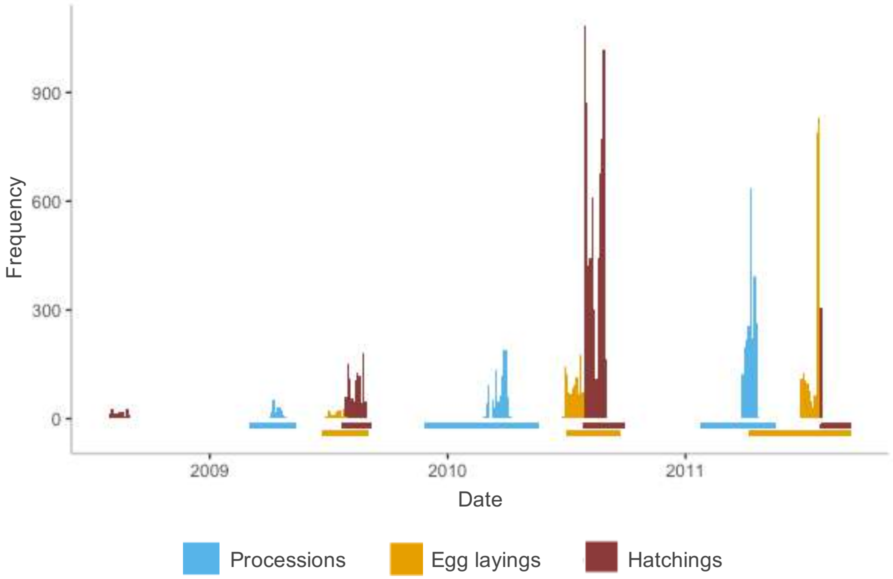


Figure 4.6: Histograms showing the frequency of simulated egg layings (orange), hatchings (red) and processions (blue) along the simulation period (29/07/2001-20/07/2008). Field observations (2009–2011) are depicted in the plot as horizontal bars below the histogram (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

4.5 Discussion

To the best of our knowledge, *INSTAR* is the first ABM simulating the population dynamics of the pine processionary moth. This is a spatially-explicit model, which constitutes an advantage in comparison to other published models such as Robinet et al. (2014), Seixas Arnaldo and Monteiro Torres (2005) or Régolini et al. (2014). The model aims to improve our understanding of the pest's population dynamics and identify gaps in our knowledge. The design and implementation of *INSTAR* constitutes an effort to synthesize the available knowledge about the target species, while it allows an easy integration of newly produced knowledge. Under a structural point of view, *INSTAR* has been built considering all the ontological stages of the target species: eggs, larvae, pupae and moths. The concepts of colony and cluster as an agent types are used to represent groups of eggs, larvae or pupae, while moths are represented as individual agents. The model is build following a modular structure with three submodel classes: development, mortality and movement. The classification of submodels into a reduced number of

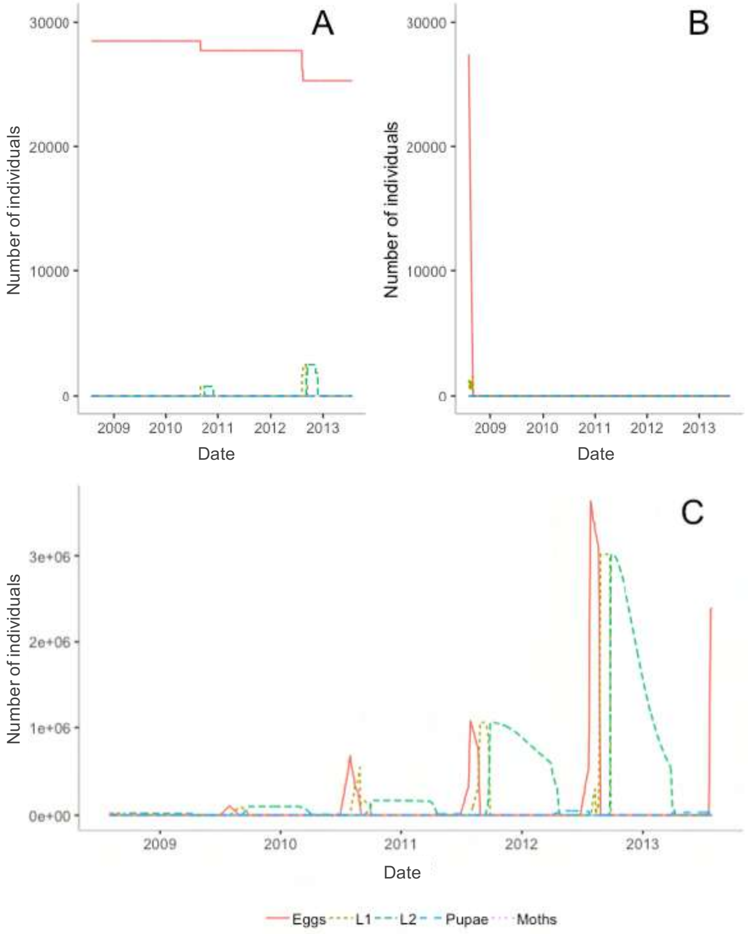


Figure 4.7: Plots showing the pest development as number of eggs (red continuous line), larvae L1 (light brown pointed line), larvae L2 (green short-dashed line), pupae (blue long-dashed line) and moths (pink pointed line) under three different scenarios: MINUS10 **(A)**, PLUS10 **(B)** and NORMAL **(C)**, for the period 2008–2013.

classes helps to overcome some of the most common critics to ABMs: the difficulties of reproducing them, standardising their structures and defining guidelines to design, calibrate and evaluate them (DeAngelis and Grimm, 2014). Thus, the modular structure of *INSTAR* eases the exchange of information among modellers as well as the comparison between models. Such a structure improves the understanding of the model and facilitates communication with non-modellers. Moreover, it could constitute a framework to build models simulating other forest pests in a wide variety of ecological systems, since it summarises the key biological processes that take place in them. As an example, movement submodels could be adjusted to simulate the dispersal and establishment of mistletoe, another common pest in pine plantations, by following Mellado and Zamora (2016).

T. pityocampa is a poikilotherm species, and therefore air temperature plays a key role in its performance. Moreover, the distribution and density of pine plantation stands has been demonstrated to be another important factor explaining the population dynamics of the species (Dulaurent et al., 2011; Li et al., 2015; Torres-Muros et al., 2017). Thus, *INSTAR* considers climate and land use as the main forcing variables or drivers. In this manuscript, the role of temperature in *INSTAR* has been calibrated and analysed. Parameters involved in development submodels have been calibrated using phenology observations from Sierra Nevada (Spain) and the difference between observed and simulated average hatching and procession date as a measure of model fit. The egg phase showed small differences (maximum 9 days) for all tested parameter values and years. The parameter value selected corresponds to the one which minimises the difference in observed and simulated average hatching date for all three years ($T_{egg-devel}$ 22 °C). Larvae phase shows important differences for different parameter values and years. This implies that larvae phase is the main responsible for the phenology within *INSTAR*. The parameter set selected for larvae development corresponds to the one which minimises the difference for all years ($T_{larvae-devel-high}$ 27 °C, $T_{larvae-devel-internal}$ 25 °C and $T_{larvae-devel-low}$ -8 °C). This set also resulted in small differences for each year separately and causes the model to successfully reproduce the species phenology through a multiple-year simulation.

Besides this, *INSTAR* behaviour when exposed to extreme climate has also been analysed. Extremely low temperatures (MINUS10 scenario) have a severe impact on the number of larvae but not on the eggs. This is explained by the fact that the egg mortality implemented in the model is only due to parasitism which is not linked with temperature. The model could be improved in this regard by also including egg mortality due to lethal temperature (following Rocha et al., 2017) and the effect of temperature on parasitism rates (following Tiberi et al., 2015). When exposed to extremely high temperatures (PLUS10 scenario), the behaviour is quite different. This scenario causes a total annihilation of the pest during the first year of the execution. In other words, an extreme increase in temperature such as the one caused by PLUS10 scenario seem to cause most cells in the landscape to reach maximum lethal temperatures. Our simulated area represents a warm region of the distribution area of the pest. Therefore, the population is probably closer to its high temperature threshold than to its lower one, resulting in this scenario causing the population collapse which cannot be observed under the MINUS10 scenario (i.e. a change of the same scale towards low temperatures does not cause as many cells to reach minimum lethal temperatures). Nevertheless, these statements should be taken cautiously. The parameter values have been taken from literature, they refer to air temperatures and represent the general knowledge of *T. pityocampa*. The actual lethal values may differ for different populations and been influenced by other factors (e.g. wind speed, shading) which can modulate the actual temperature to which larvae are exposed. Another reason for the difference between scenarios can be that at higher temperatures, eggs develop faster and hatching is anticipated, causing the larvae to be exposed to the high summer temperatures. Literature suggests that *T. pityocampa* adapts to areas with warm summers by delaying the egg phase to late summer, thus avoiding lethal temperatures (Chapter 2 in Roques, 2015). At the moment, *INSTAR* does not possess a mechanism simulating this process, since initialisation is fixed at a certain date as it is commonly done in processes which deal with seasonal and annual patterns (such as hydrological models). This limitation, however, can be overcome by calibrating the initialisation date for the area to be simulated based on field data. To sum up, phenology has been calibrated successfully according to the field observations. However, more knowledge about the drivers modulating the biological cycle of the species would be required for a more realistic modelling.

This article is focused on the phenological aspects of the processionary moth. Although this is a very important process, in order to correctly simulate the population dynamics of the pest, its spatial distribution should be addressed by calibrating and parameterising movement submodels. However, data on movements by the pine processionary moth are difficult to obtain and literature often refers to nonnatural conditions, such as flight distance measured under laboratory conditions (Sauvard and Yart in Battisti et al., 2015), or extreme values (Robredo, 1963).

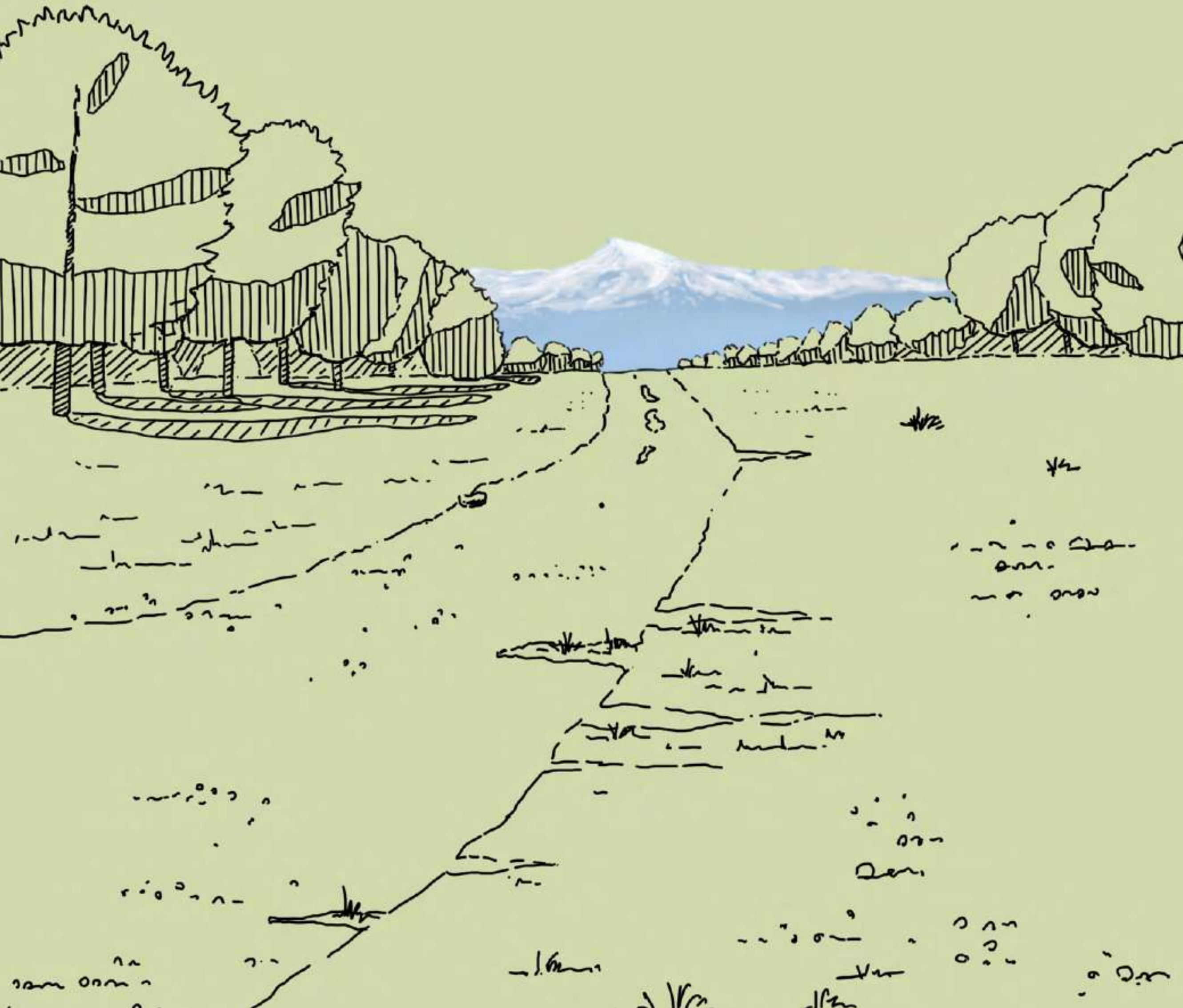
Moreover, assessing the impact of the pest at a landscape scale requires high resolution data, such as quantifying per-larvae biomass consumption. Although larvae weight gain has been studied (Avtzis, 1986), no reference for biomass consumption has been found. This has avoided a more realistic modelisation of the host-pest interaction. Due to the interest on forest health, pests are commonly monitored by assessing their impact as defoliation or other stress signals on the host (Trumbore et al., 2015). In the case of the pine processionary moth, the number of colonies is also often monitored and reported. *INSTAR* uses this type of information for the calculation of the trees carrying capacity (see section 4.3.3 and Supplementary Material S4.1). However, data at a higher resolution (i.e. number of larvae per colony at different stages) is not available and such information would be particularly valuable to improve how the host-pest interaction is modelled and to calibrate the mortality submodels. In general terms, information and field observations about movement and mortality parameters are scarce and therefore an important gap of knowledge exists in this respect.

INSTAR is focused on the processionary moth, and therefore host development is modelled in a very simple way. This submodel could be further improved by considering more a complex relationship of pine activity with climate, differences among pine species or linkages between primary production and topographic-soil features. This could be done by coupling *INSTAR* with independent models (such as the ones proposed by Faias et al., 2012) simulating stand growth and development.

Due to the inherent characteristics of ABMs, there is a high degree of uncertainty in the model and a high number of parameters, which will require calibration and parameterisation (Kelly (Letcher) et al., 2013). Thus, further work should focus on determining the parameters which have the strongest impact on model outputs (i.e. sensitivity analysis) and identifying model uncertainty sources. Once the model is fully calibrated and validated, simulations can be considered as *in silico* performed experiments that are not feasible in the real world. *INSTAR* could then help to forecast the probability of occurrence and intensity of the pest outbreaks on pine plantations under different climate and land use scenarios. Thus, in the long term, *INSTAR* could be useful for the environmental decision makers in charge of managing the large area covered by pine plantations affected by this pest.

4.6 Conclusions

Current available knowledge on *T. pityocampa* has been synthesized and integrated into *INSTAR*, an ABM aiming to simulate the population dynamics of this species. In this article, we present *INSTAR* model structure according to a standard protocol, specifically designed to document ABMs, increasing its usability and reproducibility. Moreover, we have conducted a consistency test which constitutes a first internal validation of the model. The experiments presented here assess how the model simulates the development of the pest driven by temperature. Once the model has been calibrated, it successfully reproduces the phenology observed for a given area. This means that the submodels responsible for the development within *INSTAR* are well designed and implemented. Moreover, the model behaves as expected when exposed to extreme input values through a climate stress test. Extreme high temperatures cause full annihilation of the pest before the first cycle is completed and extreme low temperatures greatly limit the pest population. Further work should focus on testing and calibration of pest spatial distribution, as well as overall sensitivity and uncertainty analysis.



Discussion

This thesis aimed to increase our understanding of Mediterranean pine plantations by means of ecological modelling. The modelling of ecological processes is highly relevant nowadays since ecosystem management is facing new challenges as a result of global change, especially in the Mediterranean Basin. Climate change is expected to have major impacts in the Mediterranean area as a result of increased aridity and higher incidence of extreme weather events (Zittis et al., 2021). Moreover, massive land use changes are rapidly transforming our ecosystems, resulting in complex effects with consequences for ecosystem services and quality of life (Quintas-Soriano et al., 2022). Advancing the understanding of ecosystems and assessing multiple future trajectories are therefore required to assist decision-making under these new conditions.

We have tackled the objectives of this thesis considering both the ecological and social dimensions of our target ecosystem. Firstly, we addressed the perspective of the stakeholder community on the socio-ecological system around Mediterranean pine plantations. In this regard, we made use of a novel participatory modelling technique which allowed us to synthesise semi-quantitative descriptions of our system. The outcomes of this exercise served to address the second and third ecological objectives, the simulation of forest and defoliator dynamics, focusing especially on the role of management and climate. By addressing each objective from a different modelling approach, we have attempted to show an overview of techniques, provided a high level of detail on methodological aspects and ensured transparency and promoted reproducibility of the modelling process by discussing the limitations and assumptions of each technique. The ecological models presented in this thesis advance our understanding of the socio-ecological system, the forest dynamics and the pine processionary moth dynamics of Mediterranean pine plantations in southeastern Spain.

Knowledge-based models to understand the socio-ecological system

Understanding the social dimension of ecosystems is highly relevant to develop successful management strategies and policies, especially in highly anthropised systems such as the Mediterranean ones (Perry and Enright, 2006). Complex socio-ecological systems can be effectively studied by eliciting and analysing stakeholders' knowledge (Aminpour et al., 2020). Knowledge co-production techniques help to generate common views of problems through the participation of all actors involved in or affected by them (e.g. Meliadou et al., 2012; Olazabal et al., 2018a; Tepes and Neumann, 2020; Xiang, 2013). Moreover, these techniques can also help to find knowledge gaps and solutions which clarify the synergies and trade-offs amongst stakeholders' objectives (Vanermen et al., 2020). In Chapter 1, we applied Fuzzy Cognitive Mapping to generate a knowledge-based model to go more deeply into the perceptions, knowledge and experiences from a variety of stakeholders to build a shared description of Mediterranean pine plantations and extract proposals for policy and management actions.

The Spanish reforestation programme has been widely criticised, resulting in passionate debates between defenders and detractors of this policy (Vadell Guiral et al., 2017). Part of the forest engineering sector criticises the negative perception that some social groups have of past pine plantations and lambast them for being uninformed and asserting biased arguments (Serrada Hierro, 2017). Considering these criticisms and debates around the Spanish reforestation programme, prior to the study we expected to find contrasting views on the management of pine plantations from stakeholders with different educational backgrounds or professional profiles. However, our results show a high level of agreement in the narratives of all three types of stakeholders: researchers, managers and socio-economic agents. Stakeholder groups express common understanding of the ecological functioning of pine plantations and the relevance of stand density as a key variable controlling multiple processes, an aspect which has also been shown in empirical ecological studies (e.g Gómez-Aparicio et al., 2009; Navarro-González et al., 2013). Stakeholder groups also propose common management actions, and in addition they provide group-specific proposals of actions, which highlight their main concerns and interests. Stakeholders highlight that the effective management of pine plantations in our study area is limited by multiple factors such as insufficient human and material resources, lack of effective knowledge transfer or gaps in the governance processes. These aspects are also identified at more general levels (e.g. ecological restoration in Europe, Cortina-Segarra et al., 2021), which in our opinion highlights how arduous ecosystem management can be.

Based on our knowledge-based model, we conclude that apparent contrasting differences observed in certain social circles could be reconciled by promoting interaction among stakeholders based on an honest interest to empathise and understand other positions. This would create an enriching environment where common points will help reconcile stakeholders whose visions are not as different as they may think and will provide innovative proposals for actions. Thus, we identify a need to implement multi- and transdisciplinary management strategies in order to improve communication and commit to a common vision on the future of pine plantations. We consider that any proposal for future actions on pine plantations will only be feasible if the perceived conflict is solved and supposedly opposing views are integrated into management objectives shared by all parties.

Interaction among stakeholders requires fluent and effective communication. However, communication between researchers and managers is one of the most pressing challenges in ecosystem management. Scientific outcomes are often unapproachable for managers due to language and publication barriers, and limited efforts are given to adapt scientific information to wider audiences. Effective communication depends on frequent and close interaction between scientists and managers, which demands enormous investments of time from groups who are usually not rewarded for it (Janse, 2008). Moreover, managers and researchers differ in their preferred channels for communication, even though they provide similar suggestions to improve it, such as clearer ways to present scientific information and clearer formulation of needs by policy-makers (Janse, 2008). The question then remains how to ensure long-term and effective interaction between researchers and managers. Based on our experience gained through the interviews with stakeholders, we propose the creation of science-policy interfaces as platforms to establish such collaborations, and would like to stress that success rates will depend on resources allocated to overcome challenges and potential tensions (Ojanen et al., 2021).

One of the main outcomes of this socio-ecological modelling exercise was the important role that the stakeholders' community assigned to silvicultural management as a measure to influence stand density, the main variable identified to control multiple and interlinked ecological processes such as regeneration, biodiversity and resilience. Navarro-Cerrillo et al. (2019) and Jiménez and Navarro (2016) have studied the effects of thinning on the resilience to drought by southeastern Spain pine plantations under a context of climate change. They concluded that thinning can serve as a silvicultural measure to adapt pine plantations to climate change. Furthermore, other factors apart from drought may be playing a role in the resilience of pine plantations and the relationship between these factors and stand density may differ. As an example, the pine processionary moth may benefit from lower density stands in Mediterranean pine plantations since that provides them with better temperature conditions for their development (Battisti et al., 2005; Régolini et al., 2014). Moreover, low stand densities can increase the risk of wind storm damage, especially in weak stands such as the ones commonly found in southeastern Spain. Therefore, although thinning is suggested as a suitable strategy to manage pine plantations and increase their resilience, more knowledge and effective transfer from science to management is required, as some stakeholders also point out. Thus, subsequent parts of this thesis tackled the simulation of forest and defoliator dynamics in order to increase our knowledge of these processes.

Process-based models to simulate forest and pest dynamics

Forest dynamics comprise multiple ecological processes operating on different spatial and temporal scales, for which process-based modelling approaches have great potential. These models aim to simulate the functioning of forest systems through the modelling of ecological processs and response variables such as biomass, diversity or species distribution. However, ecological process-based modelling is a relatively new field of research compared with other ones where modelling has a longer history and as such, current ecological process-based modelling studies are the early steps towards reliable future predictions, as has happened in other fields (e.g. in climatology, see Toth and Buizza, 2019).

Among other challenges, inherent uncertainty on the multiple components driving ecosystem dynamics such as future climate or management policies, as well as our limited understanding of ecosystem functioning limits our forecasting capacity. Under these circumstances, a frequently used option is to explore a wide range of contrasting scenarios and analyse the behaviour of response variables based on the best available knowledge. Therefore, current ecological process-based modelling (merely) aims to explore potential futures under alternative assumptions, rather than actually predict the future state of ecosystems (Duveneck and Scheller, 2016). Modellers make assumptions about plausible future trajectories of ecosystems or, in other words, they generate projections. Process-based —and specially forest—models cannot be validated for the future, but they can be *corroborated* (Bugmann, 2014) and evaluated with regard to their capacity to capture ecological processes, which allows us to simulate linked explanatory variables when environmental conditions change. Thus, process-based models are the best available tools to make projections under novel conditions since the robustness of empirical statistical models is limited to the conditions under which they are created (Scheller, 2018).

Building a process-based model is an iterative process of purpose formulation, information synthesis, consideration of assumptions, model implementation and analysis and further increasing model complexity in a delicate compromise for better estimations (i.e., the modelling cycle according to Railsback and Grimm, 2011). This process is highly enriching and makes science advance towards better estimations and identification of knowledge gaps and sources of uncertainty. On the other hand, the more complex a model is, the more effort is required to parameterise it, which makes it hard to set up and apply, and it increasingly becomes a black box for non-modellers and practitioners. Thus, a spurious increase in model complexity to augment the resemblance with the real system and a lack of transparency regarding model assumptions and limitations prevent modelling from serving society. Therefore, avoiding such practices is the best way to ensure that models are useful for decision-making (Saltelli et al., 2020).

In order to simulate the forest dynamics of Mediterranean pine plantations and the effects of management and climate, the spatially-explicit landscape process-based LANDIS-II model was implemented and applied in the study area. This Forest Landscape Model is a widely used model tested and calibrated for multiple landscapes and species (e.g. Hotta et al., 2021; McDowell et al., 2021; Olson et al., 2021; Vakili et al., 2021). The large community of users and developers and the continuous updates in model code ensure a constant improvement of model formulation.

Even though LANDIS-II documentation is a model that is very well documented (i.e., detailed and up-to-date user guides are available for all LANDIS-II extensions), setting up Forest Landscape Models is an arduous process which often hampers the application of these tools (Scheller, 2018). Along our journey as novel modellers, we decided to generate an overview of the whole procedure followed to implement and apply a Forest Landscape Model in a new area (Chapter 2). This process encompasses multiple steps: input data generation, parameterisation, species calibration and initial tests. By showing how we addressed these steps as novel users we hope to encourage other ones to apply Forest Landscape Models in new areas while ensuring the transparency and reproducibility of our modelling project.

The challenges encountered during the initialisation and calibration process of LANDIS-II in our study area were mainly related to the availability and findability of data to faithfully define initial conditions and calibrate species behaviour in a compromise between feasibility and uncertainty. Moreover, Mediterranean forests have some peculiarities which could be accounted for in further model developments. LANDIS-II initial vegetation conditions are defined by presence and age of species per cell (The LANDIS-II Foundation, 2018). For computational efficiency, cohorts instead of individual trees are simulated in each cell of the target landscape. Age is considered a proxy for biomass, which then defines priority access to resources (light, water) of high biomass cohorts over lower ones. Assigning age values to each cohort throughout a large area involves assumptions and data transformations, since age is rarely reported in large-scale forest inventories. Moreover, for Mediterranean species in particular, this age-biomass assumption may not always apply due to varying shape and tortuous growth patterns (Ameztegui et al., 2022). Therefore, to overcome these uncertainties we recommend models like LANDIS-II to move away from the use of age as the main cohort-level variable, but instead apply more measurable variables such as diameter or basal area. Besides this, in Chapter 2 we found that the inclusion of shrub communities in simulation experiments can be highly relevant in Mediterranean areas due to their important role as nurse plants (Castro et al., 2004; Gómez-Aparicio et al., 2008), but their calibration can be especially challenging since forest inventories often neglect these species and therefore the scarcity of data becomes even more evident.

Access to exhaustive field observations could improve accuracy regarding initialisation and calibration of Forest Landscape Models (Scheller, 2018). In this regard, and as an example of the above-mentioned required closer collaboration between researchers and managers —but also between modellers and field ecologists—collecting and sharing such data could be a direct way to bring together multidisciplinary teams of researchers and managers. This would eventually result in better model projections, more scientific information feeding decision-making processes and better understanding of managers' needs by researchers. Once a Forest Landscape Model is set up for a specific region, it can be applied to simulate the expected behaviour of a forest system under different scenarios.

In the case of our target ecosystem, transformation of pure even age pine plantation stands towards mixed and structurally diverse systems is encouraged to promote adaptation and increase resilience to disturbances and climate change (De-Dios-García et al., 2015; Messier et al., 2022). Thus, in Chapter 3, we simulated the future dynamics of pine plantations under three projected climate scenarios and four different management scenarios representing different approaches towards this goal.

Our results highlight the importance of considering changing climate and management on natural succession influencing the transformation of pine plantations to more mixed stands. We found agreement with empirical studies showing phenological changes due to climate change, which will stress summer stagnation but could increase the vegetation growing capacity during winter (Di Filippo et al., 2021; Gea-Izquierdo et al., 2011; Madrigal-González et al., 2018). Natural succession drives the shift of pine plantations towards oak woodlands under certain conditions (Dios et al., 2019; González-Moreno et al., 2011), but intensification of management interventions can play a key role speeding up their structural and compositional transformation (Millar and Stephenson, 2015; Mina et al., 2017). The transformation capacity is more pronounced in xeric areas where oaks show higher growing capacity over pines, probably due to more abundant seedling banks (Gómez-Aparicio et al., 2009).

Mediterranean pine plantations are expected to show high vulnerability to climate change due to their intrinsic characteristics and the expected modifications in the precipitation regime (Navarro-Cerrillo et al., 2019; Peñuelas and Sardans, 2021; Sánchez-Salguero et al., 2012b; Zittis et al., 2021). As such, predicting the future state of these forests is challenging due to the uncertainty in climate projections —exogeneous—, initial conditions —endogenous—and the influence of other drivers of change (drought, pests, fires). Simulating all these processes together is still far beyond our capacity as the uncertainties involved would be too high, but further experiments could focus on simulating these processes separately as an initial step. Simulation experiments addressing the incidence of more frequent extreme climatic events (i.e., droughts) could be performed by generating extreme climate time series since this aspect is currently known to be underestimated in climate projections (see Fischer et al., 2013). Besides this, and according to the concerns expressed by the stakeholder community (Chapter 1), the effects of disturbances such as fires and pests should be considered. Forest pests and fires represent important drivers influencing the biomass accumulation dynamics in Mediterranean forest ecosystems and climate change is expected to strongly alter their regimes (Seidl et al., 2017). Therefore, further research could evaluate an ensemble of scenarios considering not only climate projections but also natural disturbances and their interactions in our target ecosystem (e.g. Mina et al., 2022).

The pine processionary moth is the most common forest pest in Spanish pine plantations, showing population dynamics highly influenced by climatic factors and the spatial configuration of the landscape (Castagneyrol et al., 2014b; Gazol et al., 2019). Even though this species has long been studied, a process-based model describing its population dynamics on a detailed scale was still missing. In this case, we considered that a higher level of complexity was required in comparison to the forest system in order to faithfully simulate the internal dynamics of the species and its relationship with the tree hosts. Thus, Agent-Based Modelling was the chosen technique for this system as it allows studying emergent properties of the system as a result of interacting agents.

The *INSTAR* Agent-Based Model was designed to simulate the population dynamics of the pine processionary moth on a detailed scale in a spatially and temporally explicit manner (Chapter 4). The design and implementation process of *INSTAR* helped synthesise the available knowledge on the species and, by doing so, identify knowledge gaps on the population dynamics of the species. The available literature describing the influence of temperature on larvae development and mortality (e.g. Battisti et al., 2005; Démolin, 1969a; Gazol et al., 2019; Hoch et al., 2009) allowed the initial modelling of the species life cycle and phenology in relation to this factor.

Nonetheless, the scarcity of data on species displacement habits and biomass consumption limited us from a more realistic modelling of these processes and therefore further research on the species biology would be advisable to improve the simulation of these processes on a detailed scale. If these aspects are overcome, future distribution and impacts of the species under a context of climate change will be better simulated. Specifically, detailed information on biomass consumption rates could help improve predictions on defoliation rates. This is a highly relevant aspect regarding the impact of the species on tree hosts, since under a context of climate change the growing capacity of trees may be reduced and therefore the recovery capacity of trees may be compromised. Further work could also be undertaken to integrate *INSTAR* into a Forest Landscape Model. This would allow simulating defoliator dynamics together with detailed forest dynamics. This integration was not developed throughout this thesis as it required a wide adjustment of *INSTAR* structure since LANDIS-II and *INSTAR* work at very different spatial and temporal scales. Nevertheless, future work could be done in this regard.

The experience gained through the work with the LANDIS-II Forest Landscape Model and *INSTAR* Agent-Based Model has provided us with a good overview of process-based modelling approaches based on very different models. In contrast to long-lived widely used models with a broad community supporting them (i.e., LANDIS-II), *INSTAR* was “home-grown” designed and therefore its documentation was created by us based on model code, notes and discussions during the model design process, providing us with an exhaustive understanding of the internal functioning of the model. For LANDIS-II, on the other hand, we were completely dependent on publicly available model documentation, and our understanding of the model structure was developed through the setting up process based on available material and contact with model users and developers. This is the most common way for new users to start working with a model, and the reason why model documentation is so relevant.

Model documentation is commonly prepared through scientific articles describing model performance and application results. However, internal model details are often not fully reported in those publications, since the main focus in scientific articles is usually on model outcomes. Furthermore, model manuals are usually provided —although not always—but their quality may be limited as they are not necessarily systematically reviewed and assessed. Process-based model documentation can be especially challenging since no standard notation is able to describe them completely. Traditional equation-based models can be easily described through equations and parameter values, but process-based models usually require wordy descriptions of elements (individuals, landscape) and submodels (Railsback and Grimm, 2011). To address this problem, the ODD protocol was proposed to systematically describe Agent-Based Models (Grimm et al., 2010). Paradoxically, no standard protocol is applied for Forest Landscape Models and therefore these are rarely described in a standard and unified way, which obscures model assumptions, limits their use to closely isolated communities and ultimately restricts their potential impact to decision-making (Scheller, 2018).

The reasons for this lack of standard documentation are probably related to the intrinsic nature of the research and publication process. Model documentation and maintenance is time consuming but does not directly bring scientific rewards to their developers, who already know their models in detail and may not be able or willing to maintain high quality model documentation. This issue is similar to data generation, curation and documentation, which has been a poorly rewarded activity for a long time. Nowadays, however, data papers and data journals are well established ways to improve findability and accessibility to scientific data, as well as to give scientific credit to data providers (Candela et al., 2015; Lawrence et al., 2011). A similar approach could be followed for model documentation. Actually, model repositories such as ModeleR (Bonet et al., 2014) and documenting methodologies such as TRACE (Schmolke et al., 2010) have been proposed to document and store models, but also as a transparent way to report the whole modelling cycle, including parameterisation, calibration, uncertainty quantification or validation analyses, among others. Systematic model reporting through TRACE methodology in specialised journals or repositories could therefore be a way to increase transparency of the modelling process.

Modelling as a tool for management

The overarching purpose of this thesis was to increase the understanding of pine plantation functioning through the design and building of ecological models. In the long term, our goal is to build models which can assist the decision-making process. Even though the applicability of ecological models for management could be seen as a primary objective of any modelling project, creating models useful for decision-making requires integrating managers' needs from the beginning of the process, which rarely occurs.

Ecosystem management involves taking decisions considering multiple aspects: ecological, sociological, economic, etc. In this context, participatory modelling processes can be used to bring together communities of stakeholders which can learn from each other and combine their expertise into integrative management policies. Scientific and technical aspects have long been considered in ecological management, but clearly more attention is needed on other processes such as communication, information barriers or the actual execution and completion of plans. In order to address these issues, the participatory construction of knowledge-based models can be enriching processes to help bridge the gap between usually separated areas (e.g. forest interventions, public use, economic development) by serving as forums or interaction spaces where different profiles meet and learn from one another. The participatory modelling processes used in this thesis can be focused on the development of natural resources management plans, as they can help define priorities for management, identify potential conflicts, address disagreements, and determine knowledge gaps which may require further investigation.

Forest Landscape Models may also be useful tools for forest management, and are actually already used for this purpose in other contexts. As an example, the Forest Service in the USA routinely uses LANDIS-II for their planning and actively participates in its development. In our experience, however, the use of process-based models and other ecological models in our area is limited to sporadic collaboration between managers and researchers, often based on personal contact rather than systematic working routines. Moreover, the procedures followed to design natural resources management plans are subject to strict bureaucratic procedures, which could be hampering innovation and the assimilation of new knowledge. The result of this situation is that the management plans are very often based on outdated information and techniques. As an example, the volume allowed for harvesting is often based on simple calculations estimating the percentage of stockable volume every 10 years.

Although this thesis did not primarily aim to transfer the knowledge obtained to decision makers, we are very aware of the importance of the so-called "management-science interface". Thus, in order to demonstrate the capabilities of Forest Landscape Models for management, we present here some examples of how our simulation results could be directly used to feed into management decisions and intervention plans. On a medium scale (i.e., thousands of hectares, such as a medium size protected area), our results could help improve the mandatory zoning for protected areas in Andalusia. We have used our results to propose a new zoning of Sierra de Huétor Natural Park. This protected area is mainly occupied by dense pine plantations. Thus, we have classified the territory based on its diversification potential and therefore natural capacity to become mixed forests (Figure D.1). To this end, we have inferred that the areas with a higher diversification potential are those where our simulation predicts a shift of vegetation types from dense pine plantations to *Quercus* dominated or mixed stands. By contrast, areas with low diversification potential are those that, according to our model, remain as pine plantations at the end of the simulation period.

At a more detailed level, simulation outcomes could help prioritise local areas with a tendency to accumulate biomass in the short term, which can be highly useful to develop fire prevention plans (Figure D.2). Moreover, long-term projects linking science to practice and including an intermediate figure responsible for knowledge transfer could help answer other management questions such as where to expect forest decay or disturbance risks (e.g. see Stritih et al., 2021). Considering especially that forest management often suffers from resource scarcity, these knowledge-rich strategies should aim to identify the areas where interventions are mostly needed, while saving precious resources intervening in areas which may not need it.

Regarding other models such as Agent-Based Models, attention should be paid to the relevant level of detail for decision-making. In the case of *INSTAR*, this model could be further developed to become a tool for decision-making. As mentioned above, *INSTAR* is currently a research product which aids the research of different aspects of the species population dynamics. The knowledge generated through this exercise can be used to generate a new model explicitly aiming to assist decision-making by identifying sensitive forest areas and anticipating pest outbreaks. In order to do so, relevant variables for managers should be revised and implemented in the model. As an example, this new management-oriented model should incorporate degree of defoliation as an output since managers routinely consider this variable for planning (see Ros-Candeira et al., 2019), but more information is needed to improve the modelling of this aspect. Finally, the spatial and temporal scale of this new model should be adapted to management scales (hectares, months) instead of requiring the high detail scales currently used by *INSTAR* (trees, days).

To sum up, our results show that ecological modelling can be highly useful for management. We have obtained relevant results that increase our knowledge of the social and ecological components of pine plantations. We have also simulated the structure of these formations under several climatic and management

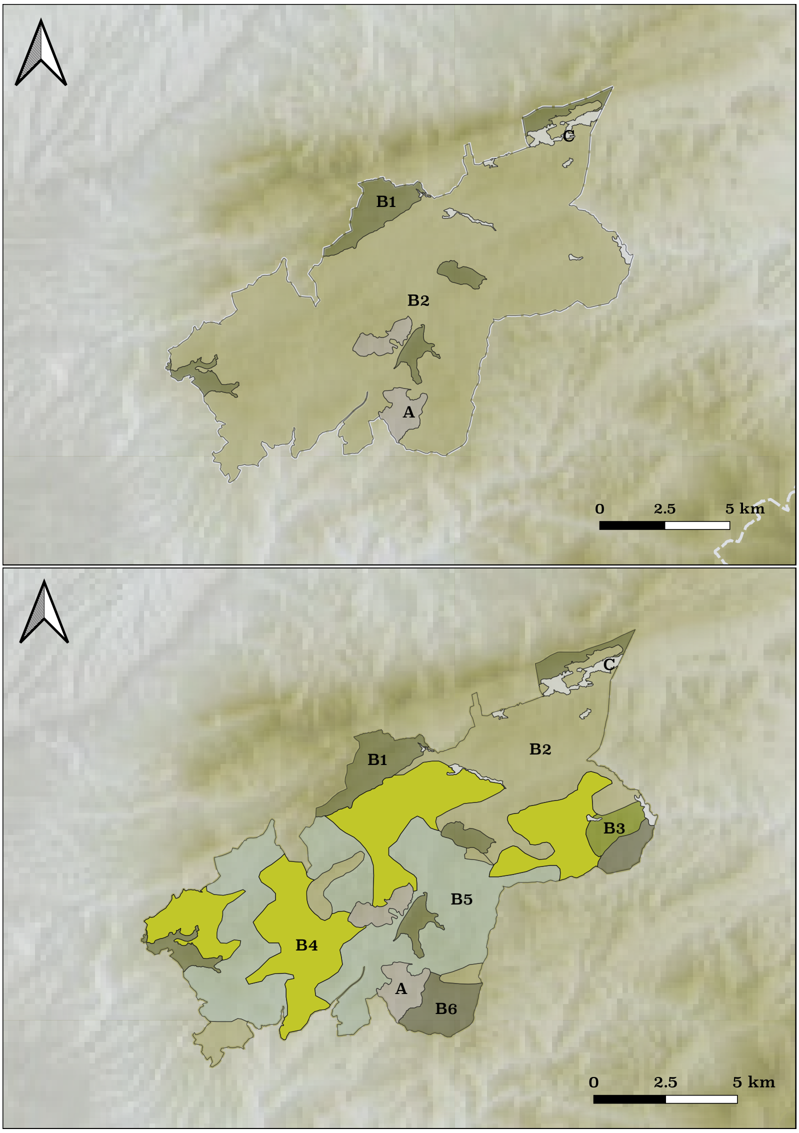


Figure D.1: Current zoning of Sierra de Huétor Natural Park (top) and proposal of new zoning (bottom). The proposal has been developed based on projected forest types by 2100 considering a conservative management scenario and climate conditions under RCP8.5 emissions scenario. A: Reserve Areas; B1: Special Regulation Areas. Areas of geological and entomological interest; B2: Special Regulation Areas - Oak woodlands; B3: Special Regulation Areas - Pine plantations with high diversification potential; B4: Special Regulation Areas - Pine plantations with intermediate diversification potential; B5: Special Regulation Areas - Pine plantations with low diversification potential; B6: Special Regulation Areas - Post-fire regeneration areas; C: Common Regulation Areas. Cultivation areas.

scenarios. Thus, we believe that this thesis has made a contribution towards a more integrated and participatory way of using modelling in forest management. However, multiple challenges need to be addressed before it becomes a routine tool in ecosystem management. These challenges involve technical aspects but also social ones, often related to lack of interaction among stakeholders and communication difficulties.

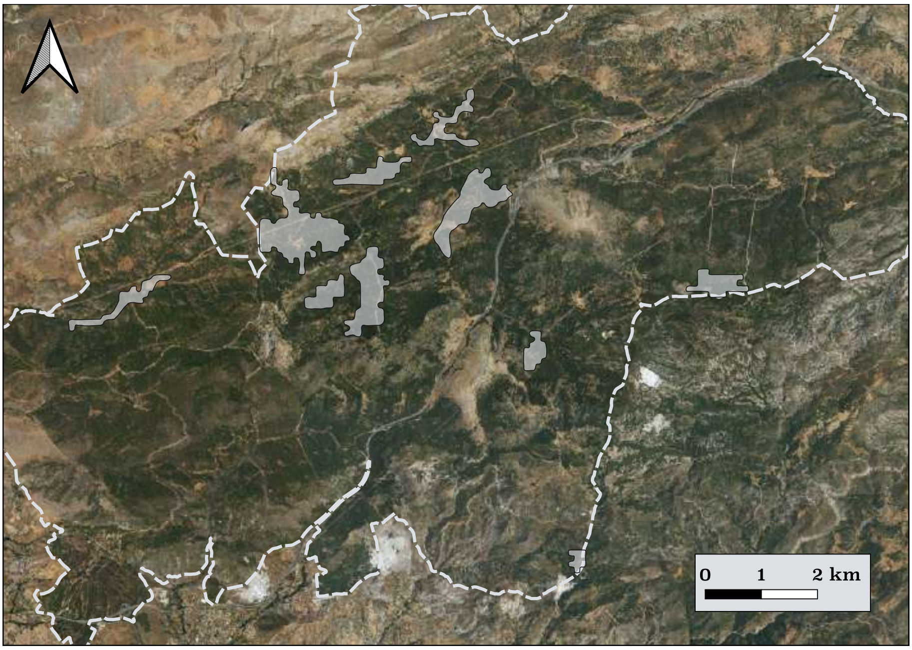


Figure D.2: Proposal of areas to intervene to prevent fire risk based on projected biomass accumulation by 2040, considering current climate conditions and no management interventions.

Conclusions

1. Knowledge-based models can be useful tools to set the scene on the management of complex socio-ecological systems. The Fuzzy Cognitive Mapping participatory technique can be used to understand the narratives of multiple stakeholders around a system or situation, therefore helping to identify potential sources of conflict and the main points of agreement. In this regard, developing a knowledge-based model can be a very convenient initial step towards the creation of communities of practice or science-policy interfaces dealing with ecosystem management.
2. The community of stakeholders within southeastern Spain pine plantations recognises stand density as a key variable describing the functioning of these ecosystems. They propose silvicultural actions to control stand density and point towards knowledge gaps in the relationship between stand density, regeneration of native vegetation and diversity.
3. In order to achieve the long-term goal of restoring pine plantations to fully functional forests, the stakeholders community identifies a need for a more integrative, multidisciplinary and socio-ecological policy in the management of these ecosystems. Stakeholders highlight drawbacks in the current governance of pine plantations, while they also call for effective knowledge transfer between science and management.
4. Our results show a high level of agreement in the narratives of researchers, managers and socio-economic agents. They express common understanding on the ecological functioning of pine plantations and also propose common management actions. In addition, they provide group-specific proposals of actions, which highlight their main concerns and interests and can serve as innovative ideas for management.

5. We advocate the need to create platforms or spaces of interaction among stakeholders to improve the management of Mediterranean pine plantations. Effective science-policy interfaces which ensure long term and fluent communication among stakeholders can be useful tools for this purpose.
6. Landscape process-based models have great potential to simulate ecosystem dynamics on multiple spatial and temporal scales with different levels of detail. The spatial component of spatially-explicit landscape process-based models and their capacity to simulate future unprecedented conditions make these models highly useful tools for ecological decision-making. However, there is a need to increase efforts in documenting and communicating complex landscape process-models as this would result in an increase in their reproducibility, application and impact.
7. Based on our simulations, climate and natural succession are identified as the main driving forces in the future development of pine plantations, while management influences forest structure and composition. Climate change is expected to cause a shift in the phenological growth pattern of Mediterranean pine plantations by reducing the growing activity during summer but anticipating the spring growing phase and enabling higher growth rates during winter.
8. In the absence of perturbations such as fires or pests, simulations show increases in total biomass over time, which would be stronger under climate change scenarios. The increase in biomass differs among species groups and climatic areas, resulting in forest type changes which are enforced by management interventions focused on the limitation of pine growth and the promotion of oaks. As a result, a shift from pine to oak woodlands is observed especially in xeric areas under intense management regimes.
9. Current available knowledge on *Thaumetopoea pityocampa* has been synthesised and integrated into *INSTAR*, an Agent-Based Model aiming to simulate the population dynamics of this species. *INSTAR* has been validated with regard to species phenology and the influence of temperature on the species lifecycle. The model behaves as expected when exposed to extreme input values. The creation of this model is an example of how available scientific information can be integrated into a research product which can help identify knowledge gaps on an ecological system.

Conclusiones

1. Los modelos basados en conocimiento pueden ser herramientas útiles para sentar las bases sobre la gestión de sistemas socio-ecológicos complejos. La técnica participativa *Fuzzy Cognitive Mapping* puede ser usada para comprender las narrativas de múltiples agentes sobre un sistema o situación, ayudando así a identificar fuentes potenciales de conflicto y principales puntos de acuerdo. En este sentido, el desarrollo de modelos basados en conocimiento puede ser un primer paso hacia la creación de comunidades de práctica o interfaces ciencia-gestión que afronten la gestión de los ecosistemas.
2. La comunidad de agentes en torno a las repoblaciones de coníferas del sudeste español distingue la densidad del pinar como una variable crucial que describe el funcionamiento de estos ecosistemas. Propone acciones silvícolas de control de la densidad y señala lagunas de conocimiento en la relación entre densidad, regeneración de vegetación nativa y diversidad.
3. Para conseguir el objetivo a largo plazo de restaurar las plantaciones de pinos a bosques completamente funcionales, la comunidad de agentes ve necesaria una política de gestión de estos ecosistemas más integradora, multidisciplinar y socio-ecológica. Los agentes subrayan obstáculos en la gobernanza actual de las plantaciones, mientras que exigen una transferencia efectiva de conocimiento entre ciencia y gestión.
4. Nuestros resultados muestran un alto grado de acuerdo en las narrativas de investigadores, gestores y agentes socio-económicos. Estos expresan una compresión común sobre el funcionamiento ecológico de las plantaciones y también proponen acciones comunes de gestión. Además, cada grupo proporciona acciones específicas, que subrayan cuáles son sus mayores preocupaciones e intereses, y pueden servir como ideas innovadoras.

5. Abogamos por la creación de plataformas o espacios de interacción entre agentes para mejorar la gestión de los pinares de repoblación. Las interfaces ciencia-gestión pueden ser herramientas útiles para este propósito, dado que aseguran una comunicación fluida y eficiente a largo plazo.
6. Los modelos de procesos de paisaje tienen gran potencial para simular las dinámicas de los ecosistemas a múltiples escalas espaciales y temporales con distinto grado de detalle. La componente espacial de los modelos de procesos espacialmente explícitos y su capacidad para simular condiciones futuras inéditas hace de estos modelos herramientas útiles para la toma de decisiones. Sin embargo, existe una necesidad de aumentar los esfuerzos en documentación y comunicación sobre modelos de procesos complejos, lo que redundaría en el aumento de su reproducibilidad, aplicabilidad e impacto.
7. Basándonos en nuestras simulaciones, el clima y la sucesión natural aparecen como los principales impulsores del desarrollo de las repoblaciones, mientras que la gestión forestal influye en la estructura y composición del bosque. Se espera que el cambio climático cambie el patrón fenológico de crecimiento de las repoblaciones, reduciendo el crecimiento en verano pero anticipando la fase de crecimiento primaveral y permitiendo mayores tasas de crecimiento durante el invierno.
8. En ausencia de perturbaciones tales como fuegos o plagas, las simulaciones muestran aumentos en la biomasa total a lo largo del tiempo, más fuertemente bajo escenarios de cambio climático. El aumento en biomasa difiere entre grupos de especies y áreas climáticas, resultando en cambios en tipos de vegetación que son reforzados por las intervenciones forestales orientadas a limitar el crecimiento de los pinos y favorecer el de las quercíneas. Como resultado, se observa un cambio de pinares a encinares, especialmente en zonas xéricas bajo intensa gestión forestal.
9. El conocimiento actual de *Thaumetopoea pityocampa* ha sido sintetizado e integrado en *INSTAR*, un modelo de agentes dirigido a simular las dinámicas poblacionales de esta especie. *INSTAR* ha sido validado en cuanto a fenología de la especie y la influencia de la temperatura en su ciclo de vida. El modelo se comporta de acuerdo a lo esperado al ser expuesto a valores de entrada extremos. La creación de este modelo es un ejemplo de cómo la información científica disponible puede ser integrada en un producto científico que ayuda a identificar lagunas de conocimiento sobre un sistema ecológico.

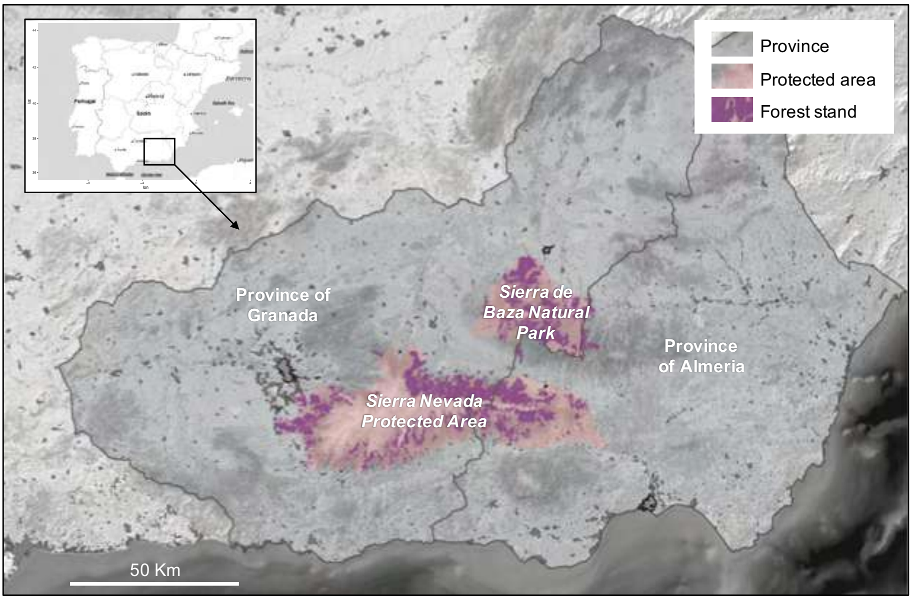
Supplementary Materials

Supplementary Material of Chapter 1

S1.1 Study area description

The pine plantations assessed in this work are located in southeastern Spain, within the Granada and Almería provinces of Andalusia region (Figure S.1). Andalusia covers 8,759,700 ha with 8.5 million inhabitants. Although it is a major biodiversity hotspot in the Mediterranean region (Estrada et al., 2011; López-López et al., 2011), eastern Andalusia suffered a very intense deforestation until the 50s of the past century. This region is especially mountainous (more than 30 % of the region is above 1,000 m a.s.l.) and the climate is mostly semiarid. Both circumstances caused a high rate of soil loss and erosion. This situation encouraged the design and implementation of a very ambitious program to plant 684,000 ha of pines. This work is focused in two protected areas that jointly share more than 10 % of the pine plantations of the region (occupying only 2.5 % of the regional area). Sierra Nevada (172,000 ha; 46,195 ha of pine plantations) and Sierra de Baza (53,600 ha; 23,800 ha of pine plantations) protected areas are the highest mountains of the Baetic mountain range, reaching 3,478 m a.s.l. They both share similar ecologic features as well as management criteria regarding pine plantations.

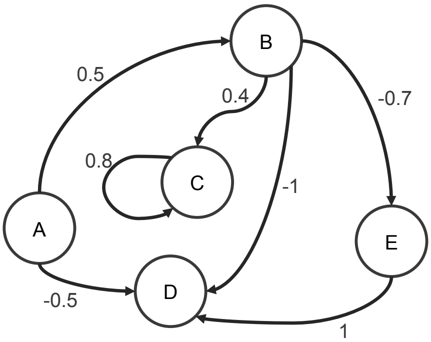
Figure S.1: Map of the study area located in the provinces of Granada and Almería in southeastern Spain. The protected areas (Sierra Nevada and Sierra de Baza) containing pine plantations are highlighted.



S1.2 FCM processing

Figure S.2: Example of Fuzzy Cognitive Map and corresponding adjacency matrix. Concepts out-degree and in-degree are included in the corresponding column and row, respectively.

MAP

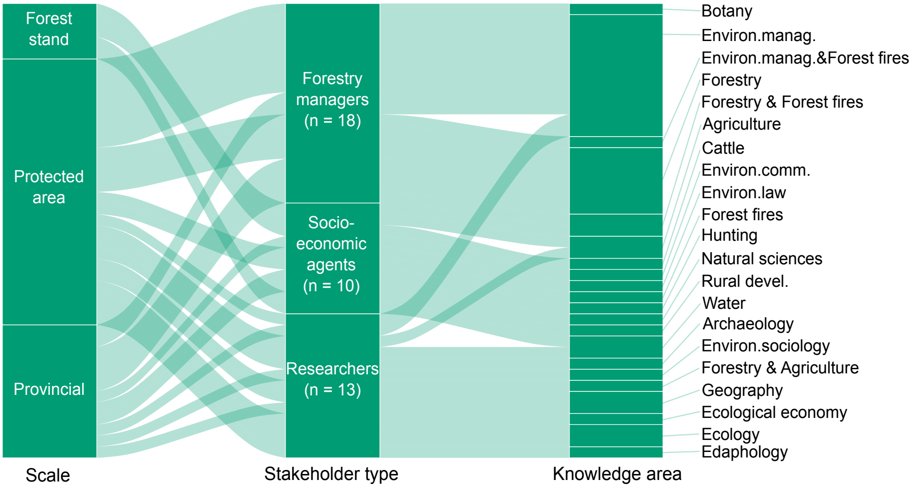


ADJACENCY MATRIX

	A	**B**	**C**	**D**	**E**	**Concepts out-degree**
A	0	0.5	0	-0.5	0	1.0
B	0	0	0.4	-1	-0.7	2.1
C	0	0	0.8	0	0	0.8
D	0	0	0	0	0	0
E	0	0	0	1	0	1
Concepts in-degree	0	0.5	1.2	2.5	0.7	

S1.3 Stakeholders' profiles

Figure S.3: Overview of stakeholder groups included in this study and their main knowledge area. In brackets, the number of individuals included in each group. ("Environ." stands for environmental; "manag." for management; "comm." for communication; and "devel." for development).



S1.4 Interviews materials

Material provided to interviewees to explain project objectives and methodology.

Collect information about pine plantations in Sierra Nevada and Sierra de Baza from expert managers, researchers and local agents

Study objectives and expected results

To collect opinions and knowledge from different types of stakeholders related to pine plantations in eastern Andalusia

Source: María Suárez Muñoz

Methodology

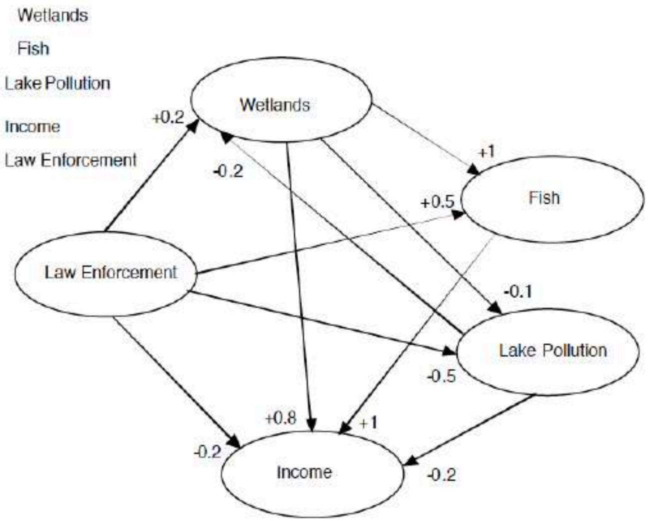
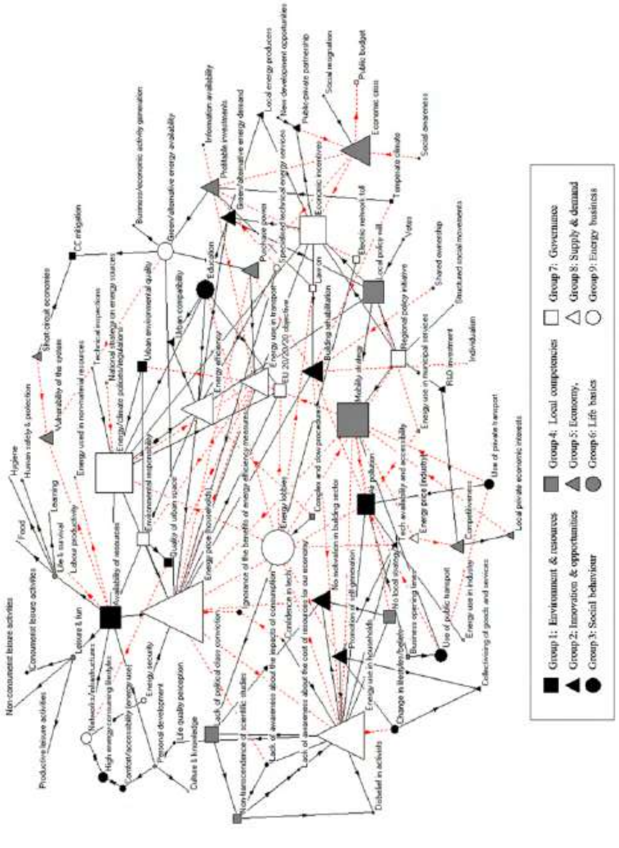


Fig. 3. Example fuzzy cognitive map.

Source: Özesmi and Özesmi, 2004



Source: Olazabal et al., 2016

STEP 1

IF WE TALK ABOUT PINE PLANTATIONS IN THIS AREA AND THEIR SURROUNDINGS, WHAT COMES UP TO YOUR MIND? HOW WOULD YOU DESCRIBE THE SITUATION?

Source: Francisco J. Bonet García (first picture), María Suárez Muñoz (second picture)

1. Write all concepts, variables or elements that come to your mind in relationship to pine plantations.
   Example: ….

2. Create a map or scheme with those elements:
    a. Identify the relationship type (+ or -):

If...	**Relationship type**
...A increases, B increases	+
...A decreases, B decreases	+
...A increases, B decreases	-
...A decreases, B increases	-

3. Define the weight of each connexion between -1 and +1, where 0 means no relationship exists and 1 means there is a strong connexion

General level	Value
Very strong relationship	**1**
Strong relationship	**0.9**
	0.8
	0.7
Intermediate relationship	**0.6**
	0.5
	0.4
Weak relationship	**0.3**
	0.2
	0.1
No relationship	**0**

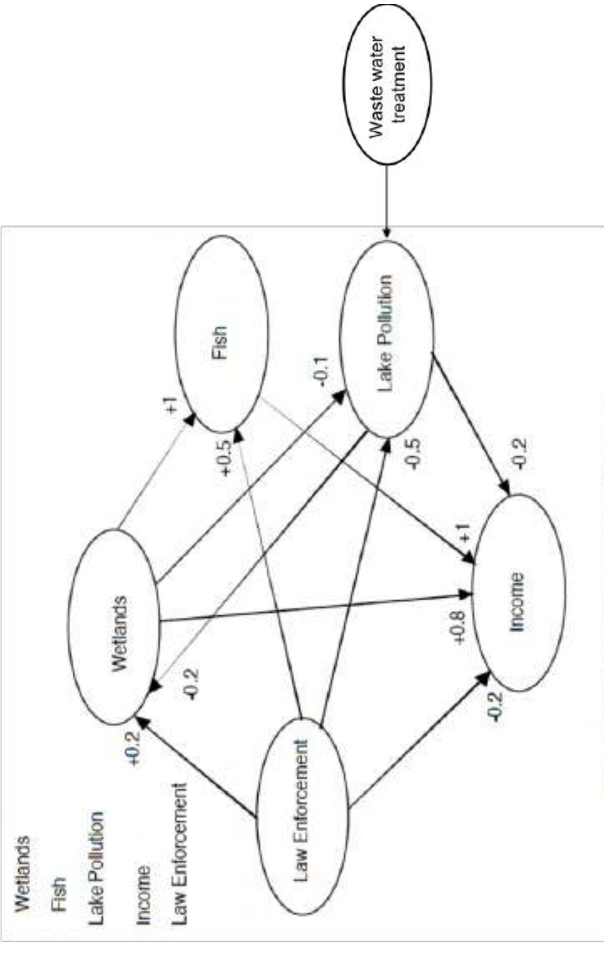


Fig. 3. Example fuzzy cognitive map.

Modified from Özesmi and Özesmi, 2004

STEP 2

WHAT COULD BE DONE TO ENHANCE THE SITUATION?

4. Write down all the elements or concepts that come to your mind.
   Example: waste water treatment

5. Add those concepts to the previous map
   a. Connect them with previous concepts
   b. Identify the type of relationship (+ or -)
   c. Define the weight of this relationship between -1 and +1
   d. If needed, add new elements to the map. Again, identify the type of relationship (+ or -) and define its weight

S1.5 Accumulation curves

Figure S.4: Accumulation curve for the full community of stakeholders.

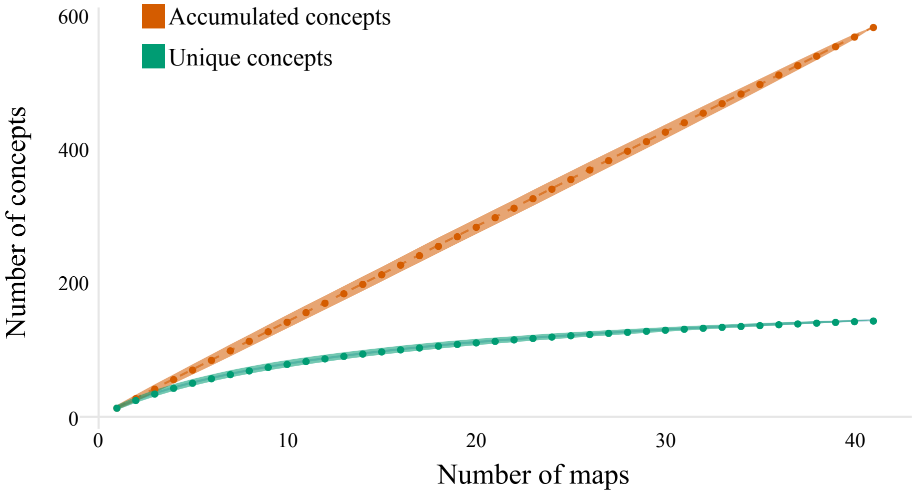


Figure S.5: Accumulation curve for the socio-economic agents.

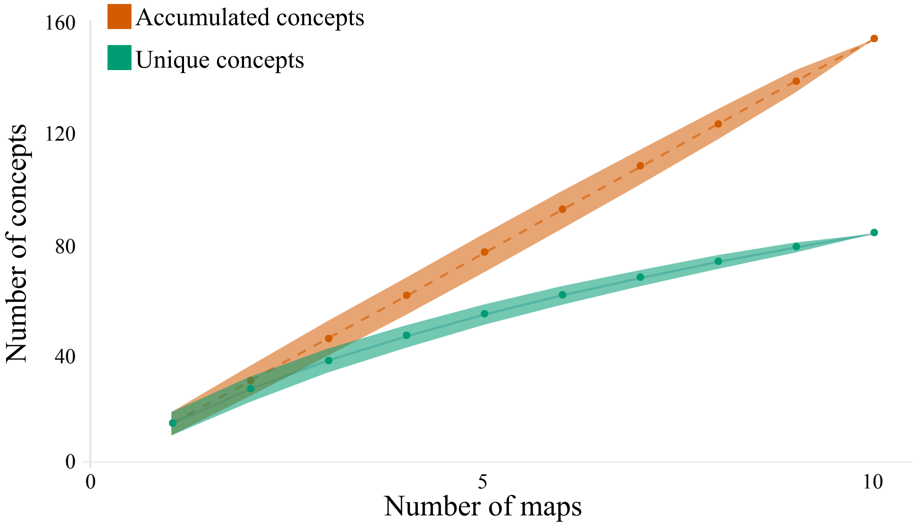


Figure S.6: Accumulation curve for the researchers.

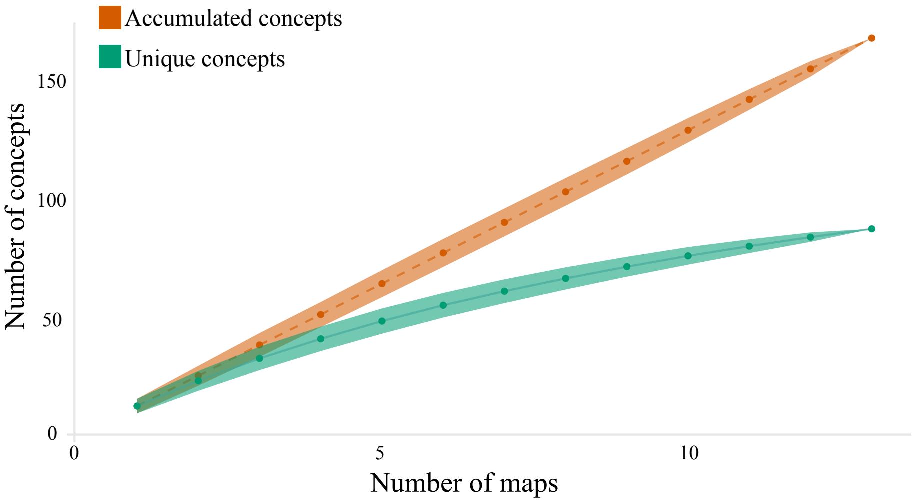
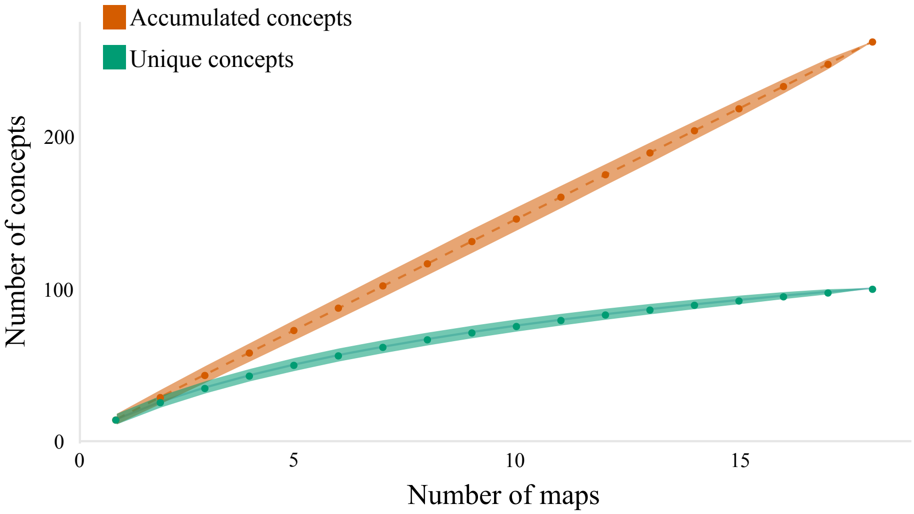


Figure S.7: Accumulation curve for the forestry managers.



Supplementary Material of Chapter 2

S2.1 Supplementary Tables

Table S.1: Age assignation table.

Species	**Height (cm)**	**Diameter (cm)**	**Cohort (years)**
P. sylvestris	< 30	< 2.5	10
P. sylvestris	30-130	< 2.5	10
P. sylvestris	> 130	< 2.5	10
P. sylvestris	> 130	2.5 - 7.5	20
P. sylvestris	> 130	7.5 - 12.5	20
P. sylvestris	> 130	12.5 - 22.5	40
P. sylvestris	> 130	22.5 - 42.5	40
P. sylvestris	> 130	> 42.5	50
P. halepensis	< 30	< 2.5	10
P. halepensis	30-130	< 2.5	10
P. halepensis	> 130	< 2.5	10
P. halepensis	> 130	2.5 - 7.5	10
P. halepensis	> 130	7.5 - 12.5	30
P. halepensis	> 130	12.5 - 22.5	40
P. halepensis	> 130	22.5 - 42.5	40
P. halepensis	> 130	> 42.5	50
P. nigra	< 30	< 2.5	10
P. nigra	30-130	< 2.5	10
P. nigra	> 130	< 2.5	10
P. nigra	> 130	2.5 - 7.5	20
P. nigra	> 130	7.5 - 12.5	30

P. nigra	> 130	12.5 - 22.5	40
P. nigra	> 130	22.5 - 42.5	40
P. nigra	> 130	> 42.5	50
P. pinaster	< 30	< 2.5	10
P. pinaster	30-130	< 2.5	10
P. pinaster	> 130	< 2.5	10
P. pinaster	> 130	2.5 - 7.5	10
P. pinaster	> 130	7.5 - 12.5	30
P. pinaster	> 130	12.5 - 22.5	40
P. pinaster	> 130	22.5 - 42.5	40
P. pinaster	> 130	> 42.5	50
Q. pyrenaica	< 30	< 2.5	10
Q. pyrenaica	30-130	< 2.5	10
Q. pyrenaica	> 130	< 2.5	10
Q. pyrenaica	> 130	2.5 - 7.5	30
Q. pyrenaica	> 130	7.5 - 12.5	40
Q. pyrenaica	> 130	12.5 - 22.5	40
Q. pyrenaica	> 130	22.5 - 42.5	50
Q. pyrenaica	> 130	> 42.5	50
Q. faginea	< 30	< 2.5	10
Q. faginea	30-130	< 2.5	10
Q. faginea	> 130	< 2.5	10
Q. faginea	> 130	2.5 - 7.5	30
Q. faginea	> 130	7.5 - 12.5	40
Q. faginea	> 130	12.5 - 22.5	40
Q. faginea	> 130	22.5 - 42.5	40
Q. faginea	> 130	> 42.5	50
Q. ilex	< 30	< 2.5	10
Q. ilex	30-130	< 2.5	10
Q. ilex	> 130	< 2.5	10
Q. ilex	> 130	2.5 - 7.5	30
Q. ilex	> 130	7.5 - 12.5	40
Q. ilex	> 130	12.5 - 22.5	40
Q. ilex	> 130	22.5 - 42.5	40
Q. ilex	> 130	> 42.5	50
Pop. nigra	< 30	< 2.5	10
Pop. nigra	30-130	< 2.5	10
Pop. nigra	> 130	< 2.5	10

Pop. nigra	> 130	2.5 - 7.5	10
Pop. nigra	> 130	7.5 - 12.5	10
Pop. nigra	> 130	12.5 - 22.5	20
Pop. nigra	> 130	22.5 - 42.5	30
Pop. nigra	> 130	> 42.5	40
J. oxycedrus	< 30	< 2.5	10
J. oxycedrus	30-130	< 2.5	10
J. oxycedrus	> 130	< 2.5	10
J. oxycedrus	> 130	2.5 - 7.5	20
J. oxycedrus	> 130	7.5 - 12.5	30
J. oxycedrus	> 130	12.5 - 22.5	30
J. oxycedrus	> 130	22.5 - 42.5	40
J. oxycedrus	> 130	> 42.5	50
J. communis	< 30	< 2.5	10
J. communis	30-130	< 2.5	10
J. communis	> 130	< 2.5	20
J. communis	> 130	2.5 - 7.5	30
J. communis	> 130	7.5 - 12.5	30
J. communis	> 130	12.5 - 22.5	40
J. communis	> 130	22.5 - 42.5	50

Table S.2: Species parameters.

Species	**Long.**	**Sex. Mat.**	**Effect. Seed Disp.**	**Max. Dist.**	**Veg. Repr. Prob**	**Sprout Age Min.**	**Sprout Age Max.**
J. communis	600	17	2	30	0.2	0	600
J. oxycedrus	600	17	2	30	0.2	0	600
P. halepensis	150	20	100	1000	0	0	0
P. nigra	400	25	100	1000	0	0	0
P. pinaster	200	20	100	1000	0	0	0
P. sylvestris	300	25	100	1000	0	0	0
Pop. nigra	90	20	240	800	1	0	50
Q. faginea	300	15	300	700	1	0	300
Q. ilex	600	15	300	700	1	0	600
Q. pyrenaica	300	15	300	700	1	0	300
short shrubs	50	8	2	30	0.2	0	50
medium shrubs	50	8	2	30	0.2	0	50
tall shrubs	50	8	2	30	0.2	0	50

Table S.2: Species parameters (cont.).

Species	**AmaxA/ AmaxB**	**FolN**	**HalfSat**	**H3**	**H4**	**PsnT Min**
J. communis	5.3/21.5	0.85	264.5	115	155	3
J. oxycedrus	5.3/21.5	0.85	264.5	115	155	3
P. halepensis	5.3/21.5	1.19	282.5	118	160	3
P. nigra	5.3/21.5	1.02	245	115	155	2
P. pinaster	5.3/21.5	1.00	245	115	155	3
P. sylvestris	5.3/21.5	1.33	266.5	110	150	1
Pop. nigra	−46/71.9	2.5	227	105	145	2
Q. faginea	−46/71.9	1.92	224.5	115	155	3
Q. ilex	5.3/21.5	1.42	199	118	160	2
Q. pyrenaica	−46/71.9	1.85	224.5	110	150	1
short shrubs	5.3/21.5	0.70	170	118	160	2
medium shrubs	5.3/21.5	0.75	175	118	160	2
tall shrubs	5.3/21.5	0.80	180	118	160	2

Table S.2: Species parameters (cont.).

Species	**PsnT Opt**	**SLW max**	**SLW Del**	**TOfol**	**k**	**Frac Fol**	**Frac BelowG**
J. communis	21	200	0	0.50	0.50	0.10	0.40
J. oxycedrus	21	200	0	0.66	0.50	0.10	0.40
P. halepensis	26	240	0	0.34	0.50	0.10	0.32
P. nigra	23	240	0	0.26	0.50	0.10	0.31
P. pinaster	25	240	0	0.24	0.50	0.10	0.32
P. sylvestris	20	240	0	0.36	0.50	0.10	0.30
Pop. nigra	31	85	0.2	1.00	0.58	0.02	0.31
Q. faginea	26	110	0.2	1.00	0.58	0.03	0.36
Q. ilex	28	150	0	0.52	0.50	0.08	0.37
Q. pyrenaica	22	80	0.2	1.00	0.58	0.03	0.34
short shrubs	27	100	0	0.75	0.50	0.10	0.35
medium shrubs	27	100	0	0.75	0.50	0.10	0.35
tall shrubs	27	100	0	0.75	0.50	0.10	0.30

S2.2 LANDIS-II and PnET-Succession species-specific parameters and sources

Definitions based on Gustafson and Miranda (2019) and Scheller et al. (2007).

Long.: Longevity, species' maximum age. Unit: years. Source: data from Serrada et al. (2008) for all species except for Junipers and shrubs. *Pinus* spp. were given a low value within the reported range, since trees growing in pine plantations are expected to grow less than under optimal conditions. *Juniperus* spp. were given the same longevity as the maximum longevity species (*Q. ilex*) to avoid biomass overestimations, given that *Juniperus* spp. have often reported longevities above 1000 years. Shrubs were given a relatively short longevity for the same reason.

Sex. Mat.: Age at which the species matures sexually. Unit: years. Source: Serrada et al. (2008), TRY database (Fitter and Peat, 1994; Kattge et al., 2020; Kleyer et al., 2008; Paula et al., 2009). Data for *Juniperus* spp. corresponding to reported sexual maturity for *J. communis* according to TRY database. *Pinus* spp. based on sources and decreased since trees growing in pine plantations are expected to reach maturity later than under optimal conditions. *Pop. nigra* based on Serrada et al. (2008). *Quercus* spp. based on Serrada et al. (2008) for *Q. ilex*. Shrubs given a default low value.

Effect. Seed Disp.: Species' effective distance for dispersing seeds. Units: meters. Source: *Juniperus* spp. data for *Juniperus occidentalis* according to Cassell et al. (2019), *Pinus* spp. data corresponding to values for *P. sylvestris* according to Newton et al. (2013). *Quercus* spp. from Cantarello et al. (2017). Shrubs given same value as *Juniperus* spp.

Max. Dist.: Species' maximum distance for dispersing seeds. Units: meters. Source: *Juniperus* spp. data for *Juniperus occidentalis* according to Cassell et al. (2019), *Pinus* spp. data corresponding to values for *P. sylvestris* according to Newton et al. (2013). *Quercus* spp. from Cantarello et al. (2017). Shrubs given same value as *Juniperus* spp.

Veg. Repr. Prob: Probability that the species resprouts. Units: none. Source: *Juniperus* spp. given a certain level of resprouting probability as *Juniperus* spp. have a weak capacity to resprout after fire (R. Navarro, pers. communication); *Pinus* spp. and *Quercus* spp. based on TRY database (Fitter and Peat, 1994; Hill et al., 2004; Kattge et al., 2020; Liebergesell et al., 2016; Sophie et al., 2005; Valladares Conde, 2005). Shrubs given a certain resprouting capacity as they represent a heterogeneous group.

Sprout Age Min: Minimum age required for the species to resprout. Units: years. Source: in the lack of data, the resprouting age was assumed to cover the whole lifespan of the species, given that it has the capacity to resprout (Vegetative reproduction probability > 0).

Sprout Age Max: Maximum age required for the species to resprout. Units: years. Source: in the lack of data, the resprouting age was assumed to cover the whole lifespan of the species, given that it has the capacity to resprout (Vegetative reproduction probability > 0).

AmaxA/AmaxB: Intercept and slope of relationship between foliar N and maximum net photosynthetic rate, such that $Amax = AmaxA + AmaxB \times FolN$. Units: $\mathrm{nmolCO_2\,g^{-1}leaf\,s{-}1}$. Source: default starting value for evergreen/deciduous species (Gustafson and Miranda, 2019). Shrubs functional groups are assumed to behave as evergreen.

FolN: Foliar nitrogen content. Units: %. Source: except for *J. communis* (same value as *J. oxycedrus*) and *Pop. nigra*, which is given the average value for *Populus* spp. according to Gustafson and Miranda (2019), all other species are based on based on TRY database (Adler et al., 2014; Adriaenssens, 2012; Atkin et al., 2015; Blonder et al., 2011; Campbell et al., 2007; Chen et al., 2013; Cornelissen, 1996; Cornelissen et al., 2003; Cornelissen et al., 2004; Craine et al., 2009; Falster et al., 2015; Fitter and Peat, 1994; Freschet et al., 2010; Garnier et al., 2006; Kattge et al., 2009; Kattge et al., 2020; Kerkhoff et al., 2006; Lukeš et al., 2013; Maire et al., 2015; Medlyn et al., 1999; Milla and Reich, 2011; Niinemets, 2001; Ogaya and Peñuelas, 2003; Ordoñez et al., 2010; Pierce et al., 2013; Quested et al., 2003; Reich et al., 2009; Reich et al., 2008; Rolo et al., 2012; Verguts et al., 2012; Walker, 2014; Wright et al., 2004).

HalfSat: Half saturation light level for photosynthesis. Units: $\mu\mathrm{mol\,m^{-2}\,s^{-1}}$. Source: based on shade tolerance by Niinemets and Valladares (2006): *Juniperus* spp. value for *J. communis*; *Pinus* spp. values for *P. nigra*, *P. sylvestris* and *P. halepensis*; *Q. ilex* value for *Q. ilex*; *Q. faginea* and *Q. pyrenaica* average value for *Q. cerris*, *Q. petraea*, *Q. pubescens* and *Q. robur* (European deciduous *Quercus* spp.) and *Pop. nigra* value for *Pop. nigra*. Shrubs given a high tolerance to shade to allow their growth under the canopy. Shade tolerance was rescaled to recommended range 100-300 (Gustafson and Miranda, 2019).

H3: Water stress parameters according to Feddes et al. (1978). Units: m pressure head. Source: based on drought tolerance by Niinemets and Valladares (2006): *Juniperus* spp. value for *J. communis*; *Pinus* spp. values for *P. nigra*, *P. sylvestris* and *P. halepensis*; *Quercus* spp. value for *Q. ilex* and *Pop. nigra* value for *Pop. nigra*. *Q. faginea* and *Q. pyrenaica* adjusted within the rest of the species range.

Shrubs given a high tolerance to drought as typical shrub species are sclerophyll drought-resistant ones. Drought tolerance was rescaled to recommended range 100-118 (Gustafson and Miranda, 2019).

H4: Water stress parameters according to Feddes et al. (1978). Units: m pressure head. Source: based on drought tolerance by Niinemets and Valladares (2006): *Juniperus* spp. value for *J. communis*; *Pinus* spp. values for *P. nigra*, *P. sylvestris* and *P. halepensis*; *Quercus* spp. value for *Q. ilex* and *Pop. nigra* value for *Pop. nigra*. *Q. faginea* and *Q. pyrenaica* adjusted within the rest of the species range. Shrubs given a high tolerance to drought as typical shrub species are sclerophyll drought-resistant ones. Drought tolerance was rescaled to recommended range 140-160 (Gustafson and Miranda, 2019).

PsnTMin: Minimum average daytime temperature for photosynthesis. Units: °C. Source: *Pinus* spp., *Quercus* spp. and *Pop. nigra* values based on coldest month and average year temperatures for each species (Serrada et al., 2008). *Juniperus* spp. given default values. Shrubs given intermediate warm values.

PsnTOpt: Optimal average daytime temperature for photosynthesis. Units: °C. Source: *Pinus* spp., *Quercus* spp. and *Pop. nigra* values based on warmest month and average year temperatures for each species (Serrada et al., 2008). *Juniperus* spp. given default values. Shrubs given intermediate warm values.

SLWmax: Maximum specific leaf weight at the top of canopy. Units: $\mathrm{g\,m^{-2}}$. Source: values given by comparison with species from the same genus/shape form. *Quercus* spp. adjusted following observations by Rafa Navarro (pers. communication).

SLWDel: Rate of change in specific leaf weight from the top of a canopy layer to the bottom. Units: $\mathrm{g^{-1}}$fol. Source: default starting value for evergreen/deciduous species (Gustafson and Miranda, 2019).

TOfol: Turnover of foliage; fraction of foliage biomass lost per year. Units: $prop.year^{-1}$. Source: calculated based on leaf longevity reported by TRY database (Adler et al., 2014; Diaz et al., 2004; Fitter and Peat, 1994; Kattge et al., 2009; Kattge et al., 2020; Wright et al., 2004). Deciduous species are given value 1, as maximum turnover should not exceed this value. Shrubs functional groups given an intermediate value within the range of all other species.

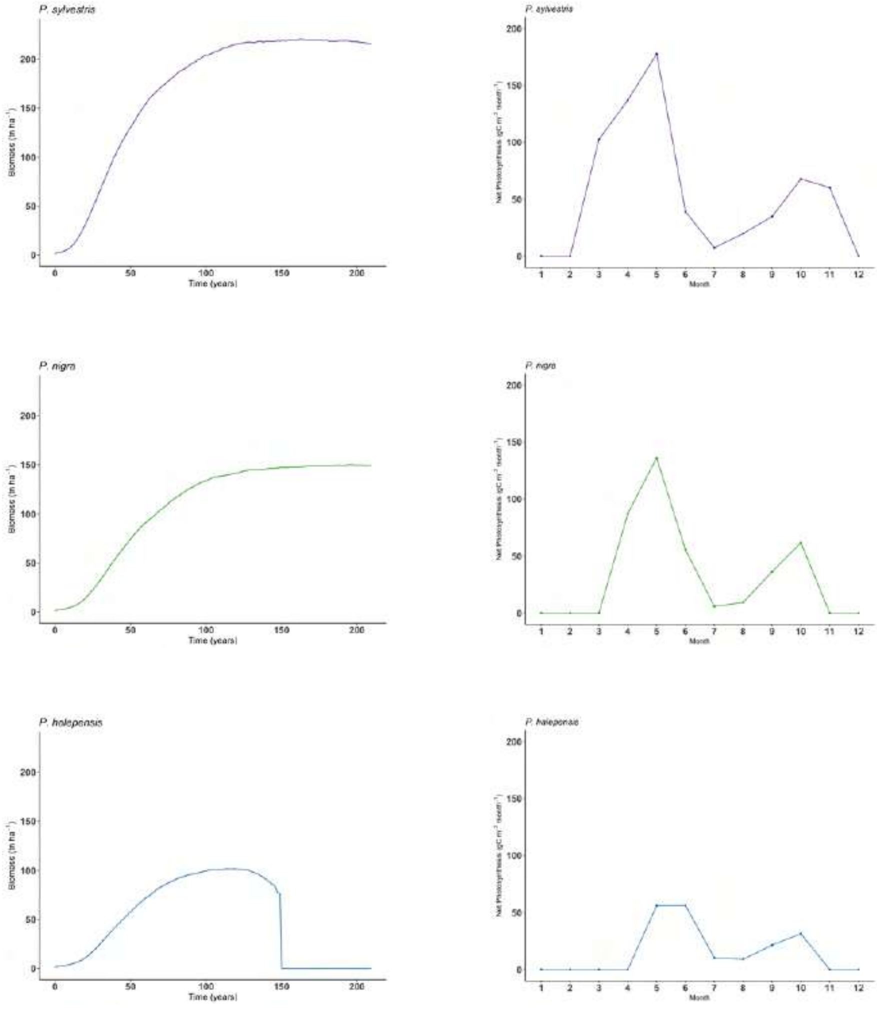
k: Canopy light attenuation constant; light extinction coefficient. Units: none. Source: default starting value for evergreen/deciduous species (Gustafson and Miranda, 2019). Shrubs functional groups are assumed to behave as evergreen.

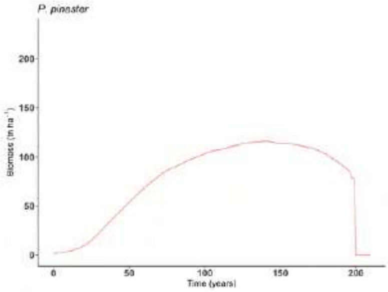
FracFol: Fraction of the amount of active woody biomass (above and belowground) that is allocated to foliage per year. Units: $prop.year^{-1}$. Source: default starting value for evergreen/deciduous species (Gustafson and Miranda, 2019). *Quercus* spp. subsequently adjusted during calibration to reduce differences in biomass estimations. Shrubs functional groups are assumed to behave as evergreen.

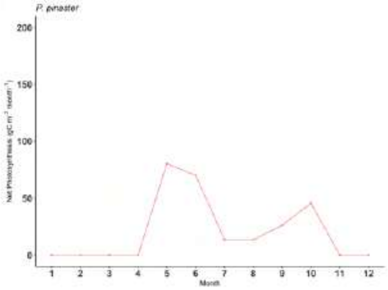
FracBelowG: Fraction of non-foliar biomass that is belowground (root pool). Allocations vary at each time step to maintain this fraction. Source: data from Montero et al. (2005) rescaled to recommended 0.3-0.4 range (Gustafson and Miranda, 2019). Shrubs functional groups are assumed to have an intermediate value.

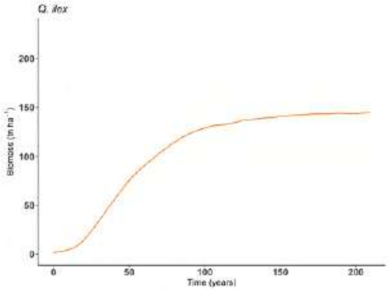
S2.3 Supplementary Figures

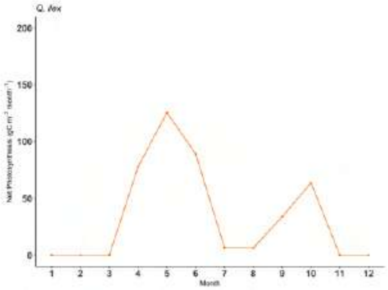
Figure S.8: Single species simulations results: total biomass (left panels) and monthly photosynthesis (right panels). Each simulation consisted on a single cohort of the corresponding species growing on a single-cell landscape (1 ha) under average historical climate corresponding to climate region 1 (see below). Monthly photosynthesis is calculated as the monthly average among all months for which the species is alive.

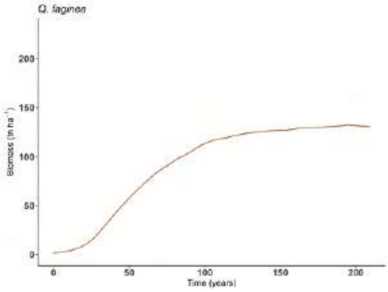


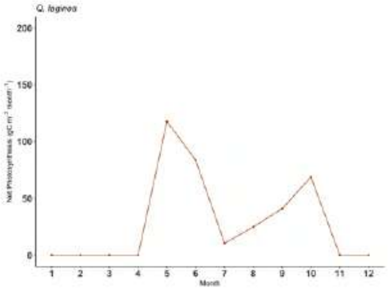

P. pinaster
Biomass (tn ha-1)
0
50
100
150
200
Time (years)

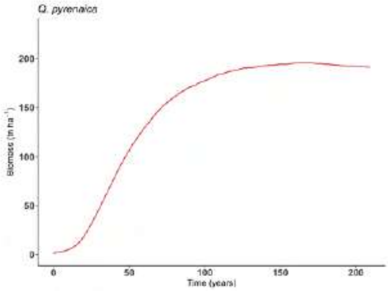

P. pinaster
Net Photosynthesis (gC m-2 month-1)
0
50
100
150
200
1
2
3
4
5
6
7
8
9
10
11
12
Month

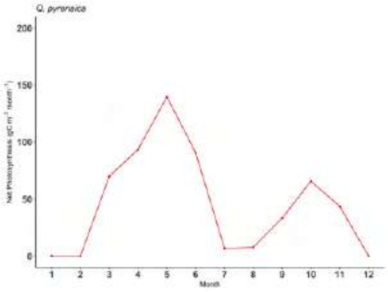

Q. ilex
Biomass (tn ha-1)
0
50
100
150
200
Time (years)

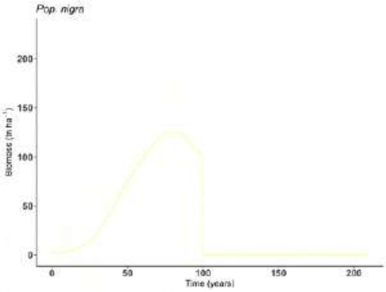

Q. ilex
Net Photosynthesis (gC m-2 month-1)
0
50
100
150
200
1
2
3
4
5
6
7
8
9
10
11
12
Month

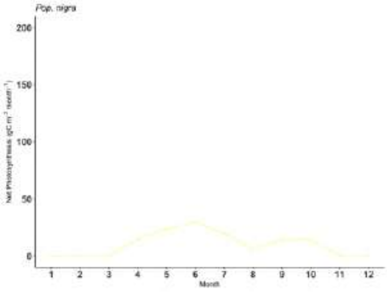

Q. faginea
Biomass (tn ha-1)
0
50
100
150
200
Time (years)

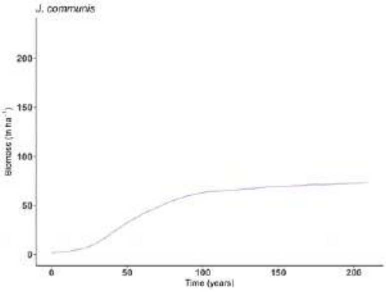

Q. faginea
Net Photosynthesis (gC m-2 month-1)
0
50
100
150
200
1
2
3
4
5
6
7
8
9
10
11
12
Month

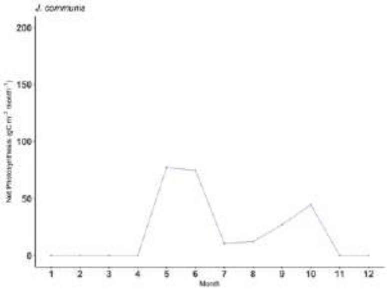

Q. pyrenaica
Biomass (tn ha-1)
0
50
100
150
200
Time (years)

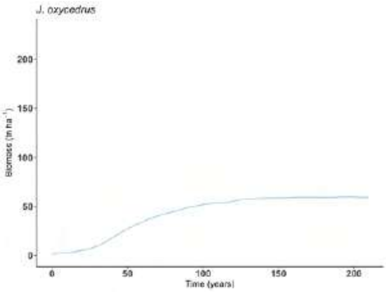

Q. pyrenaica
Net Photosynthesis (gC m-2 month-1)
0
50
100
150
200
1
2
3
4
5
6
7
8
9
10
11
12
Month


Pop. nigra
Biomass (tn ha-1)
0
50
100
150
200
Time (years)


Pop. nigra
Net Photosynthesis (gC m-2 month-1)
0
50
100
150
200
1 2 3 4 5 6 7 8 9 10 11 12
Month


J. communis
Biomass (tn ha-1)
0
50
100
150
200
Time (years)


J. communis
Net Photosynthesis (gC m-2 month-1)
0
50
100
150
200
1 2 3 4 5 6 7 8 9 10 11 12
Month


J. oxycedrus
Biomass (tn ha-1)
0
50
100
150
200
Time (years)

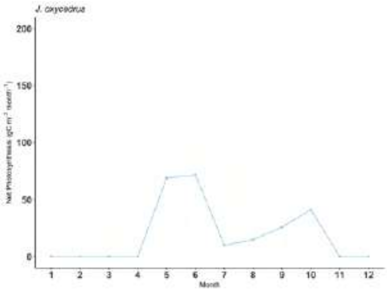
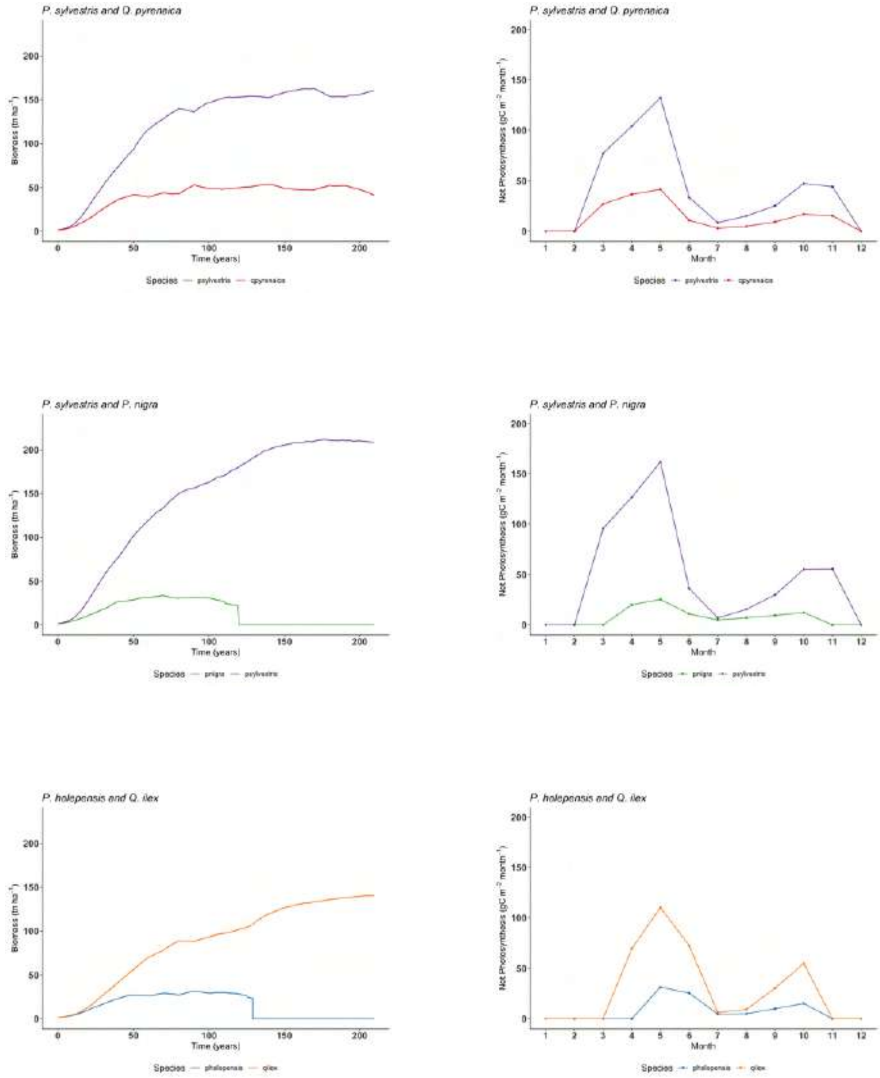

J. oxycedrus
Net Photosynthesis (gC m-2 month-1)
0
50
100
150
200
1 2 3 4 5 6 7 8 9 10 11 12
Month

Figure S.9: Groups of species simulation results: total biomass (left panels) and monthly photosynthesis (right panels). Each simulation consisted on one cohort of each of the corresponding species growing on a single-cell landscape (1 ha) under average historical climate corresponding to climate region 1 (see below). Monthly photosynthesis is calculated as the monthly average among all months for which the species is alive. Note that in the shrubs simulation (last two panels) short, medium and tall shrubs are present, with very similar values of biomass and photosynthesis rates.



P. sylvestris and Q. pyrenaica

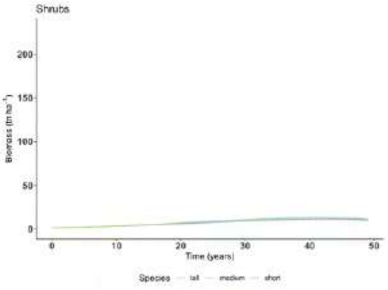
P. sylvestris and Q. pyrenaica

P. sylvestris and P. nigra

P. sylvestris and P. nigra

P. halepensis and Q. ilex

P. halepensis and Q. ilex


Shrubs
200
150
100
50
0
Biomass (tn ha⁻¹)
0
10
20
30
40
50
Time (years)
Species
tall
medium
short

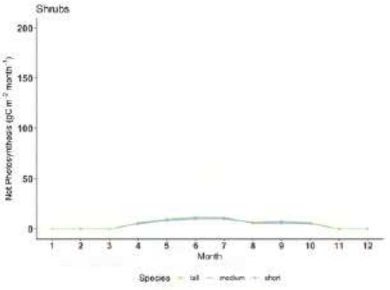

Shrubs
200
150
100
50
0
Net Photosynthesis (gC m⁻² month⁻¹)
1
2
3
4
5
6
7
8
9
10
11
12
Month
Species
tall
medium
short

Figure S.10: Comparison of simulated (lines) *versus* observed (dots) Relative Growth Rates (RGR) relative to biomass. For the simulation results, the RGR corresponds to the slope coefficient in the linear model biomass as a function of age. The RGR observation data correspond to NFI data from single-species dominated plots within Sierra Nevada. Biomass was calculated from single-tree measurements using allometric equations from Montero et al. (2005). Observed RGR was calculated as: $RGR = \frac{\ln biomass_{NFI3} - \ln biomass_{NFI2}}{time_{NFI3} - time_{NFI3}}$

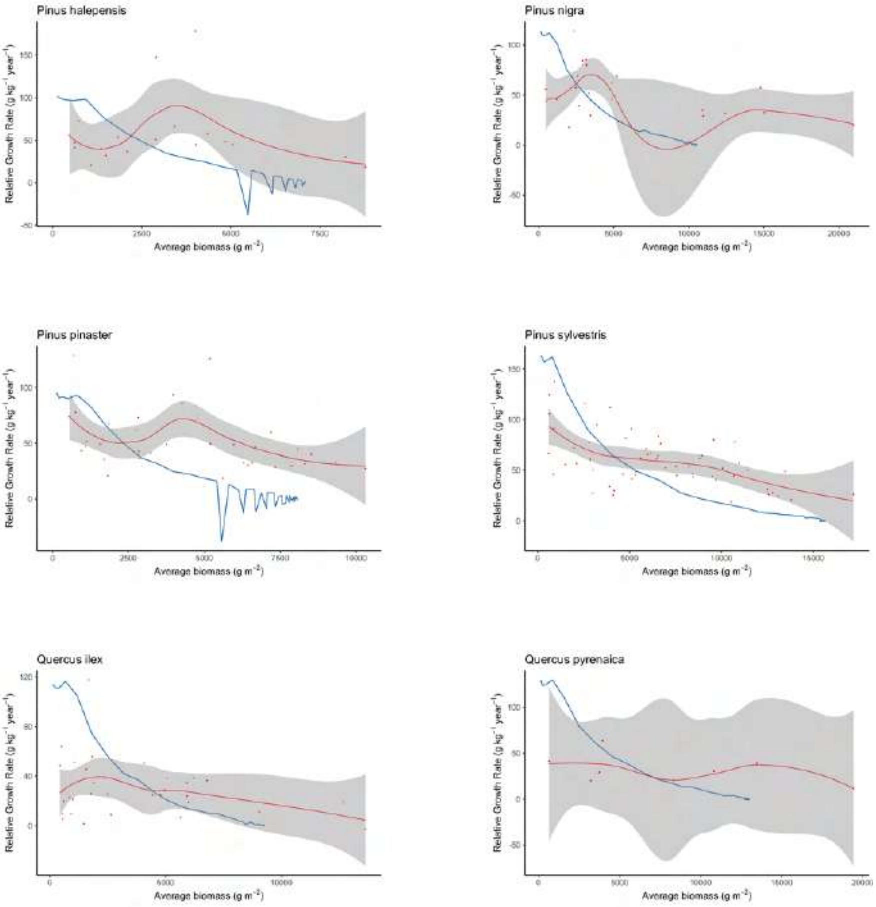


Figure S.11: Temperature conditions for climate regions.

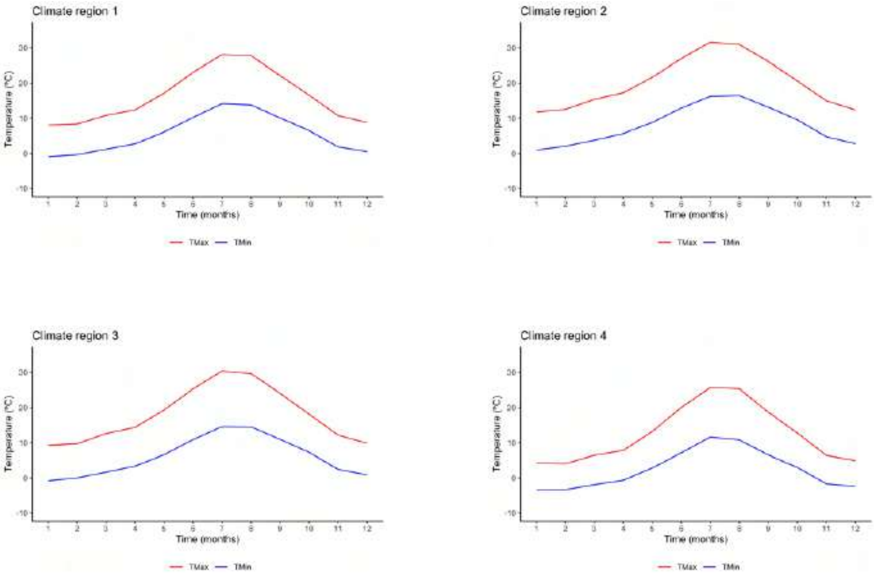


Figure S.12: Precipitation conditions for climate regions.

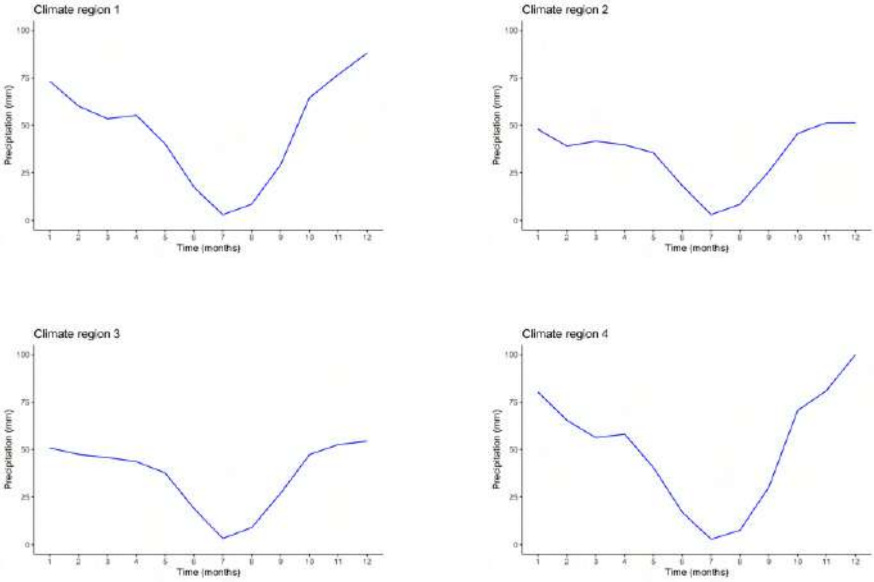


Figure S.13: PAR conditions for climate regions.

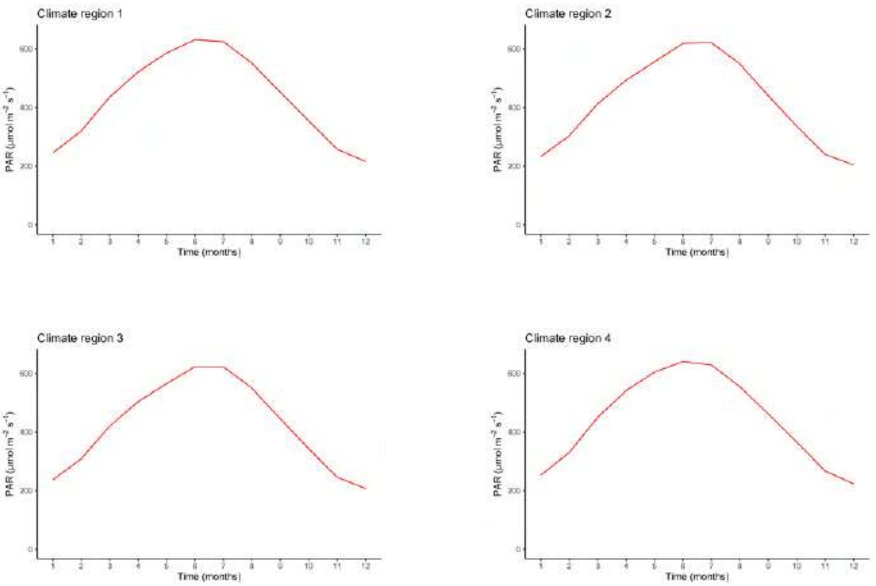
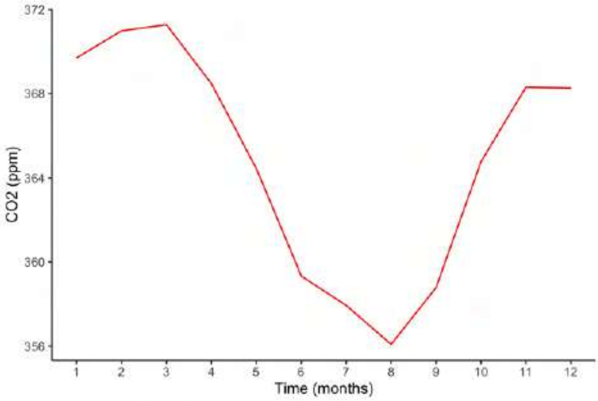


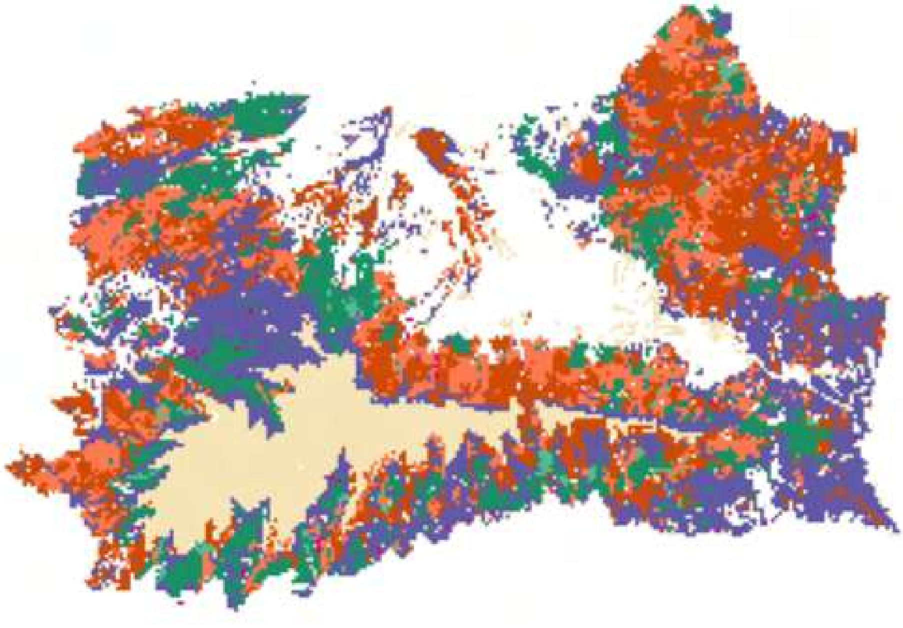
Figure S.14: CO2 conditions for all climate regions.



Supplementary Material of Chapter 3

S3.1 Initialization and calibration of LANDIS-II and PnET-Succession extension

Figure S.15: Current distribution of forest types.



To calibrate species-specific parameters, we compared site-level simulations with empirical biomass estimations. Site-level simulations are those where a single cohort of each species is grown on one-cell. Further details on these single cell simulations can be found in Suárez-Muñoz et al. (2021). Following the approach recommended by the model developers, simulated growth patterns for each species were compared with species biomass estimations to calibrate the most influential parameters (Gustafson and Miranda, 2021).

Empirical biomass values were derived from silvicultural schemes proposed by Campos and Díaz-Balteiro (2015) for *Pines* spp. (*P. nigra*, *P. halepensis*, *P. pinaster* and *P. sylvestris*), *Quercus* spp. (*Q. ilex*, *Q. faginea* and *Q. pyrenaica*) and *Juniperus oxycedrus*. These schemes were produced by extensive field observations and literature revision and correspond to the expected growth patterns of the species in the Andalusia region, southern Spain. The proposed silvicultural schemes provide stand density and average diameter for each species rotation period.

We estimated aboveground biomass using allometric equations published by Montero et al. (2005), which were developed for the most common tree species growing in Spain. Moreover, other biomass estimations were also considered for *P. sylvestris* (Rojo y Alboreca and Montero González, 1996), *P. nigra* (Bautista et al., 2001) and *P. halepensis* (Montero et al., 2000). For the tree species with no merchantable value or considered of minor importance (*Populus nigra*, *Juniperus communis* and shrubs), silvicultural schemes were only available for an extremely short rotation period corresponding to non-natural growth patterns (e.g. 14 years for *Pop. nigra*) or data was not available whatsoever. We therefore parameterized such species comparatively to other species of the same genus (Cantarello et al., 2017; Cassell et al., 2019; Loudermilk et al., 2013) and from expert's knowledge.

Calibration of the most influential species parameters was done following Gustafson and Miranda (2021) and PnET-Succession developers' recommendations (M. Duveneck, E. Gustafson, pers. comm.). In general terms, HalfSat was rescaled and FolN was tuned to adjust simulated species growth patterns to observations. Besides, FracFol, SLWmax and FracBelowG were also calibrated. Moreover, PsnTMax, as well as LeafOnMinT, were given species-specific values, while PsnTMin was modified correspondingly to simulate growth limitation due to extremely high or low temperatures. Finally, parameter EstRad, denoting limitation to establishment due to light conditions, was also incorporated to the list of species-specific parameters by assigning the maximum fRad value obtained in the calibration runs (Gustafson and Miranda, 2021).

Species-specific parameters required for both LANDIS-II and PnET-Succession are provided in Table S.3. Moreover, Figures S.16-S.22 show the growth curve of each species compared to empirical biomass values used for the calibration. Details for each species are provided in each figure caption.

Table S.3: LANDIS-II and PnET-Succession extension species parameters. FolN: Nitrogen foliar content; HalfSat: Photosynthesis half saturation light level; PsnTMin, PsnTOpt, PsnTMax: photosynthesis minimum, optimal and maximum average daytime temperature; LeafOnTMin: Minimum temperature for active growing season; H3, H4: Water stress parameters according to Feddes et al. (1978); SLWmax: Maximum specific leaf weight at the top of canopy; Tofol: foliage turnover; FracFol: Foliage fraction; FracBelowG: Fraction of non-foliar biomass below ground (Gustafson and Miranda, 2021).

Species	**Long.** (years)	**Sex. Mat.** (years)	**Effect. Seed Disp.** (m)	**Max. Dist.** (m)	**Veg. Repr. Prob**	**Sprout Age Min.** (years)	**Sprout Age Max.** (years)
J. communis	600	17	2	30	0.2	0	600
J. oxycedrus	600	17	2	30	0.2	0	600
P. halepensis	150	20	100	1000	0	0	0
P. nigra	400	25	100	1000	0	0	0
P. pinaster	200	20	100	1000	0	0	0
P. sylvestris	300	25	100	1000	0	0	0
Pop. nigra	90	20	240	800	1	0	50
Q. faginea	300	15	300	700	1	0	300
Q. ilex	600	15	300	700	1	0	600
Q. pyrenaica	300	15	300	700	1	0	300
short shrubs	80	8	2	30	0.2	0	50
medium shrubs	80	8	2	30	0.2	0	50
tall shrubs	80	8	2	30	0.2	0	50

Table S.3: LANDIS-II and PnET-Succession extension species parameters (cont.).

Species	**FolN** (%)	**HalfSat** (μmol $\mathrm{m^{-2}\,s^{-1}}$)	**EstRad** (prop.)	**Psn TMin** (℃)	**Psn TOpt** (℃)	**Psn TMax** (℃)
J. communis	0.80	421	0.60	5	21	38
J. oxycedrus	0.80	421	0.60	5	21	38
P. halepensis	2.60	450	0.58	5	26	39
P. nigra	2.90	390	0.61	4	23	38
P. pinaster	2.60	390	0.62	5	25	39
P. sylvestris	2.30	425	0.59	3	20	38
Pop. nigra	2.70	362	0.63	4	31	38
Q. faginea	3.00	358	0.64	5	26	39
Q. ilex	2.90	317	0.68	4	28	40
Q. pyrenaica	3.00	358	0.63	3	22	38
short shrubs	0.70	271	0.69	4	27	40
medium shrubs	0.75	279	0.69	4	27	40
tall shrubs	0.80	287	0.68	4	27	40

Table S.3: LANDIS-II and PnET-Succession extension species parameters (cont.).

Species	**LeafOn MinT** (℃)	**H3** (m)	**H4** (m)	**SLW max** ($\mathrm{g\,m^{-2}}$)	**TOfol** ($prop.\ year^{-1}$)	**Frac Fol** ($prop.\ year^{-1}$)	**Frac BelowG** (prop.)
J. communis	3	115	155	200	0.50	0.07	0.35
J. oxycedrus	3	115	155	200	0.66	0.07	0.35
P. halepensis	3	118	160	240	0.34	0.08	0.315
P. nigra	2	115	155	240	0.26	0.06	0.31
P. pinaster	3	115	155	240	0.24	0.07	0.315
P. sylvestris	1	110	150	240	0.36	0.06	0.31
Pop. nigra	2	105	145	85	1.00	0.023	0.31
Q. faginea	3	115	155	160	1.00	0.02	0.33
Q. ilex	2	118	160	180	0.52	0.04	0.34
Q. pyrenaica	1	110	150	100	1.00	0.022	0.32
short shrubs	2	118	160	100	0.75	0.09	0.32
medium shrubs	2	118	160	100	0.75	0.09	0.32
tall shrubs	2	118	160	100	0.75	0.09	0.30

Figure S.16: Growth pattern for *P. halepensis*. Green continuous line shows simulated values; lines with points show empirical biomass estimations for two different site qualities for Andalusia (based on Campos and Díaz-Balteiro, 2015) and Spain (based on Montero et al., 2000).

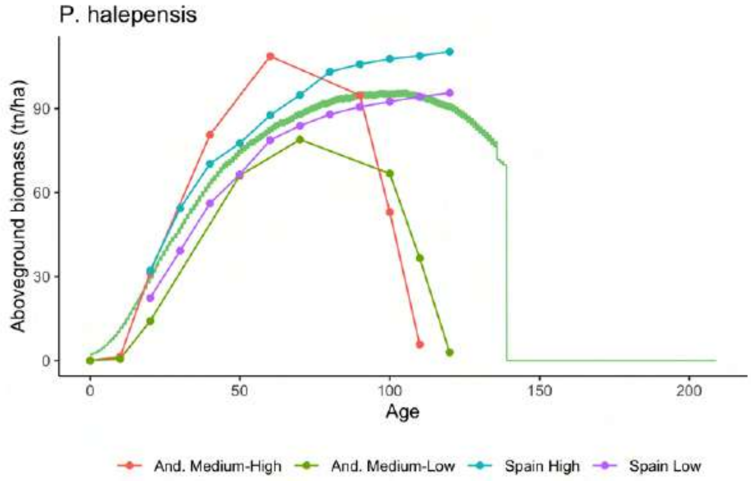


Figure S.17: Growth pattern for *P. nigra*. Green continuous line shows simulated values; lines with points show biomass estimations at two different site qualities for Andalusia (based on Campos and Díaz-Balteiro, 2015) and Cazorla (based on Bautista et al., 2001).

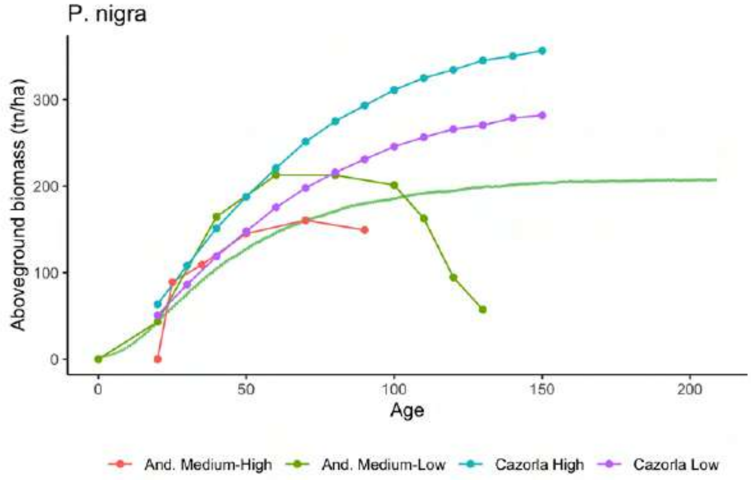


Figure S.18: Growth pattern for *P. pinaster*. Green continuous line shows simulated values; lines with points show biomass estimations at two different site qualities for Andalusia (based on Campos and Díaz-Balteiro, 2015).

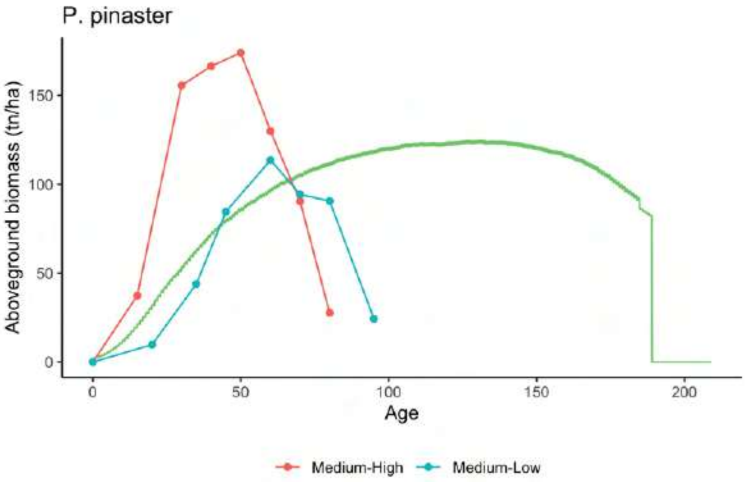


Figure S.19: Growth pattern for *P. sylvestris*. Green continuous line shows simulated values; lines with points show biomass estimations at two different site qualities for Andalusia (based on Campos and Díaz-Balteiro, 2015) and Guadarrama (based on Rojo y Alboreca and Montero González, 1996).

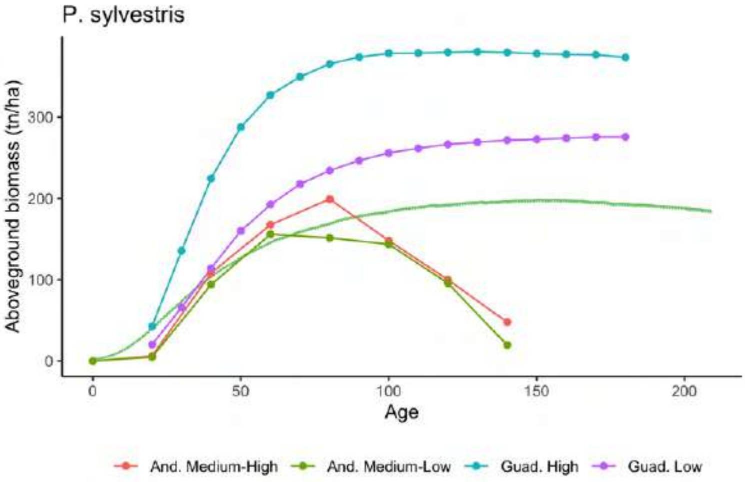


Figure S.20: Growth pattern for *Q. ilex*. Green continuous line shows simulated values; lines with points show biomass estimations at two different site qualities for Andalusia (based on Campos and Díaz-Balteiro, 2015). We calibrated parameters with medium-high quality curves because these conditions represent better what is found in our study area.

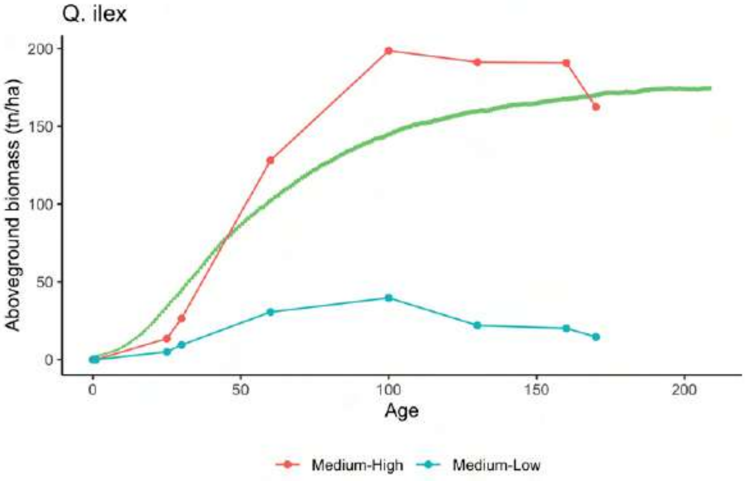


Figure S.21: Growth pattern for *Q. pyrenaica*. Green continuous line shows simulated values; lines with points show biomass estimations for high and low-high forests in Andalusia (based on Campos and Díaz-Balteiro, 2015).

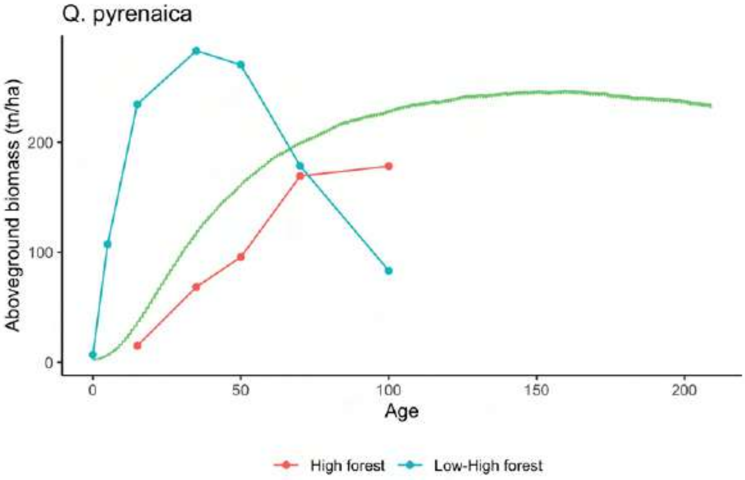
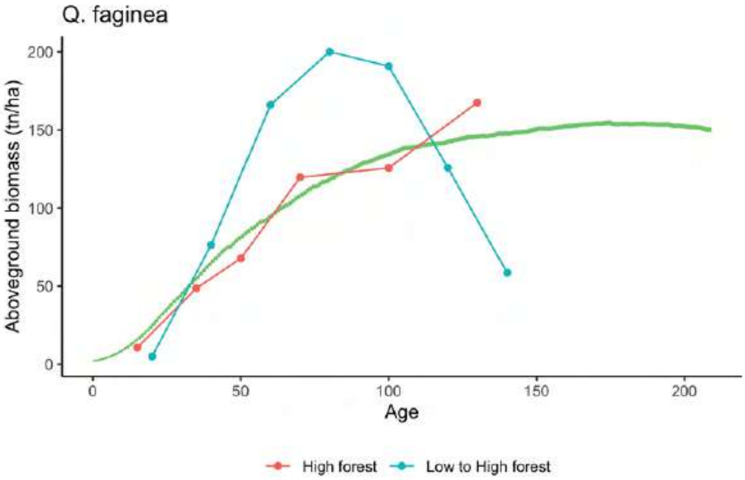


Figure S.22: Growth pattern for *Q. faginea*. Green continuous line shows simulated values; lines with points show biomass estimations for high and low-high forests in Andalusia (based on Campos and Díaz-Balteiro, 2015).



S3.2 Climate scenarios

S3.2.1 Climate data sources and analysis

Precipitation, maximum and minimum temperature monthly data were obtained from Karger et al. (2020). These data provide monthly precipitation and temperature for four downscaled global circulation models at 0.049 ° resolution for a historical period (1950-2005) and two future projections (2005-2100): RCP4.5 and RCP8.5.

The historical period data were analysed by comparing them to data from meteorological stations located in the study area (Figures S.23-S.25). Precipitation data were further bias-corrected through quantile mapping (Lucatero et al., 2018; Teutschbein and Seibert, 2012, see description of the methodology below).

Figure S.23: Comparison of maximum temperature observed and modelled for four different global circulation models.

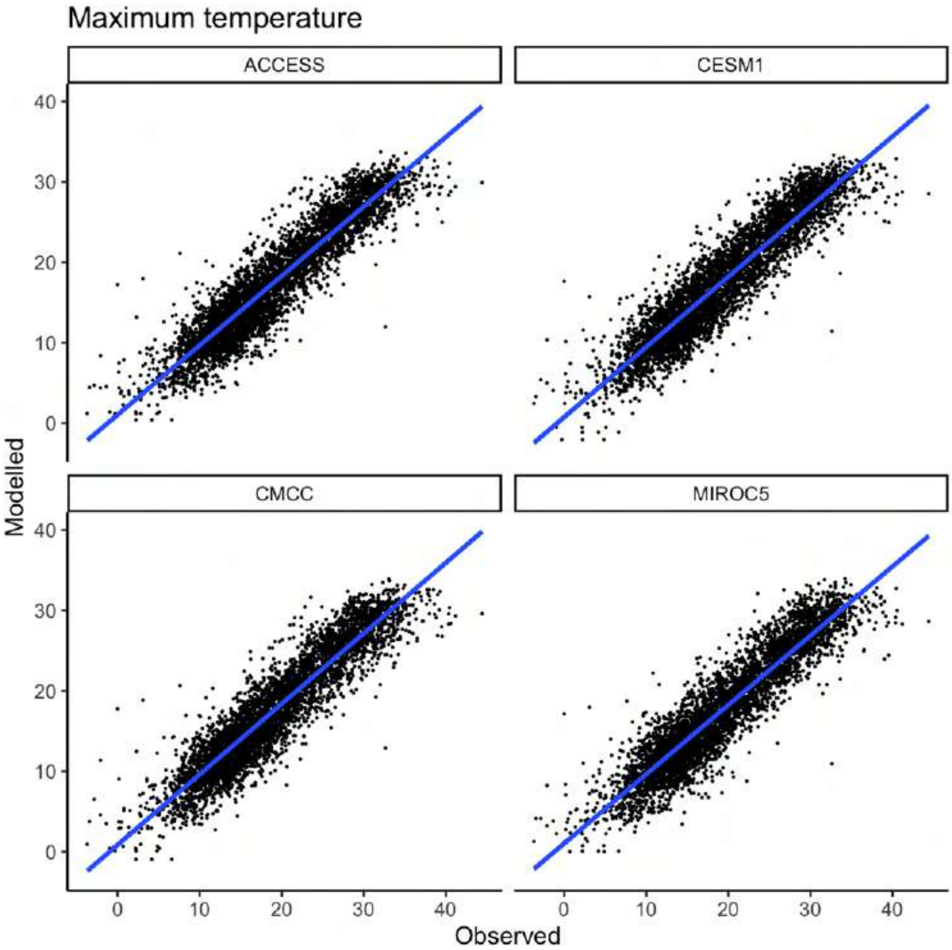


Figure S.24: Comparison of minimum temperature observed and modelled for four different global circulation models.

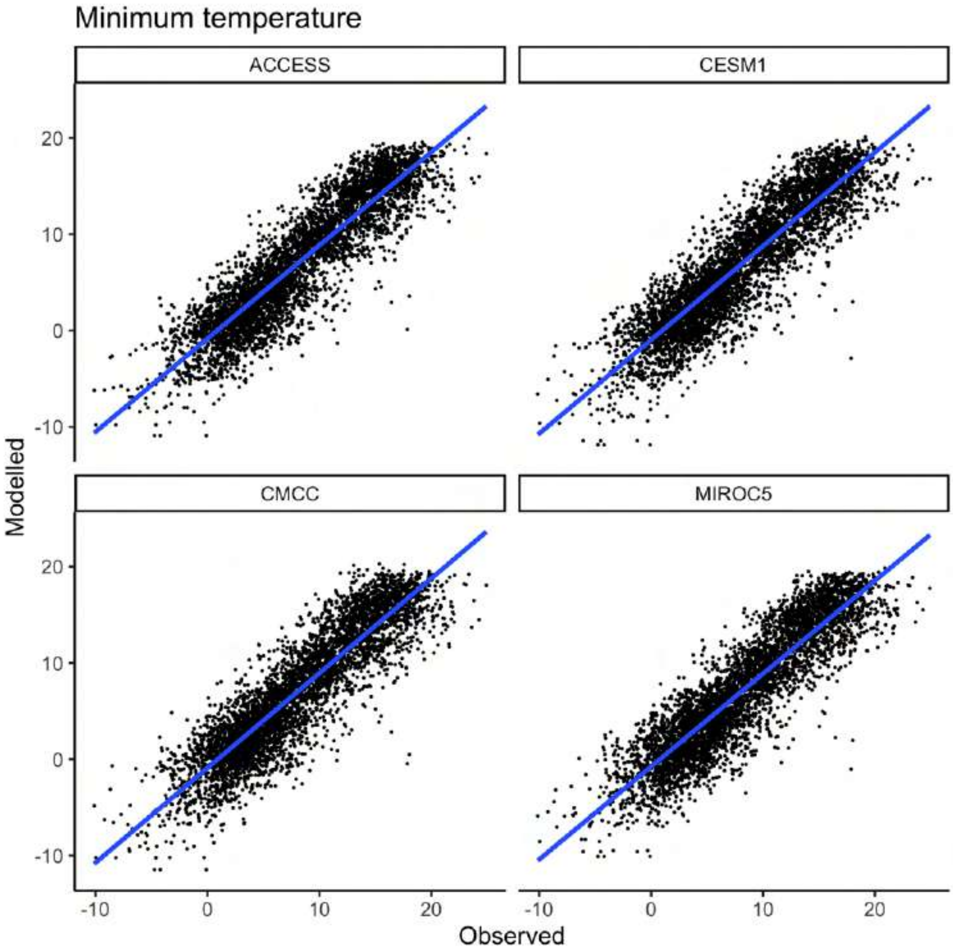
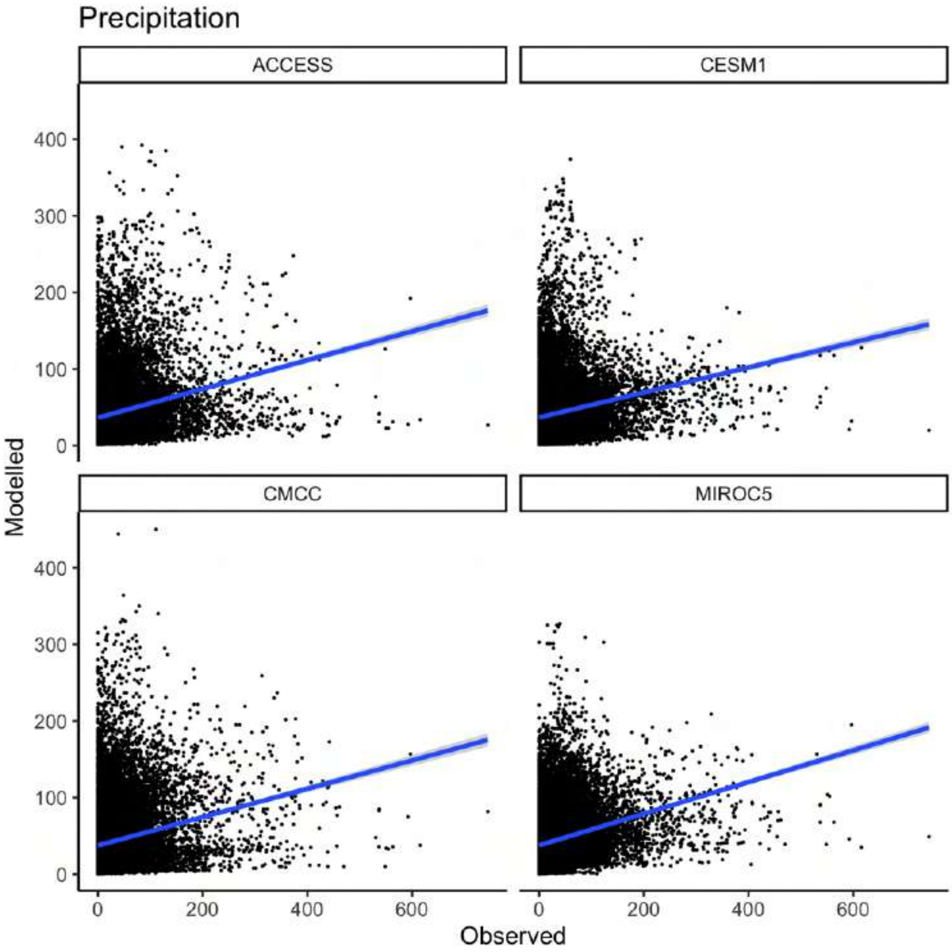


Figure S.25: Comparison of precipitation observed and modelled for four different global circulation models.



Precipitation bias-correction

Bias-correction of precipitation data was done based on precipitation observations from 98 meteorological stations within the study area. Daily precipitation data were analysed and those stations which had missing data were filled if possible in order to have as many data as possible which increases the success of the bias correction methodology. Since monthly corrections are to be established for each climate region, the data available for each one of them are scarce in some cases. Thus, for those days of negligible precipitation, each missing value was replaced by the average value among the data from the meteorological stations within the same climate region. This filling was only applied when there were at least 5 stations with data for that day, and the average among them was 2 mm or less. By doing so, a higher number of values are available for the bias-correction, which improves its accuracy, but large errors are avoided as only null or low precipitation days are filled up. Once the data filling was completed, monthly precipitation was calculated for each station. Finally, for each month in the series (1950-2005) the average precipitation among all climate stations within the region was calculated and compared with the average modelled data for each climate model. After this process, we obtained 49 or more data for each month for climate regions 1, 2 and 3 (corresponding to the years 1950 to 2006), while climate region 4 remained with of 31 values per month as in this region —at the highest elevation—very few meteorological stations are found. Nevertheless, this region is mainly non-forested and therefore its influence on forest dynamics is limited.

After data preparation, we applied a quantile mapping method, which is commonly used as a bias correction method and generally leads to good performance compared to other simple bias correction methods (Crochemore et al., 2016). In this case, quantile mapping consists of correcting the values according to their location in the monthly probability density function. It applies different corrections coefficient to each value within one month depending on their frequency of occurrence. Therefore, low values and high values are corrected differently. Moreover, the correction is independent for each month of the year. Further details of the quantile mapping method can be found in Teutschbein and Seibert (2012). Figures S.26 and S.27 show the seasonal pattern of modelled data and observations before and after the correction for each climate region, respectively.

Figure S.26: Observed (OBS) and modelled (MOD) monthly precipitation for each climate region before applied bias-correction method. The different lines for MOD indicate the different global circulation models evaluated.

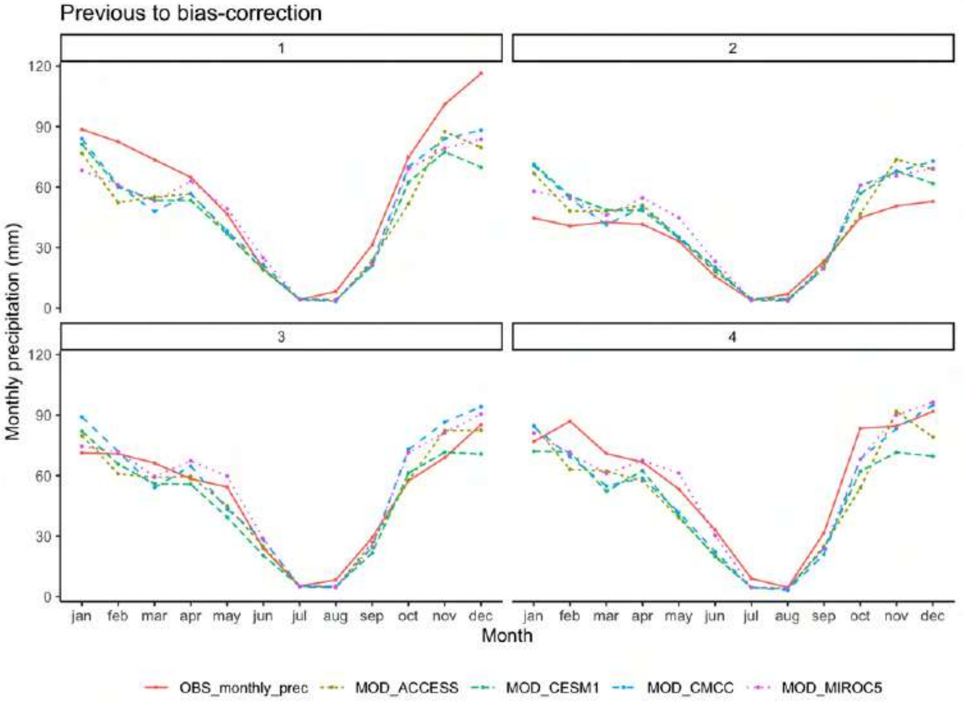
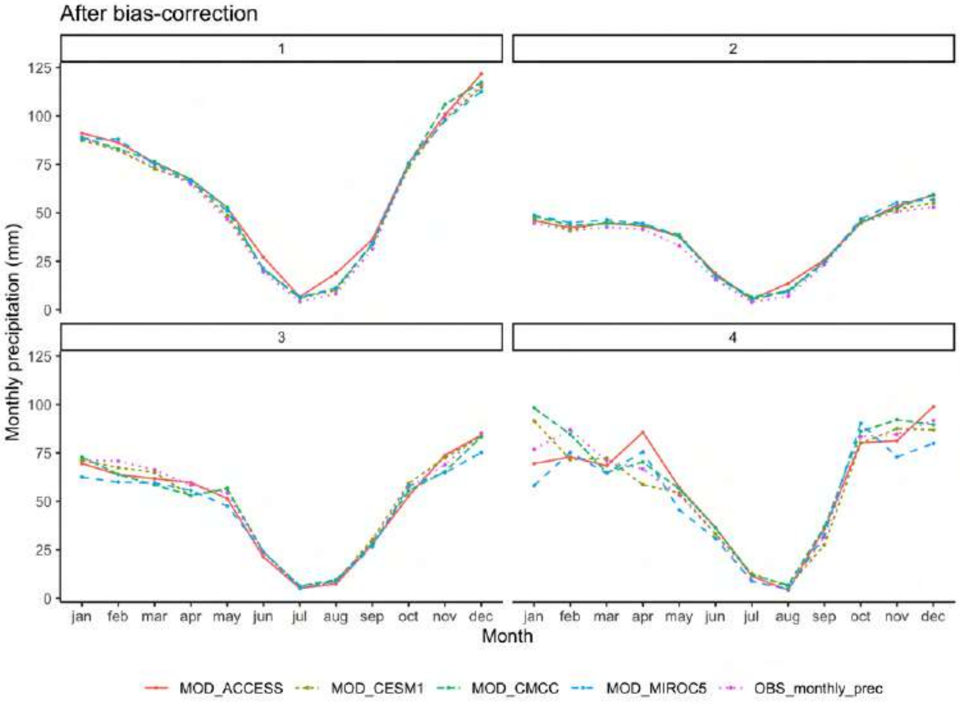


Figure S.27: Observed and modelled monthly precipitation for each climate region after applied bias-correction method.



S3.2.2 Climate time series

The time series for each climate region were generated as the average cells within a region (see Suárez-Muñoz et al., 2021, for details about climate regions definition). A current climate scenario was generated by randomly sampling data from years within the historical period. Years previous to 1950, only used during the spin-up phase, were given the average monthly value of the historical period for all three climate scenarios (Current, RCP4.5, RCP8.5). In the lack of major differences among models, MIROC5 global circulation model data were used for this study. Figures S.28-S.30 show the annual time series for each climate region for maximum temperature, minimum temperature and precipitation. Figures S.31-S.33 show the average temperature of February, July and November for one climate region as an overview of the seasonality changes under each climate scenario.

Figure S.28: Maximum annual temperature for each climate region and scenario.

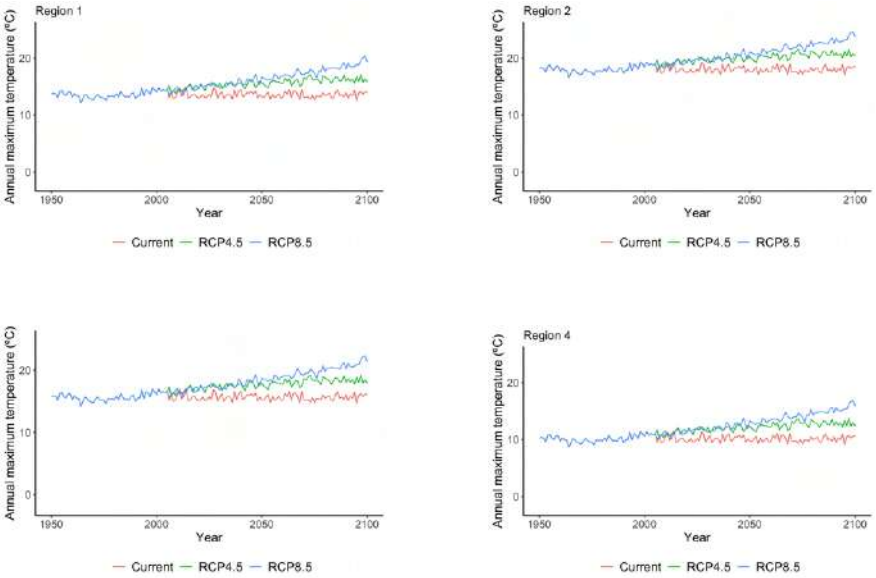


Figure S.29: Minimum annual temperature for each climate region and scenario.

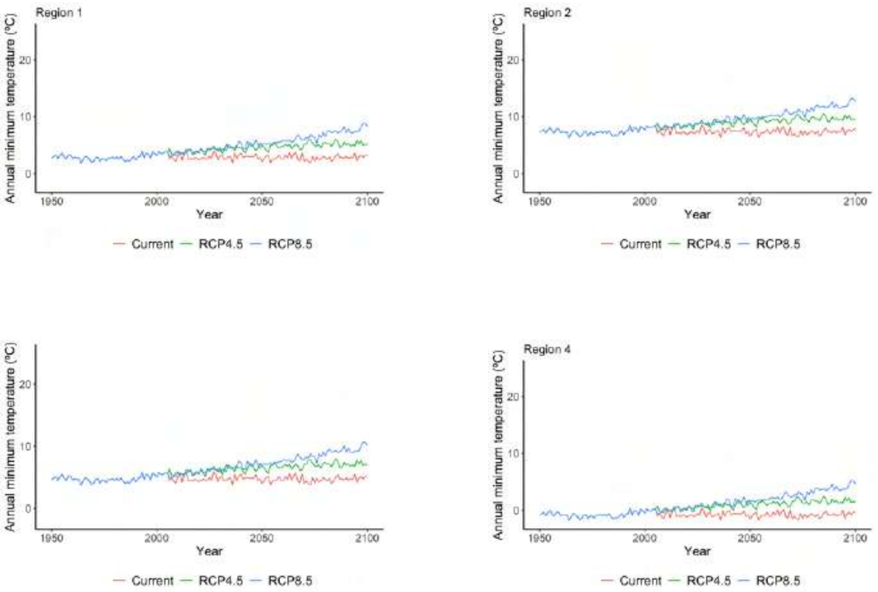


Figure S.30: Annual precipitation for each climate region and scenario. Time-series generated after applying bias-correction.

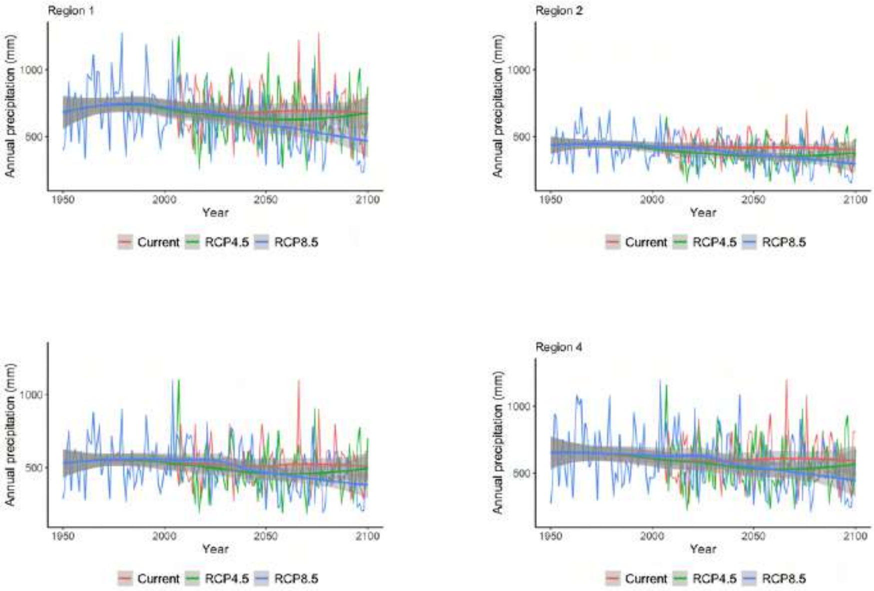


Figure S.31: February average temperature for each climate region and scenario.

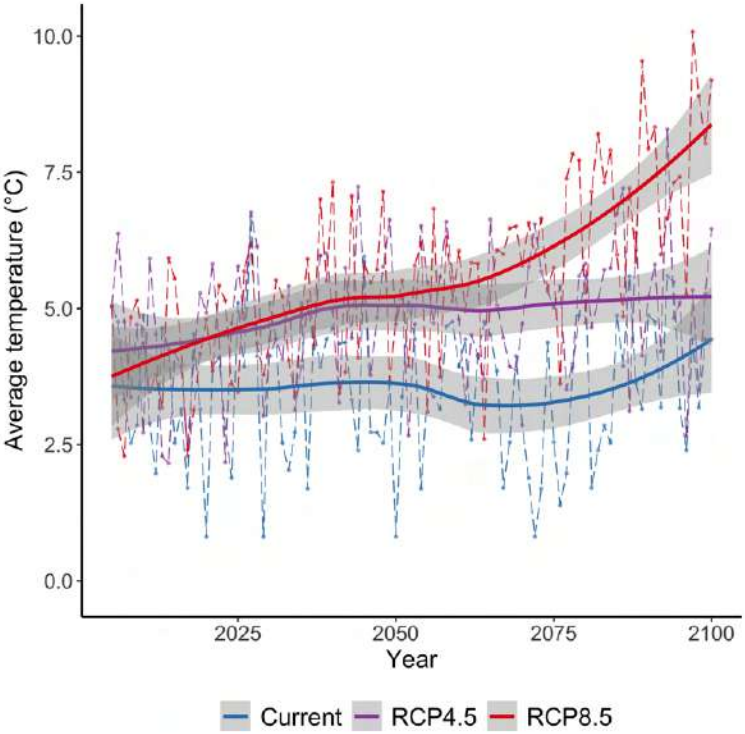


Figure S.32: July average temperature for each climate region and scenario.

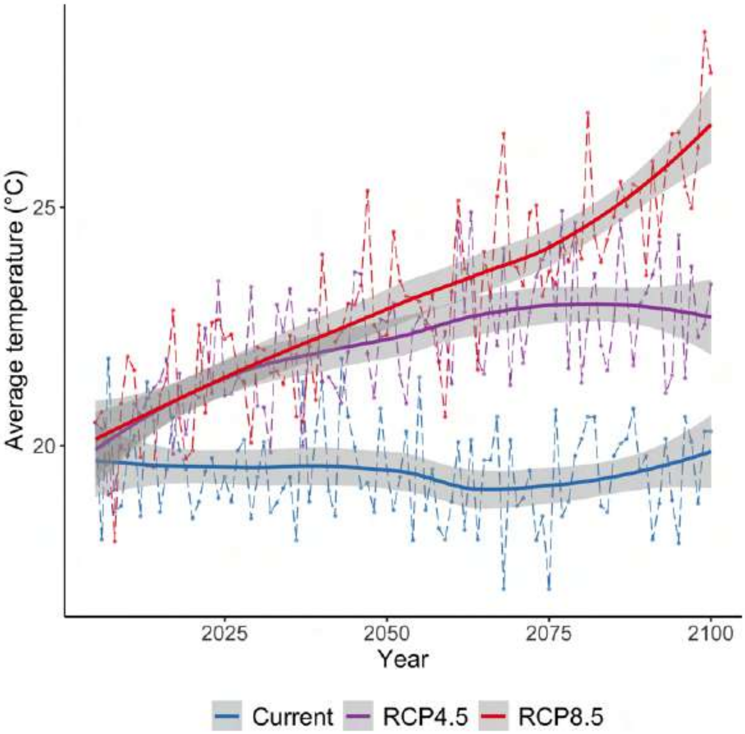
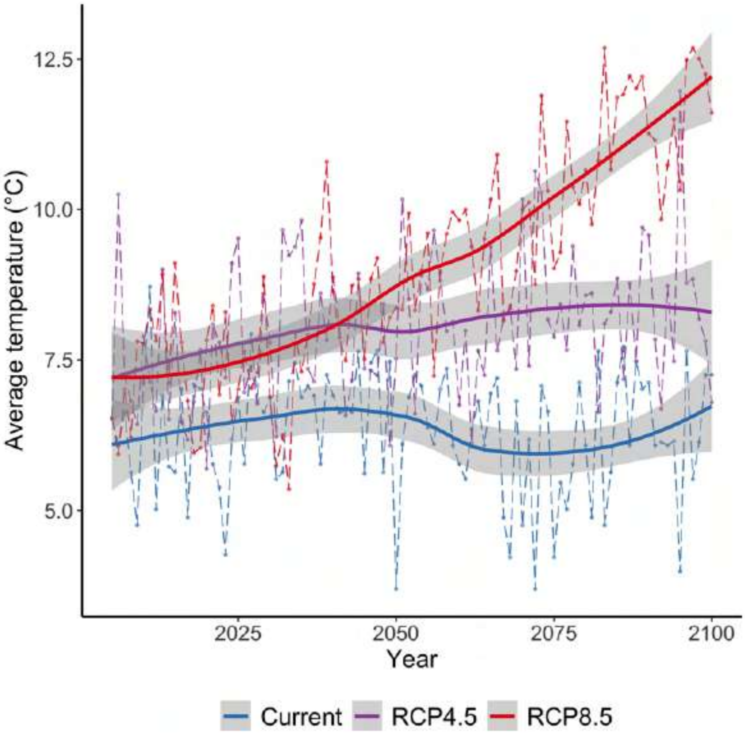


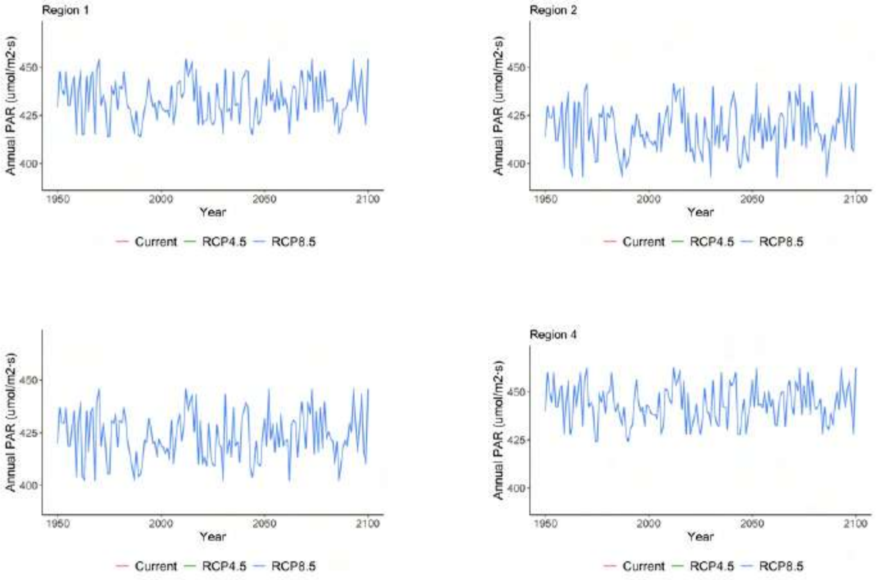
Figure S.33: November average temperature for each climate region and scenario.



PAR data source and preparation

PAR data were obtained from Cornes et al. (2018) version 20.0e. These data report global radiation at 0.1 ° resolution for the period 1981-2017. The complete time series was generated by random sampling years with data available and aggregation of gridded data by climate region in order to comply with LANDIS-II requirements. Figure S.34 shows the PAR time series for each climate region.

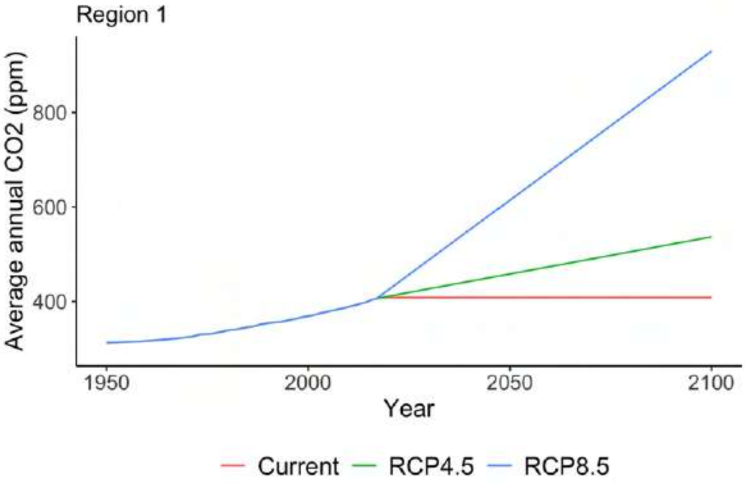
Figure S.34: PAR timeseries for each climate region and scenario.



CO_2 data source and preparation

CO_2 concentrations were obtained from Mina et al., 2021. These data correspond to single-point time series compiled by the Institute for Atmospheric and Climate Science at ETH Zürich (https://www.co2.earth/historical-co2-datasets). Scenarios RCP4.5 and RCP8.5 were generated by linearly increasing CO_2 concentrations until the projected levels according to the two RCP scenarios. Current climate scenario corresponds to CO_2 concentrations for 2018. CO_2 concentrations are considered equal for all four climate regions (Figure S.35).

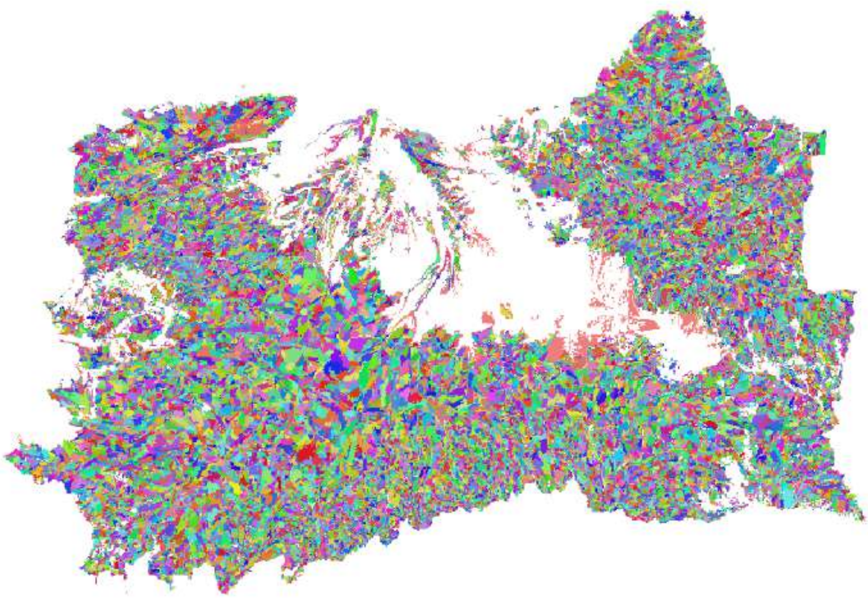
Figure S.35: CO_2 concentrations timeseries for each climate scenario.



S3.3 Management scenarios

S3.3.1 Maps of stands and management units

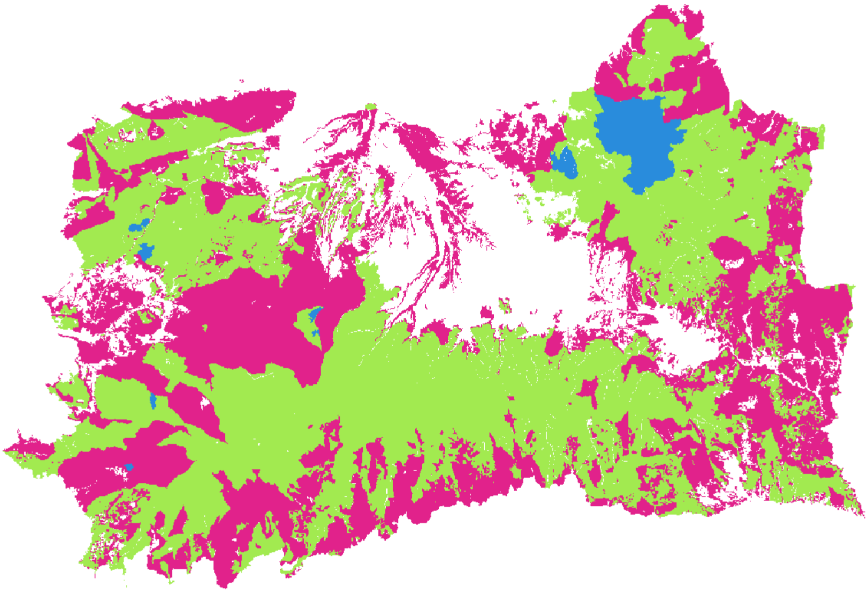
Figure S.36: Stands map based on vegetation polygons (source: vegetation map of Andalusia 1:10.000). Stands have an average of 7.9 ha (minimum 1 ha and maximum 504 ha, not considering one single stand of 8378 ha of abandoned crops and shrublands).



S3.3.2 Management scenarios conceptual ideas and descriptions

The non-management scenario represents a common situation in large areas of the territory in our region, where deficient management is usually a result of limited budget dedicated to forest management, among other reasons. Under this scenario no prescriptions are applied, except for a background browsing disturbance.

Figure S.37: Management units: private (pink), public (green), reserve (blue).



The conservative scenario is highly driven by the precautionary principle: managers are often inclined to prevent risks of post harvesting mortality due to windstorms or snowfalls in weakened stands. This scenario reproduces traditional silvicultural schemes where *Pinus* spp. are applied three subsequent thinning treatments (precommercial thinning, first and second thinning) and a regeneration felling throughout their rotation period (Serrada et al., 2008). Apart from these conifer treatments, coppice treatments are applied to *Quercus* spp. in small areas of the landscape. Under this scenario there is a low amount of biomass removed and a small proportion of area affected.

The proactive scenario is derived from the idea that over-precautionary management causes little or no effect on pine plantations and therefore it is not sufficient to produce a change in terms of species composition. Managers consider that a certain, relatively high thinning intensity is needed to promote the regeneration of broad-leaved species, and therefore ensure the transformation of these stands to mixed-species forests. Thus, under this scenario, higher amounts of biomass are removed while the proportion of area affected remains the same for pine prescriptions as in the conservative scenario.

The proactive-plus scenario does not represent a change in the conceptual approach, but a stronger commitment from the public administration to put forest policies into practice. It represents a situation where the amount of biomass being removed per cell is the same as under the proactive scenario, but more resources are allocated to forest management and therefore broader areas of the landscape are treated.

Under all scenarios a background browsing prescription is applied. This prescription emulates small-scale disturbances which constitute small removal of biomass from oaks, pines and shrubs.

Details of the simulated harvested biomass by species and cohort's age class for the silvicultural prescriptions applied in each management scenario. The effect of browsing was applied equally for all scenarios.

Table S.4: Implementation of the silvicultural prescriptions for each management scenario. Details of the harvested biomass by prescription in Table S.5.

Scenario	**Prescription**	**Maximum percentage of area affected every 10 years**
Non-manag.	Browsing	2.5 % of the whole landscape.
Conservative	Conifer treatments: Pre-comm. thinning, First thinning, Second thinning, Regeneration felling	Conifer treatments sum up to 7.5 % of the public non-reserve area, while 1.875 % of the private non-reserve area is affected by first thinning.
	Coppice	1 % in public non-reserve area.
	Browsing	2.5 % of the whole landscape.
Proactive	Conifer treatments: Pre-comm. thinning, First thinning, Second thinning, Regeneration felling	Conifer treatments sum up to 7.5 % of the public non-reserve area, while 1.875 % of the private non-reserve area is affected by first thinning.
	Coppice	3 % in public non-reserve area.
	Browsing	2.5 % of the whole landscape.
Proactive-plus	Conifer treatments: Pre-comm. thinning, First thinning, Second thinning, Regeneration felling	Conifer treatments sum up to 15 % of the public non-reserve area, while 3.75 % of the private non-reserve area is affected by first thinning.
	Coppice	3 % in public non-reserve area.
	Browsing	2.5 % of the whole landscape.

Table S.5: Conifer treatments - Precommercial thinning. Stand selection: Stands with at least 50 % of their cells with presence of any *Pinus* spp. between 20 and 35 years old.

	Conservative scenario	**Proactive and Proactive-plus scenarios**
	Cohort removal:	Cohort removal:
P. sylvestris	1-10 (35 %) 11-20 (30 %) 21-30 (25 %)	1-10 (70 %) 11-20 (60 %) 21-30 (50 %)
P. halepensis	1-10 (35 %) 11-20 (30 %) 21-30 (25 %)	1-10 (70 %) 11-20 (60 %) 21-30 (50 %)
P. pinaster	1-10 (35 %) 11-20 (30 %) 21-30 (25 %)	1-10 (70 %) 11-20 (60 %) 21-30 (50 %)
P. nigra	1-10 (35 %) 11-20 (30 %) 21-30 (25 %)	1-10 (70 %) 11-20 (60 %) 21-30 (50%)

Table S.6: Conifer treatments - First thinning. Stand selection: Stands with at least 50 % of their cells with presence of any *Pinus* spp. between 35 and 60 years old.

	Conservative scenario	**Proactive and Proactive-plus scenarios**
	Cohort removal:	Cohort removal:
P. sylvestris	31-50 (40 %) 51-400 (35 %)	31-50 (80 %) 51-400 (70 %)
P. halepensis	31-40 (40 %) 41-400 (35 %)	31-40 (80 %) 41-400 (70 %)
P. pinaster	31-40 (40 %) 41-400 (35 %)	31-40 (80 %) 41-400 (70 %)
P. nigra	31-50 (40 %) 51-400 (35 %)	31-50 (80 %) 51-400 (70 %)

Table S.7: Conifer treatments - Second thinning. Stand selection: Stands with at least 50 % of their cells with presence of any *Pinus* spp. between 50 and 80 years old.

	Conservative scenario	**Proactive and Proactive-plus scenarios**
	Cohort removal:	Cohort removal:
P. sylvestris	61-80 (40 %) 81-400 (35 %)	61-80 (80 %) 81-400 (70 %)
P. halepensis	51-60 (40 %) 61-400 (35 %)	51-60 (80 %) 61-400 (70 %)
P. pinaster	51-60 (40 %) 61-400 (35 %)	51-60 (80 %) 61-400 (70 %)
P. nigra	61-80 (40 %) 81-400 (35 %)	61-80 (80 %) 81-400 (70 %)

Table S.8: Conifer treatments - Regeneration felling. Stand selection: Stands with at least 50 % of their cells with presence of any *Pinus* spp. between 70 and 130 years old.

	Conservative scenario	**Proactive and Proactive-plus scenarios**
	Cohort removal:	Cohort removal:
P. sylvestris	91-110 (45 %) 111-400 (40 %)	91-110 (90 %) 111-400 (80 %)
P. halepensis	71-80 (40 %) 81-400 (30 %)	71-80 (80 %) 81-400 (70 %)
P. pinaster	71-80 (40 %) 81-400 (30 %)	71-80 (80 %) 81-400 (70 %)
P. nigra	91-110 (45 %) 111-400 (40 %)	91-110 (90 %) 111-400 (80 %)

Table S.9: Coppice. Stand selection: Stands with at least 50 % of their cells with presence of any *Quercus* spp. between 20 and 50 years old.

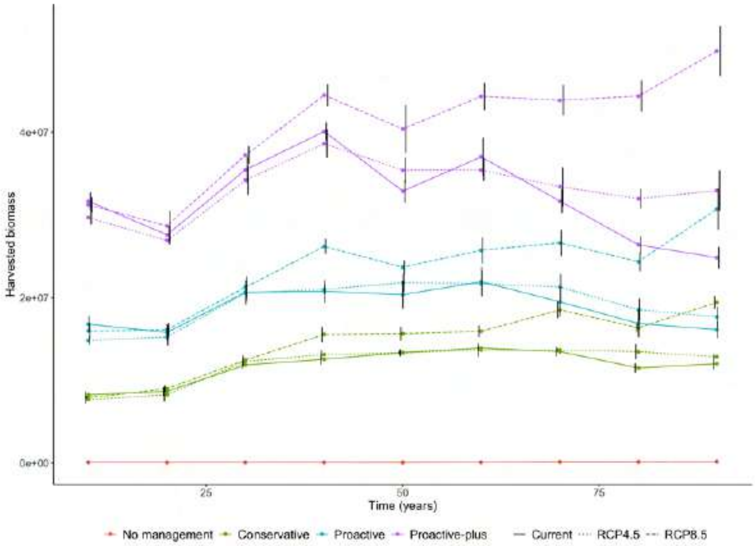
	Conservative, Proactive and Proactive-plus scenario
	Cohort removal:
Q. ilex	1-10 (40 %) 11-20 (35 %) 21-30 (30 %)
Q. faginea	1-10 (40 %) 11-20 (35 %) 21-30 (30 %)
Q. pyrenaica	1-10 (40 %) 11-20 (35 %) 21-30 (30 %)

Table S.10: Browsing. Stand selection: random.

	All management scenarios
	Cohort removal:
Tall shrubs	1-50 (40 %) 51-80 (30 %)
Medium shrubs	1-80 (55 %)
Short shrubs	1-80 (70 %)
Q. ilex	1-10 (30 %) 11-20 (20 %)
Q. faginea	1-10 (30 %) 11-20 (20 %)
Q. pyrenaica	1-10 (20 %) 11-20 (10 %)
P. halepensis	1-10 (40 %)
P. pinaster	1-10 (40 %)
P. sylvestris	1-10 (40 %)
P. nigra	1-10 (40 %)

S3.3.3 Executed harvesting

Figure S.38: Harvested biomass through time for each climate and management scenario.



S3.4 Results

Figure S.39: Average monthly net photosynthesis of the area covered by pine plantations across climate and management scenarios. Beginning period corresponds to the average among the first three simulation time steps (years 2005, 2010, 2015) and the End period to the last three time steps (years 2090, 2095, 2100). Ribbon represents the standard deviation among time steps from the mean values of five replicates.

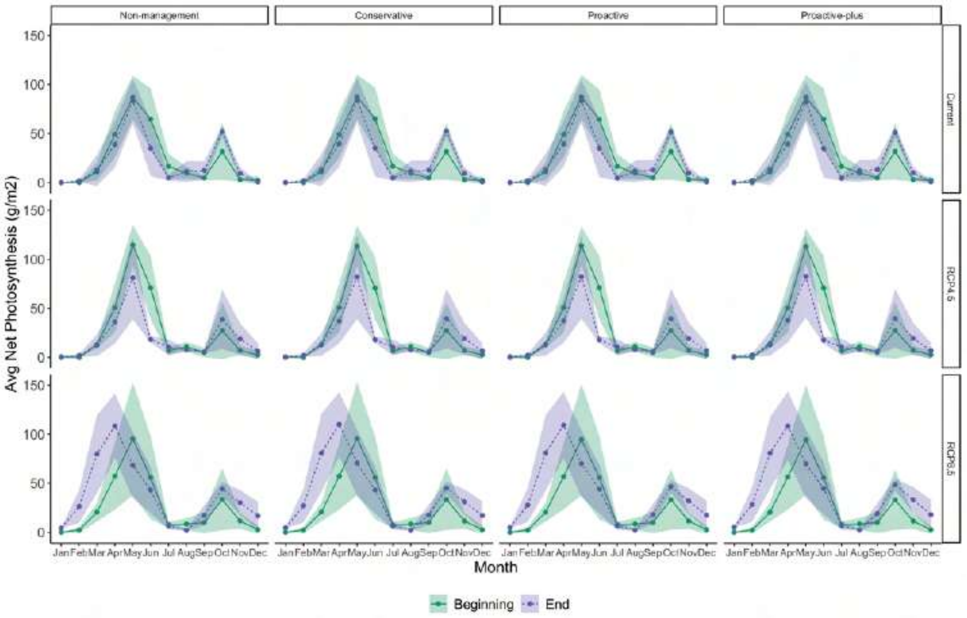


Figure S.40: Above ground biomass of pines and oaks through time at landscape level (the region initially covered by planted pine forests) for all climate and management scenarios. Values correspond to mean across 5 replicates and error bars, when visible, represent standard deviation.

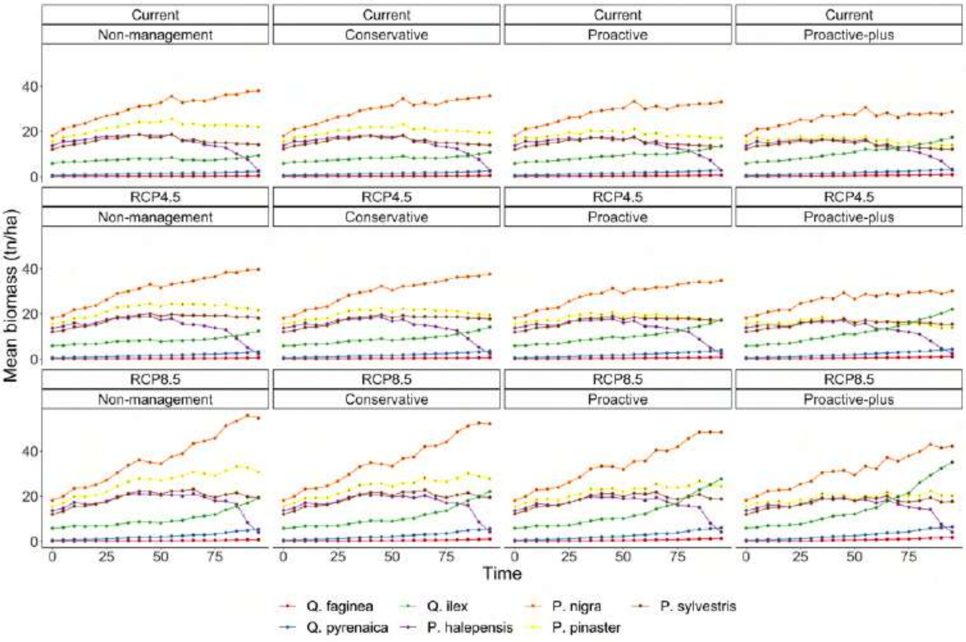


Figure S.41: Total above ground biomass trend through time as Kendall's tau statistic. Mann-Kendall trend calculated over the average total biomass maps among replicates for each timestep. Significance levels (p-values) can be found in Figure S.42.

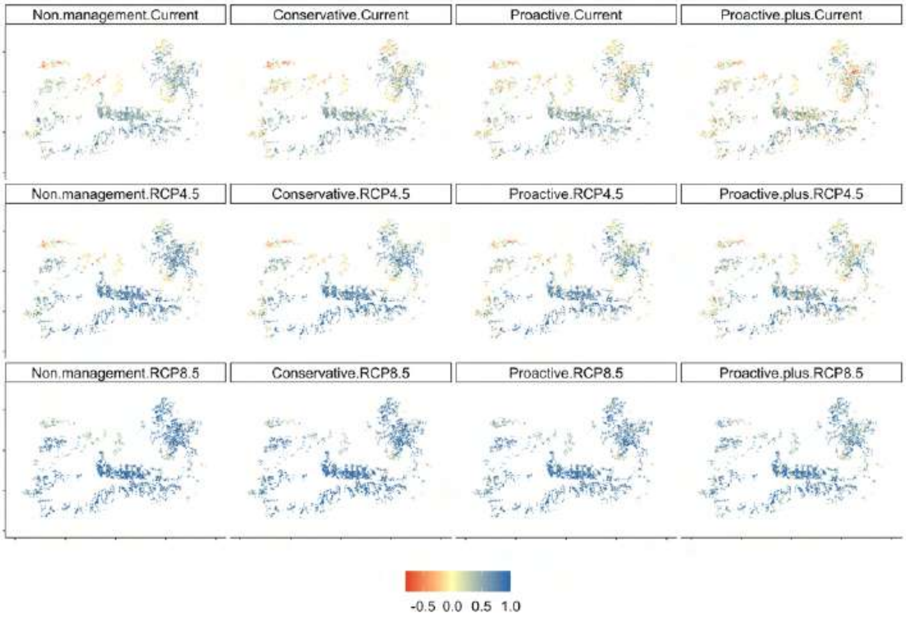


Figure S.42: Significance (p-value) of Kendall's tau statistic for total above ground biomass trend through time. Trend calculated over the average biomass maps among replicates.

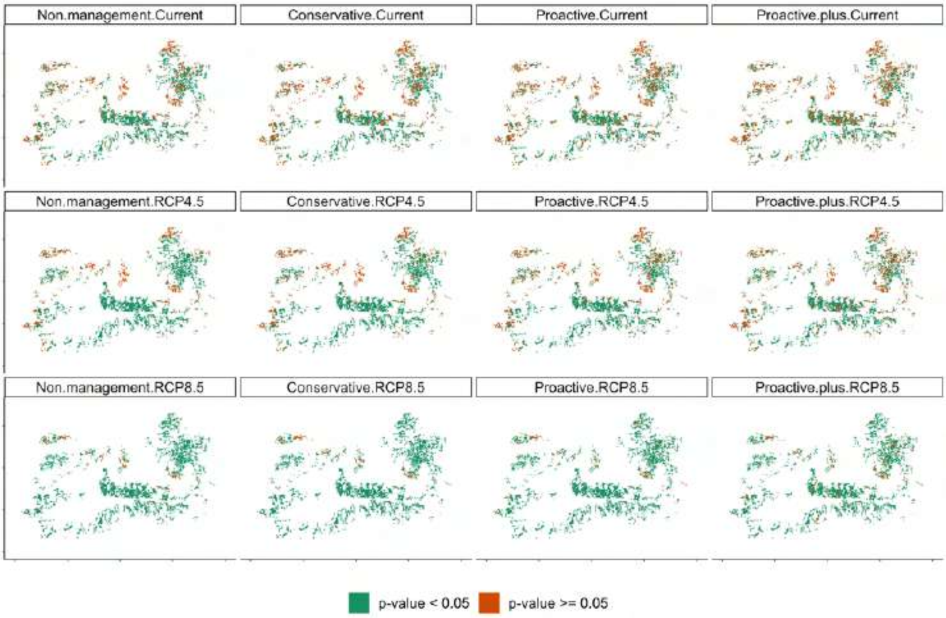


Figure S.43: Pines above ground biomass trend through time as Kendall's tau statistic. Mann-Kendall trend calculated over the average total biomass maps among replicates for each timestep. Significance levels (p-values) can be found in Figure S.44.

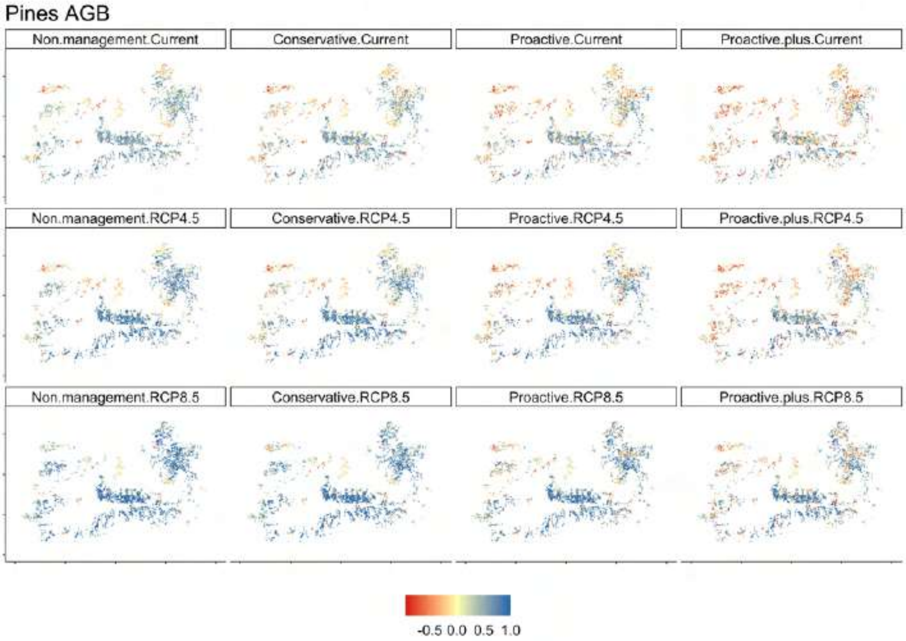


Figure S.44: Significance (p-value) of Kendall's tau statistic for pines above ground biomass trend through time. Trend calculated over the average biomass maps among replicates.

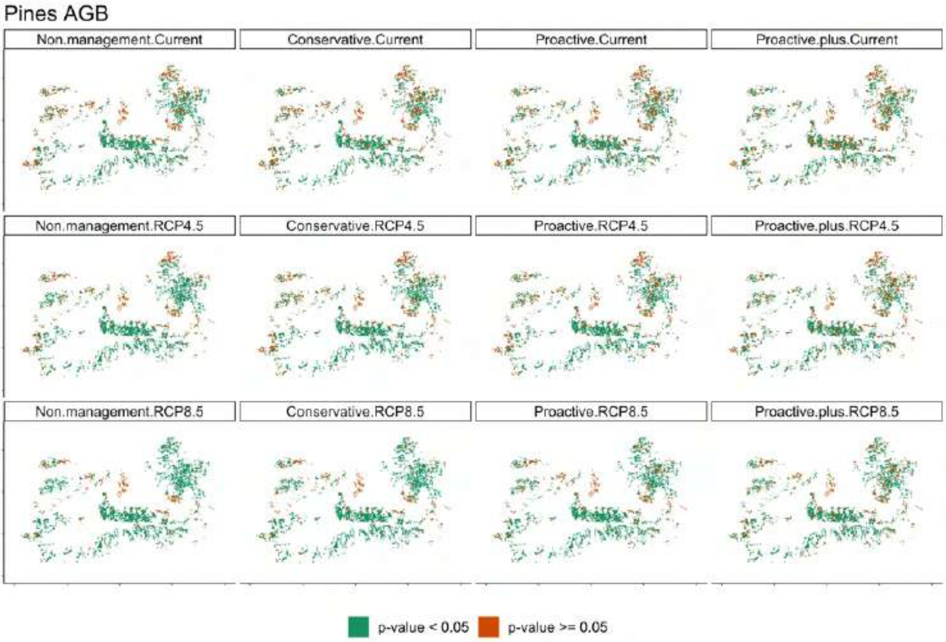


Figure S.45: Oaks above ground biomass trend through time as Kendall's tau statistic. Mann-Kendall trend calculated over the average total biomass maps among replicates for each timestep. Significance levels (p-values) can be found in Figure S.46.

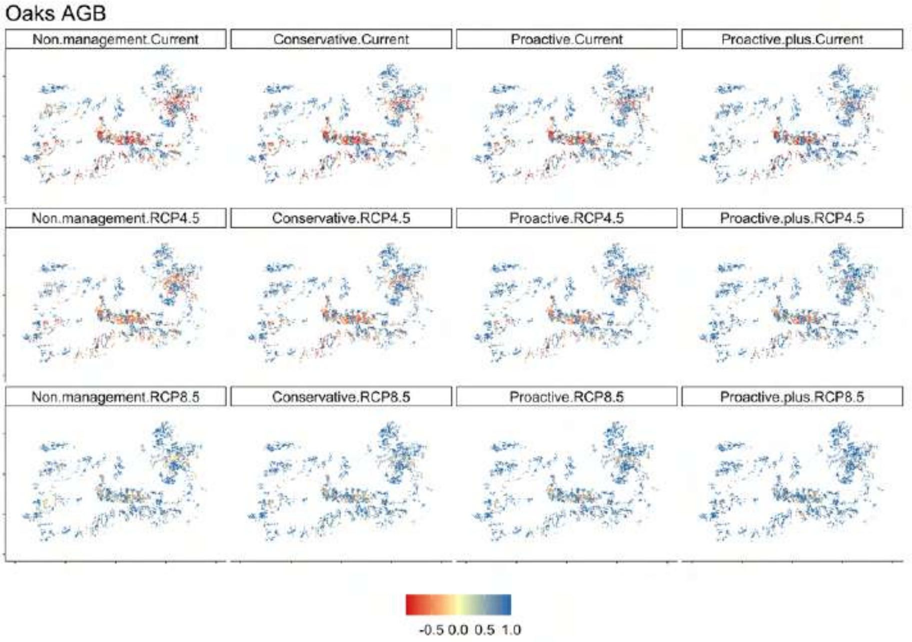


Figure S.46: Significance (p-value) of Kendall's tau statistic for oaks above ground biomass trend through time. Trend calculated over the average biomass maps among replicates.

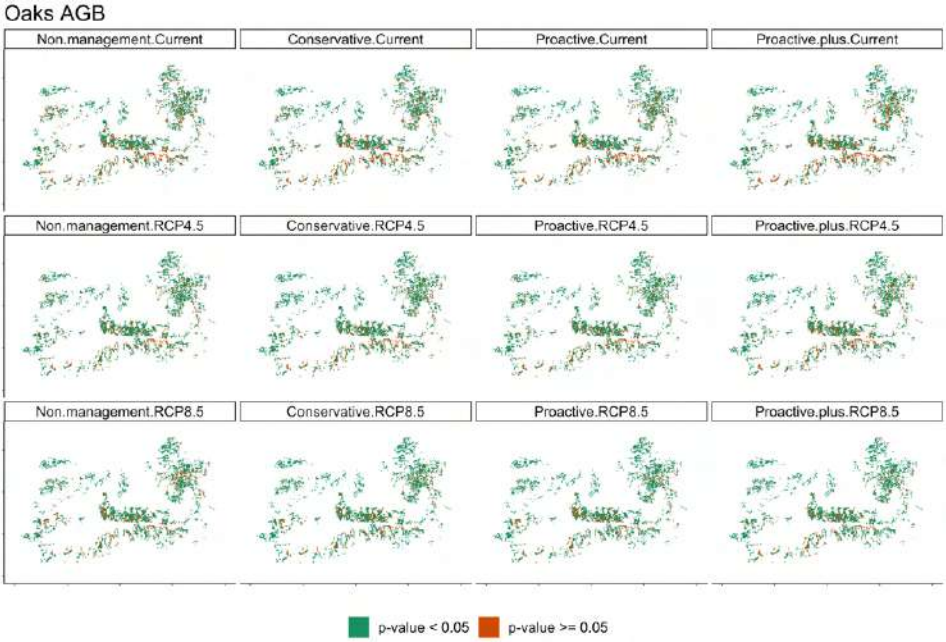


Figure S.47: Forest type maps across management and climate scenarios at initial year of simulation (2005). Map corresponds to one replicate.

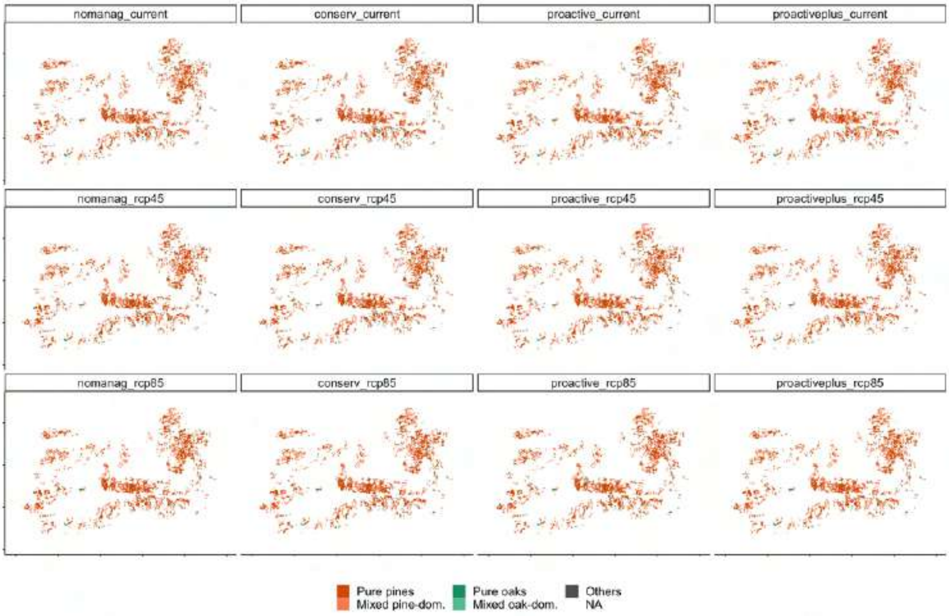


Figure S.48: Forest type maps across management and climate scenarios at final year of simulation (2100). Map corresponds to one replicate.

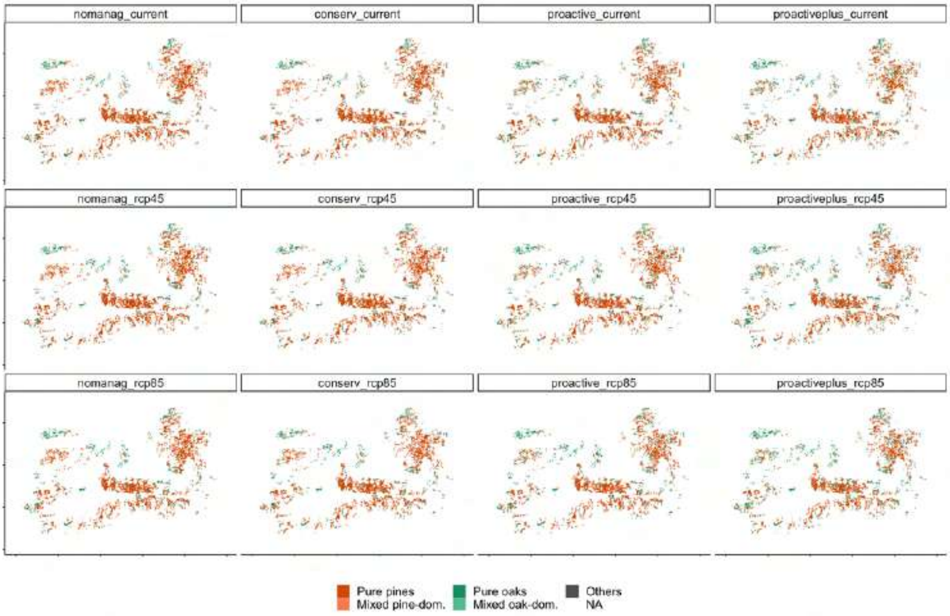


Table S.11: Percentage of area covered by each forest type at initial (2005) and final (2100) year of simulation. Mean±standard deviation among five replicates.

Harvest scenarios	**Climate scenarios**	**Forest type**	**Initial**	**Final**
Non-manag.	Current	Pure pines	61.2±1.2	63.9±0.2
Non-manag.	Current	Mixed pine dom.	34.0±1.1	17.6±0.3
Non-manag.	Current	Pure oaks	1.5±0.1	6.9±0.2
Non-manag.	Current	Mixed oak dom.	1.0±0.1	8.9±0.2
Non-manag.	Current	Shrublands	1.8±0.0	0.1±0.0
Non-manag.	Current	Mixed no dom.	0.1±0.0	0.7±0.0
Non-manag.	Current	Empty	0.4±0.0	1.9±0.0
Non-manag.	RCP4.5	Pure pines	60.3±1.0	59.6±0.4
Non-manag.	RCP4.5	Mixed pine dom.	34.9±1.0	19.1±0.4
Non-manag.	RCP4.5	Pure oaks	1.6±0.1	7.7±0.3
Non-manag.	RCP4.5	Mixed oak dom.	0.8±0.2	10.2±0.4
Non-manag.	RCP4.5	Shrublands	1.8±0.0	0.2±0.0
Non-manag.	RCP4.5	Mixed no dom.	0.1±0.0	0.8±0.0
Non-manag.	RCP4.5	Empty	0.4±0.0	2.4±0.0
Non-manag.	RCP8.5	Pure pines	60.4±0.7	53.8±0.5
Non-manag.	RCP8.5	Mixed pine dom.	34.8±0.7	22.9±0.5
Non-manag.	RCP8.5	Pure oaks	1.5±0.0	9.5±0.2
Non-manag.	RCP8.5	Mixed oak dom.	0.9±0.0	10.3±0.2
Non-manag.	RCP8.5	Shrublands	1.8±0.1	0.2±0.0
Non-manag.	RCP8.5	Mixed no dom.	0.1±0.0	1.1±0.1
Non-manag.	RCP8.5	Empty	0.4±0.1	2.2±0.1
Conservative	Current	Pure pines	60.9±1.3	59.4±0.2
Conservative	Current	Mixed pine dom.	34.2±1.2	21.0±0.3
Conservative	Current	Pure oaks	1.5±0.1	6.8±0.2
Conservative	Current	Mixed oak dom.	1.0±0.2	10.1±0.2
Conservative	Current	Shrublands	1.9±0.0	0.1±0.0
Conservative	Current	Mixed no dom.	0.1±0.0	0.7±0.0
Conservative	Current	Empty	0.4±0.0	1.9±0.1
Conservative	RCP4.5	Pure pines	60.9±0.9	54.8±0.3
Conservative	RCP4.5	Mixed pine dom.	34.3±0.8	22.7±0.3
Conservative	RCP4.5	Pure oaks	1.6±0.1	7.8±0.2
Conservative	RCP4.5	Mixed oak dom.	0.9±0.2	11.5±0.2
Conservative	RCP4.5	Shrublands	1.9±0.0	0.2±0.0
Conservative	RCP4.5	Mixed no dom.	0.1±0.0	0.8±0.0

Conservative	RCP4.5	Empty	0.4±0.0	2.3±0.0
Conservative	RCP8.5	Pure pines	60.6±0.8	49.3±0.2
Conservative	RCP8.5	Mixed pine dom.	34.3±0.7	26.3±0.1
Conservative	RCP8.5	Pure oaks	1.6±0.1	9.8±0.3
Conservative	RCP8.5	Mixed oak dom.	1.1±0.6	11.2±0.2
Conservative	RCP8.5	Shrublands	1.9±0.0	0.2±0.0
Conservative	RCP8.5	Mixed no dom.	0.1±0.0	1.0±0.1
Conservative	RCP8.5	Empty	0.4±0.0	2.2±0.1
Proactive	Current	Pure pines	61.0±1.3	55.5±0.2
Proactive	Current	Mixed pine dom.	34.3±1.3	19.9±0.4
Proactive	Current	Pure oaks	1.5±0.1	8.9±0.4
Proactive	Current	Mixed oak dom.	0.8±0.1	13.0±0.2
Proactive	Current	Shrublands	1.8±0.1	0.1±0.0
Proactive	Current	Mixed no dom.	0.1±0.0	0.7±0.0
Proactive	Current	Empty	0.4±0.1	1.9±0.0
Proactive	RCP4.5	Pure pines	59.9±0.7	51.3±0.3
Proactive	RCP4.5	Mixed pine dom.	35.2±0.5	21.5±0.3
Proactive	RCP4.5	Pure oaks	1.5±0.0	9.8±0.2
Proactive	RCP4.5	Mixed oak dom.	1.1±0.2	14.1±0.3
Proactive	RCP4.5	Shrublands	1.9±0.0	0.2±0.0
Proactive	RCP4.5	Mixed no dom.	0.1±0.0	0.9±0.1
Proactive	RCP4.5	Empty	0.4±0.0	2.3±0.0
Proactive	RCP8.5	Pure pines	61.0±0.8	46.2±0.3
Proactive	RCP8.5	Mixed pine dom.	34.3±0.8	24.4±0.5
Proactive	RCP8.5	Pure oaks	1.6±0.1	11.8±0.3
Proactive	RCP8.5	Mixed oak dom.	0.8±0.3	14.2±0.2
Proactive	RCP8.5	Shrublands	1.8±0.0	0.2±0.0
Proactive	RCP8.5	Mixed no dom.	0.1±0.0	1.1±0.1
Proactive	RCP8.5	Empty	0.4±0.0	2.2±0.0
Proactive-plus	Current	Pure pines	60.1±1.3	49.1±0.5
Proactive-plus	Current	Mixed pine dom.	35.2±1.4	20.5±0.7
Proactive-plus	Current	Pure oaks	1.5±0.1	11.8±0.3
Proactive-plus	Current	Mixed oak dom.	0.8±0.1	16.0±0.3
Proactive-plus	Current	Shrublands	1.8±0.1	0.1±0.0
Proactive-plus	Current	Mixed no dom.	0.1±0.0	0.6±0.0
Proactive-plus	Current	Empty	0.4±0.1	1.8±0.0
Proactive-plus	RCP4.5	Pure Pines	61.3±0.7	45.6±0.3
Proactive-plus	RCP4.5	Mixed pine dom.	34.0±0.8	21.4±0.5

Proactive-plus	RCP4.5	Pure oaks	1.5±0.0	13.1±0.3
Proactive-plus	RCP4.5	Mixed oak dom.	0.9±0.1	16.8±0.5
Proactive-plus	RCP4.5	Shrublands	1.8±0.1	0.1±0.0
Proactive-plus	RCP4.5	Mixed no dom.	0.1±0.0	0.8±0.0
Proactive-plus	RCP4.5	Empty	0.4±0.1	2.2±0.0
Proactive-plus	RCP8.5	Pure pines	60.5±1.2	41.1±0.3
Proactive-plus	RCP8.5	Mixed pine dom.	34.7±1.2	23.1±0.7
Proactive-plus	RCP8.5	Pure oaks	1.5±0.1	15.0±0.4
Proactive-plus	RCP8.5	Mixed oak dom.	0.9±0.2	17.4±0.4
Proactive-plus	RCP8.5	Shrublands	1.9±0.0	0.2±0.0
Proactive-plus	RCP8.5	Mixed no dom.	0.1±0.0	1.1±0.0
Proactive-plus	RCP8.5	Empty	0.4±0.0	2.1±0.0

Supplementary Material of Chapter 4

S4.1 Model assumptions

Like every model, *INSTAR* is a simplification of the real system it attempts to simulate. This simplification implies taking assumptions which are described in this section, organised by topics or submodels.

S4.1.1 Clutch size

Clutch size is one of the best-known parameters of *T. pityocampa* life cycle, with abundant references from their whole geographical distribution being available. In this work we have used local data (Sierra Nevada) from Torres Muros (2015). The model allows for adjusting the clutch size value, therefore enabling area-specific simulations.

S4.1.2 NPP rate

Food quality and quantity have been repeatedly cited as a key factor for determining the cyclic outbreaks of *T. pityocampa*: once food is consumed, the food available for the next generation is scarce and/or of low quality, and then the *T. pityocampa* population starves. Unfortunately, matching needle quality and quantity with larval consumption in a dynamic way is still puzzling. Needle biomass depends on pine size, but also on previous defoliation, and this in turn determines quality (a complete defoliation causes complete lack of old needles for the next generation of larvae) (Hódar et al., 2004).

Here, we modelled the needle production/consumption and the needle quality as a percentage of existing needle biomass, depending on pine size. A healthy pine which was not defoliated in the previous season has between 57 % and 100 % needle biomass. A pine which suffered defoliation during the previous season will have needle biomass levels below 57 % (which we called $Ql_{threshold}$). By the end of the defoliating season trees are classified as "defoliated" or "not defoliated" based on this threshold. Therefore we are assuming that a pine generates up to 43 % of needles in a growing season and that up to 57 % grew in a previous season. The cohort division of needles was defined based on Muukkonen (2005b). Muukkonen (2005b) provides data on pine needle survival by needle cohort for *Pinus sylvestris*. Then, the program calculates the decrease in needle availability as larvae consume them according to the initial number of colonies standing at the tree and the carrying capacity estimated for the tree according to its height (see section 4.3.3). After winter defoliation, needle quality is set based on its biomass content at that moment (above or below 57 %) and its quantity is increased daily between April and August by a constant growth rate (NPP, see Table 4.2) which is 43 % of the total needle biomass as suggested by Muukkonen (2005b) (see section 4.3.3).

S4.1.3 Predation and parasitism on eggs, larvae, pupae and moths

Data on *T. pityocampa* predation and parasitism on larvae, pupae and moths are abundant regarding the identity of predators and parasites but not regarding the intensity of predators-parasites interactions (Barbaro and Battisti, 2011; Battisti, 1989; Battisti et al., 2015; Charbonnier et al., 2014). Therefore such interaction could not be modelled. In some cases, such as pupae mortality (see below), parasitism is included within a whole parameter of phase mortality, but it is not included as a separate parameter. In the case of egg mortality, non-hatched eggs are estimated based on data from Torres Muros (2015) (see section 4.3.3).

S4.1.4 Colony merging and splitting

The size of a colony determines its thermic inertia against low temperatures. For this reason, larvae coming from different cohorts often merge into one colony. Even though implementing a submodel to simulate colony merging within a tree would be feasible, such procedure would increase the computing needs of the model, without improving the accuracy of the simulation since, to our knowledge, no publication reports data about mortality or development rate based on number of individuals within a colony, probably due to impediments to count them. Nevertheless, Démolin (1969a) provided an estimation of the integrated temperature (i.e. the temperature inside the colony) and the maximum temperature and insolation hours for an average size colony and this variable is implemented within *INSTAR* and used within the development submodels. Similarly, a colony may split when procession takes place, resulting in more than one burial spot. Nevertheless, this process is not included in the model as, again, it would increase the computing needs of the model, without improving the accuracy of the simulation. The burial spot defines pupae mortality based on number of trees per cell, which are 30 x 30 m. It is thus unlikely that two processions from the same tree bury in different cells and therefore have different mortality rates.

S4.1.5 Procession distance

There is a great scarcity of data in the literature regarding procession distance. In the lack of better information, we decided to use the maximum displacement (37 m) as $Procession_{max-distance}$ (see section 4.3.3) reported by Robredo (1963). The author did not mention sample size and deviation, neither average value.

S4.1.6 Pupae mortality

Pupae mortality is calculated based on Torres-Muros et al. (2017), using the average rate of final survival depending on the burial habitat. By doing so causes of mortality are not detailed within the modelisation. See submodel description in section 4.3.3.

S4.1.7 Mating success

There is no available specific data for *T. pityocampa* on mating success. Considering that the emergence of male and female moths is apparently well synchronised, with the males attracted toward females by sexual pheromones, the effect of pheromone traps as effective control measurements against populations is poor, and unfecunded egg batches found in the wild are apparently scant, all of which suggests that mating success is very high. Perhaps in situations of very low population density some Allee effect could emerge, with individuals failing to mate because of the mismatch between individuals, but this is probably a rare situation. Rhainds (2010) in his review suggests 95 % successful mating for Lepidoptera in general, which is the figure we used (see section 4.3.3).

S4.1.8 Female moth flight capacity: mating distance and oviposition distance

This is one of the greatest debates on *T. pityocampa*. It is agreed that males fly more than females. The work of Démolin (1969b) states that female moths make a short flight after emergence and a long flight after mating. However, he never published sample size, mean and variability. In the initial flight, female moths fly upwards 2-3 m (sometimes 30 m), find their direction, and then fly to the pine chosen for mating, usually one close by but sometimes 500 m away. The distance for the oviposition flight was experimentally determined, by placing 100 pupae in a site free of *T. pityocampa*, and then recording the distance at which egg batches were laid. One was found 2 km away, and 7 "within a radius of 300 m" (Démolin, 1969b). Note that seven egg batches within a radius of 300 m means that the farthest of seven egg batches is at 300 m, but the other six are at shorter distances. Nevertheless, for years these have been the single figures available for female moth flight capacity. Conversely, in a study on egg batch parasitism in Greece, Schmidt (1990) states that "normally (females) cannot fly before egg-laying". His statement vividly contrasts with Dèmolin's data, and in general it has been ignored, probably because Schmidt did not offer data in this respect, and just expressed an opinion.

Recently, Sauvard and Yart (see in Battisti et al., 2015) tested the potential flight capacity of both male and female *T. pityocampa* moths in laboratory, by means of a flight mill. According to their results, "the dispersal potential of *T. pityocampa* measured on a flight mill appeared significantly more important than the estimations of previous studies based on empirical observations or rough experiments of release-recapture". Their experiments during 2008-2009 show a mean flight distance of 10.9 km (up to 41 km) and 1.9 km (up to 10.5 km) for males and females, respectively. In subsequent years (2009-2010 and 2010-2011), the mean distance was 17 and 24 km on average and a maximum of 61 and 56 km for males, and an average of 5.6 and 5.1 km and maximum values up to 27 and 24 km for females, respectively.

Although obvious, it should be noted that the maximum flight capacity of a moth in a laboratory situation does not represent at all the usual flight behaviour in the wild. While these studies increased the figure of the maximum flight distance reached by moths, fitting well the maximum speed of colonisation of natural populations, a kernel distribution of flight frequencies within already established populations is lacking, and this is key for modelisation. In our opinion, the data available fit in a leptokurtic curve with a short-distance mode and a long right tail reaching several kilometres, that is, a vast majority of females make short-distance flights, and a few make quite long ones. Thus, the boundaries of the distribution (i.e., the longest flights) are rather well determined, but the figure for the most frequent flight and how frequent it is cannot be stated based on the present state of knowledge.

Since here we present simulations of *INSTAR* in a closed environment of 450 x 360 m (16.2 ha) and we are more interested in the short-scale dynamics of a pre-existing population rather than in colonisation of new areas on a wide scale, we use a flight distance for female moths of 100 m, at the very lower side of the kernel, in agreement with the "few dozen meters" of Démolin (1969b). If the model is used in the future to explore colonisation over wide areas, a more complex kernel can be implemented.

S4.1.9 Carrying capacity

The amount of foliage that a *T. pityocampa* caterpillar requires to complete its larval development in field conditions is, as far as we know, unknown. To get an estimate of how many larvae can develop in a given pine, field data were collected and incorporated into the model. Pine height was selected as a proxy for tree biomass, and number of winter colonies as a proxy for *T. pityocampa* population. Thus, within the framework of a different study on the population dynamics of this species (J.A, Hódar, unpublished results), 336 trees from 28 different plots were checked for four consecutive winters (2015-2018) at the end of the defoliation period (February-March). For each tree, the percent of defoliated tree biomass was estimated by an experienced observer and the number of winter colonies was recorded.

From these observations, highly defoliated (~90 %) but not completely defoliated trees (100 %) were selected, since we were interested in the number of winter colonies that can develop feeding on a single the tree without reaching food depletion. A little amount of foliage in trees ensured that trees with an excessive number of winter colonies, which could starve by lack of food, were not considered. Due to the cyclic population dynamics in the area, infestation was relatively low during the years of the study for plots with *Pinus nigra* and *P. sylvestris*. The requirement of ~90 % defoliation in the years of study was fulfilled for 20 trees of *P. halepensis* located in a recent pine plantation near Sierra Nevada Protected Area (ca. 10 km off the Protected Area limits, see Supplementary Material S4.5).

Based on these observations, the number of winter colonies per tree was related to the height of the tree. Thus, the estimate of how many colonies are needed to completely defoliate a tree depending on its size (height) can be calculated according to the resulting equation:

$$cc = 11.63 \cdot \ln \text{height} - 4.60$$
$$R^2 = 0.65$$

being cc, carrying capacity, the number of colonies that a pine can host.

The goodness of fit could be probably improved by adjusting the pine species to the characteristics of the area in which the model is run, and using a better estimation of tree size (e.g. volume, by using both height and canopy diameter). Nevertheless, only tree height was used in order to minimise the number of parameters needed to run the model. In any case, these improvements can be easily incorporated as soon as new and better data become available.

S4.2 Direction coefficients

It is known (not published data based on field expertise) that infestations are more common in SW and W orientation of each tree, while NW, S, SE and E show intermediate levels and N and NE are usually low. Thus, coefficients are assigned to each orientation in order to quantify their suitability for moth oviposition within each tree at the initialisation step. The higher the value, the more suitable the tree is for the moth oviposition.

Direction	**Angle °**	**Coefficient**
North	0	-50
NE	45	-80
E	90	-95
SE	135	-50
S	180	-10
SW	225	-5
W	270	-10
NW	315	-5

S4.3 Hydrometeorological model (WiMMed)

Daily maps of meteorological variables (maximum and minimum temperature) for the simulated area were obtained from the hydrometeorological model WiMMed (Herrero et al., 2014). This is a distributed physical model which simulates the hydrological cycle. It generates maps of several meteorological variables: soil moisture, snow cover, runoff, stream flows, etc., from point-based meteorological data and distributed parameters related to vegetation, surface, physicochemical soil properties and information about groundwater.

WiMMed uses the following daily meteorological information as input data: cumulative precipitation; maximum, minimum and mean temperatures; total cumulative solar radiation; mean relative moisture and mean wind speed. WiMMed includes algorithms for spatial interpolation of these meteorological variables, which consider the available knowledge regarding the topography influence over each individual variable. By doing so, uncertainty in the estimation of these variables is reduced when data are scarce or show high spatial variability. In the case of temperatures, all available stations are used to calculate the linear relationship between maximum and minimum temperature with elevation for each day. Afterwards, residuals (difference between relationship and measurements taken at the stations) are interpolated for each day based on Inverse Distance Weighting (IDW) with the closest 5 stations. More information regarding methods and algorithms for meteorological interpolation can be found in Herrero et al. (2011).

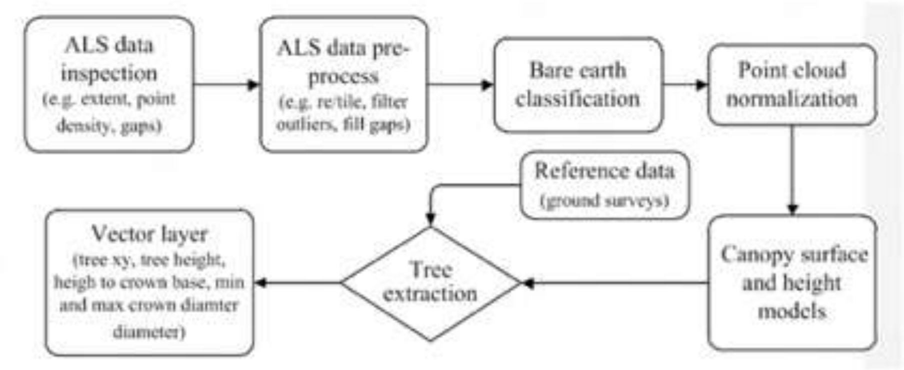
Among all WiMMed outputs, only temperatures were used in this study. In order to generate such maps, a model calibrated for Sierra Nevada in previous studies was used (Herrero et al., 2007; Pérez-Palazón et al., 2014; Pimentel et al., 2015). Temperature data came from 30 meteorological stations with records ranging from January 2001 to June 2014. Stations belong to 4 sensing networks: "Agencia Estatal de Meteorología" (AEMET), "Red de Información Agroclimática de la Junta de Andalucía" (RIA-JA), "Red de Seguimiento del Cambio Global del Organismo Autónomo de Parques Nacionales" (OAPN), and "Red del Proyecto Guadalfeo" (RPG), from the University of Córdoba and University of Granada. The stations are well distributed throughout the space and elevation gradient, being the highest at 3,097 m a.s.l. Time series have been corrected and filled using algorithms based on linear correlations among data.

S4.4 Airborne laser scanning data processing

Airborne Laser Scanning (ALS) data acquired within the Spanish National Plan for Aerial Orthophotography (PNOA, by its Spanish language acronym) were used to extract the individual tree layer used as input for the *INSTAR* model (see features of entity host in Table 4.1). Over the study area, the ALS flight was carried out in 2014. Data were delivered in LASer (LAS) binary file format containing X and Y coordinates (UTM Zone 30 ETRS 1989) and, ellipsoidal elevation Z (ETRS 1989), with up to four returns measured per pulse from REDIAM. The ALS nominal point density was 0.5 $points\ \mathrm{m}^{-2}$ with a vertical accuracy of less than 0.20 m. The data were provided as tiled (2 x 2 km) classified point clouds.

The data were examined for extent, point density, consistency, overlaps, and gaps (Figure S.49). Overlapped points (from adjacent scanning lines) were removed to avoid deriving skewed metrics and speed computation. Gap filling was achieved by merging data from additional flight lines when available.

Figure S.49: Flowchart of Airborne Laser Scanning (ALS) data processing and tree layer generation.



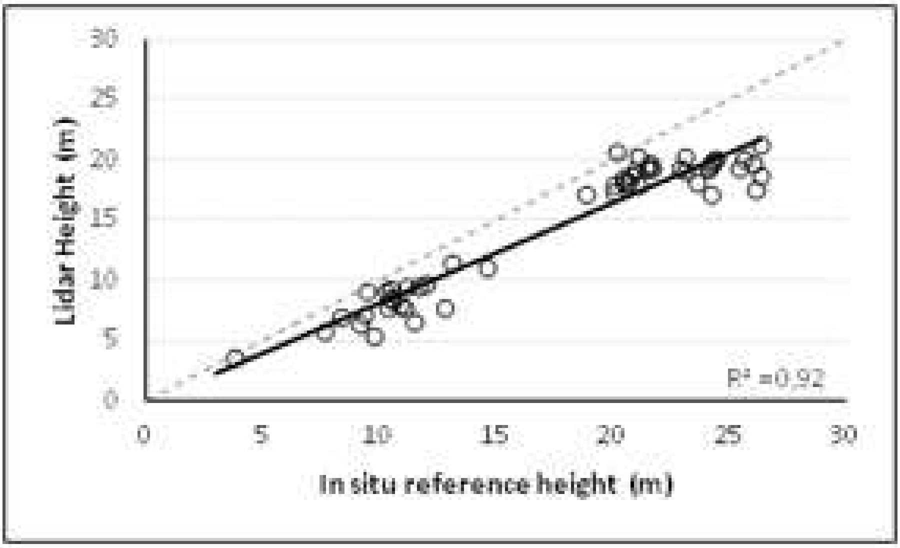
The accuracy of the existing point classification (e.g., ground, vegetation) was assessed and deemed insufficient for the purpose (i.e., identification of individual trees). Therefore, the tiled point clouds were re-classified (ground and non-ground) using the open source Multiscale Curvature Classification (MCC) algorithm (Evans and Hudak, 2007). All non-ground returns were considered vegetation over areas with no man-made features such as forests. The MCC algorithm was designed for forested environments on rough surfaces and was proved to produce the highest success rates at identifying ground and non-ground returns particularly for similar ALS flights (Evans and Hudak, 2007; Montealegre et al., 2015). Depending on flight characteristics, ALS point densities and topography, different scale and curvature parameters are optimal. The values of these parameters were determined by iterative tests with a scale parameter of 2 and a curvature parameter of 0.3 resulting in the least confusion between ground and vegetation points. With ground points classified, digital elevation models (DEM) were interpolated and used to compute the height above ground (i.e. normalised height) for the remaining points (i.e., vegetation heights). The normalised point cloud data were used to produce the canopy surface model (CSM, 2 m spatial resolution) needed to identify the individual trees present within the landscape.

The local maxima algorithm (i.e., Canopy Maxima), implemented in Fusion (an open software developed and maintained by R.J. McGaughey from USDA Forest Service), was used to identify the individual trees. The algorithm, similar to that reported in Popescu et al. (2002), uses a canopy height model to identify the local maxima within a variable-sized evaluation window. The window size is derived from the canopy height through the coefficients of a polynomial type function. These coefficients were adapted to the local conditions using field data collected in the study area (tree height, crown base height, and minimum and maximum canopy diameter). The coefficients were computed using data for all species. The threshold for tree identification was set to 4 m (trees below the threshold were ignored as the algorithm cannot cope with heavily intermingled crowns).

The agreement between the height recorded in the field and the ALS-derived height was computed using 52 trees clearly visible in the LiDAR data. Overall, the RMSE was 3.7 m with a negative bias (underestimation of field measurements) of 2.3 m. The relative RMSE for the heights was 21.7 %. Such values are within the expected range since the point cloud density was low which reduced the probability of hitting the crown apex.

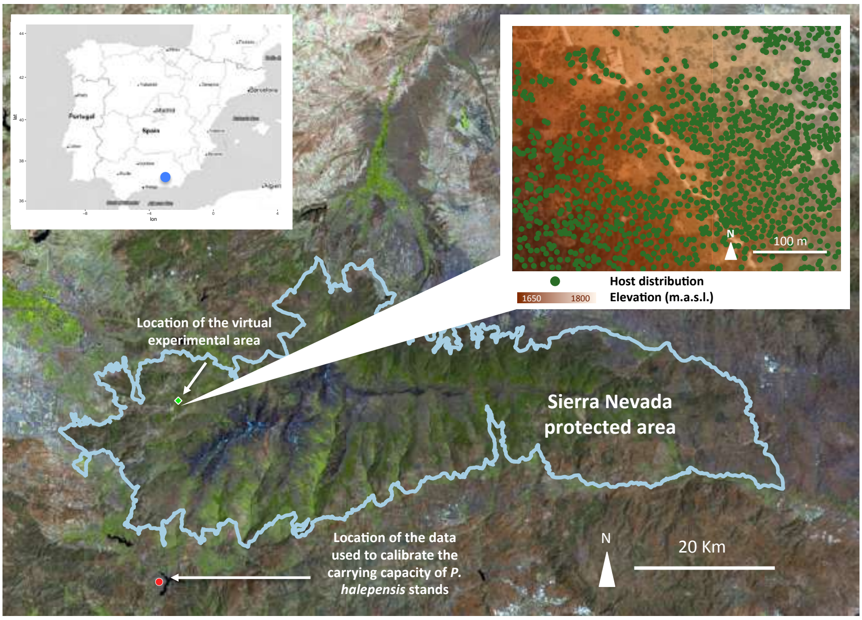
The overall tree extraction performed relatively well in areas where tree density was low (relative RMSE of 26 %) when compared with dense areas (relative RMSE of 47 %). It should be noted that the presented error metrics may be unstable as we only had four areas with *in situ* tree counts.

Figure S.50: Agreement between *in situ* and ALS-derived tree height (based on 60 individual measurements). The 1:1 line (perfect agreement) is in grey.



S4.5 Study area

Figure S.51: Map of the virtual experimental area location. Red dot indicates the location of the data used to calibrate the carrying capacity of *Pinus halepensis* stands. Detail image shows distribution of hosts as green spots.



S4.6 Phenology calibration

Figure S.52: Difference between observed and simulated average procession date, in number of days. Data refer to season 2008/2009 for each combination of parameters $T_{larvae-devel-high}$ and $T_{larvae-devel-internal}$. $T_{larvae-devel-low}$ fixed to -8 °C.

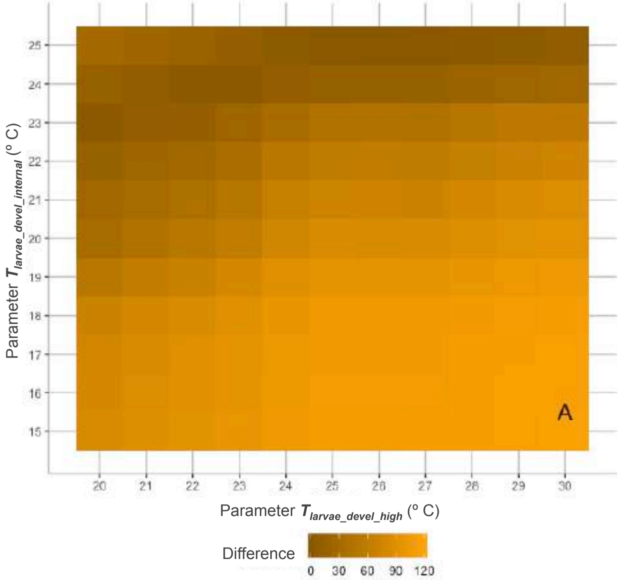


Figure S.53: Difference between observed and simulated average procession date, in number of days. Data refer to season 2009/2010 for each combination of parameters $T_{larvae-devel-high}$ and $T_{larvae-devel-internal}$. $T_{larvae-devel-low}$ fixed to -8 °C.

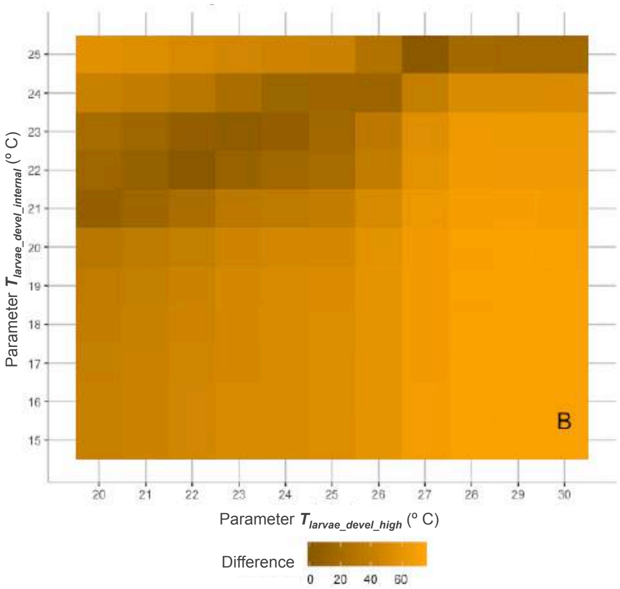


Figure S.54: Difference between observed and simulated average procession date, in number of days. Data refer to season 2010/2011 for each combination of parameters $T_{larvae-devel-high}$ and $T_{larvae-devel-internal}$. $T_{larvae-devel-low}$ fixed to -8 °C.

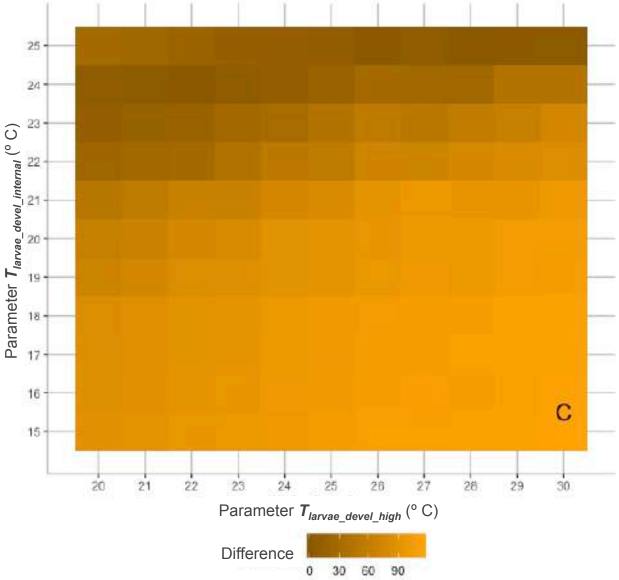
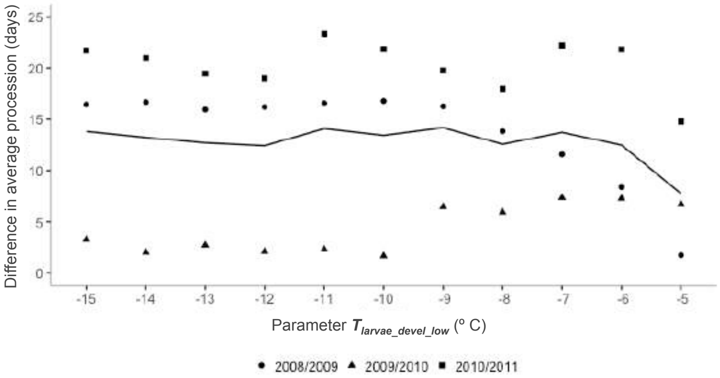


Figure S.55: Difference between observed and simulated average procession date, in number of days along $T_{larvae-devel-low}$ gradient. Data for each season (points) and across seasons (line) for parameter $T_{larvae-devel-high}$ fixed to 22 ℃ and parameter $T_{larvae-devel-internal}$ fixed to 23 ℃.



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