Dinámica post-incendio de la madera muerta e implicaciones de su manejo para las comunidades de insectos

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Y así fuimos nacidos nosotros,
los hijos de los días,
los averiguadores,
los buscadores de la vida.

(El Génesis, según los mayas)

Eduardo Galeano

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La presente tesis está basada en los siguientes artículos:

I. Molinas-González, C. R., A. B. Leverkus, S. Marañón-Jiménez, J. Castro. 2017. Fall rate of burnt pines across an elevational gradient in a Mediterranean mountain. *European Journal of Forest Research* 136:401–409.

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II. Molinas-González, C. R., J. Castro, A. B. Leverkus. 2017. Deadwood decay in a burnt Mediterranean pine reforestation. *Forests* 8:1–10.

Factor de impacto: 1.956

III. Molinas-González, C. R., J. Castro, A. González-Megías, A. B. Leverkus. 2019. Effects of post-fire deadwood management on soil macroinvertebrate communities. *Forests* 10:1046.

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Resumen

Los incendios recurrentes son una de las principales características de los ecosistemas mediterráneos. La recuperación de los procesos ecológicos y las comunidades bióticas tras este tipo de perturbación son procesos cuya duración depende de una multitud de factores. Entre ellos, la cantidad y calidad de los legados biológicos es de particular relevancia dado su efecto promotor sobre los ciclos biogeoquímicos y la sucesión secundaria. La madera quemada es uno de los legados estructurales más relevantes tras un incendio y, con diferencia, el más abundante en términos de biomasa, representando uno de los componentes de mayor importancia en los bosques de todo el mundo.

El manejo de la madera quemada tiene la capacidad de afectar diferentes aspectos de la dinámica post-incendio debido a que implica un importante cambio estructural del medio. En especial, cuando el manejo post-incendio incluye la extracción de la madera se produce una disminución en la cantidad y una modificación en la calidad de la materia orgánica en descomposición. El tipo de manejo que se plantee tras un incendio en relación a la madera quemada podría por tanto afectar a diferentes aspectos de la sucesión post-incendio como el reciclado de nutrientes y la recuperación de la biodiversidad.

En la presente tesis, he estudiado la dinámica post-incendio a medio plazo (10 años tras los tratamientos de la madera y 11 desde el incendio). He medido los efectos del manejo de la madera muerta sobre 1) la tasa de caída de arbolado, 2) la descomposición de la madera y 3) la abundancia y diversidad de macroartrópodos edáficos. Para ello, he utilizado un diseño experimental que consta de tres parcelas dispuestas a lo largo de un gradiente altitudinal, en cada una de las cuales se establecieron tres réplicas de tres tratamientos que difieren en el grado de manejo de la madera muerta: 1) Extracción, que implicó el corte de todos los árboles y triturado de las ramas; 2) Intervención intermedia, que corresponde a un corte parcial de la masa arbórea, dejando toda la biomasa in situ; y 3) No intervención, donde todos los árboles fueron dejados en pie y no se realizó ningún tipo de actuación.

En el capítulo 1, analizo la tasa de caída de arbolado tras el incendio. Aquí compruebo que la tasa de caída alcanzó al 100% de los árboles tras

5.5 años. Esta tasa de caída varió en función del diámetro de los árboles y la estructura impuesta por el tipo de manejo, independientemente de la altitud a la que se encontraban. A partir de estos resultados, se pudieron comprender mejor dos aspectos fundamentales de la dinámica del sistema. Primero, se esclareció el tiempo transcurrido para pasar de una estructura vertical a una horizontal. Segundo, se esclareció la estructura del hábitat resultante de distintos tipos de manejo, ya que el manejo determinó el tiempo de permanencia de los árboles.

En el capítulo 2 determino la tasa de descomposición de la madera muerta a través de un gradiente altitudinal. La descomposición es un proceso natural que determina el retorno de los nutrientes almacenados en la madera y que eventualmente se depositarán en el suelo. En este capítulo se pudo comprobar que la madera muerta perdió, en promedio, el 25% de su masa tras 10 años de estar en contacto con el suelo. La velocidad de este proceso varió en función del diámetro de los troncos, ya que los de mayor tamaño alcanzaron un mayor estado de descomposición. Como resultado, se sugiere que la descomposición de la madera muerta podrá proveer al suelo de los nutrientes almacenados en su interior. En este capítulo se concluyó que la descomposición es un proceso cuya velocidad varía a lo largo del gradiente altitudinal y que permitirá asegurar la rotación de los nutrientes entre la madera muerta y los suelos.

En el capítulo 3 analizo las implicaciones del manejo de la madera muerta sobre la abundancia y diversidad de las comunidades de macroartrópodos edáficos. Entre los resultados obtenidos, destaca que no sacar la madera quemada tuvo un efecto positivo, aunque muy pequeño, sobre la abundancia y riqueza de macroartrópodos edáficos. Este efecto probablemente resultó de que eliminar la madera quemada disminuyó la diversidad de microhábitats resultantes de los complejos procesos de caída y descomposición de la madera, así como la cantidad de recursos resultantes de su descomposición, disponibles para los macroartrópodos.

Como conclusión final, el manejo post-incendio afectó no solo a la cantidad de madera muerta disponible sino a su dinámica a lo largo del tiempo. Por un lado, la extracción de la madera elimina un componente mayoritario de biomasa en paisajes post-incendio que de otra forma cae al suelo de manera natural en un período de tiempo relativamente corto. Por otra parte, los troncos de mayor tamaño tuvieron una mayor tasa de descomposición que troncos de menor tamaño, probablemente debido a la presencia de una fauna especializada. En su conjunto, las características ecológicas derivadas de la manipulación de la madera post-incendio pueden repercutir en la recuperación de los macroartrópodos edáficos incluso una década después del manejo post-incendio.

Part I

Prólogo | Prologue

1. Introducción general

1.1 Perturbaciones

Los incendios son una de las perturbaciones naturales más importantes en los ecosistemas terrestres (Archibald et al., 2013; Bowman et al., 2009; Pausas and Keeley, 2009). Esto es así en sabanas tropicales (Pivello, 2011), bosques boreales (Hutto *et al.*, 2016) y bosques mediterráneos (Keeley *et al.*, 2012).

Los incendios ocurren en casi cualquier parte del mundo y se caracterizan por un determinado régimen (Bowman *et al.*, 2009, 2011). Dada una combinación de características relacionadas con la cantidad de combustible y el clima, el régimen de incendios de un ecosistema se caracteriza por una frecuencia, intensidad, estacionalidad y extensión de cada incendio, así como su variabilidad, a escala local (Archibald *et al.*, 2013; Hutto *et al.*, 2016; Pausas, 2019).

En función de la influencia de un determinado régimen de incendios sobre diferentes comunidades vegetales, se puede diferenciar entre ecosistemas dependientes, sensibles e independientes del fuego (Myers, 2006; Shlisky *et al.*, 2008). Dentro de los dependientes, como los de tipo mediterráneo, las especies han desarrollado rasgos adaptativos asociados a un régimen de incendios (He *et al.*, 2016; Pausas, 2019). Esto permite a las comunidades de tipo mediterráneo poseer una alta resiliencia a los incendios, siempre y cuando éstos ocurran dentro de los rangos naturales de su régimen (Díaz-delgado *et al.*, 2002).

El ser humano ha influido en el régimen natural de incendios en diferentes partes del mundo (Bird *et al.*, 2008; Bowman *et al.*, 2011; Doerr & Santín, 2016; Myers, 2006; Scott *et al.*, 2016). La fragmentación del paisaje y la deforestación han determinado que ecosistemas que rara vez habían experimentado incendios se estén quemando con mayor periodicidad e intensidad (Chen *et al.*, 2011; Cochrane & Barber, 2009; Myers, 2006; Pivello, 2011; Krawchuk *et al.*, 2009). Por el contrario, la exclusión del fuego puede determinar cambios en la estructura (Collins *et al.*, 2011) y la composición en ecosistemas asociados al fuego (Knuckey *et al.*, 2016; Nagel & Taylor, 2005; Swaine *et al.*, 1992). Los cambios en la ocurrencia y las características de los incendios pueden, a su vez, interactuar con otros factores, tales como el cambio climático (Dale *et al.*, 2001), el establecimiento de especies no nativas (Coffman *et al.*, 2010) y el manejo post-incendio (Bowd *et al.*, 2018), y producir consecuencias ecológicas imprevisibles (Leverkus *et al.*, 2018a; Foster *et al.*, 2016).

En la región mediterránea, la interacción entre el clima (Cramer *et al.*, 2018), la vegetación, el manejo (Pausas & Fernández-Muñoz, 2012) y otras características del paisaje han creado unas condiciones que se traducirán en una mayor frecuencia e intensidad de incendios (Cramer *et al.*, 2018; Keeley & Pausas, 2019; Ruffault *et al.*, 2016). Entre otros motivos, los paisajes se han vuelto más inflamables por la acumulación de combustible (Pausas & Fernández-Muñoz, 2012), debido principalmente al abandono de tierras agrícolas, la ganadería, las repoblaciones del siglo XX (Moreno *et al.*, 2014) y a la conectividad a nivel de paisaje de parches inflamables (Garrido Mesa, 2019). Todo esto genera que en muchos casos se superen los esfuerzos de prevención y extinción de los incendios (Turco *et al.*, 2017). Por lo tanto, el conocimiento de la dinámica post-incendio de la madera muerta y de las implicaciones de su manejo para las comunidades de plantas y animales se hace cada vez más necesario (Leverkus *et al.*, 2018a; Thorn *et al.*, 2018).

Dado que los incendios forestales pueden tener efectos negativos sobre los valores socio-económicos y naturales (Alcasena *et al.*, 2017; Bodi *et al.*, 2012) e incluso suponer una amenaza para los paisajes forestales de la región mediterránea (Costa *et al.*, 2011; Dupire *et al.*, 2019; Koutsias *et al.*, 2013; Michetti & Pinar, 2019; Pausas & Fernández-Muñoz, 2012), es necesario establecer pautas de manejo post-incendio que favorezcan la regeneración del ecosistema (Pons & Rost, 2017; Raftoyannis & Spanos, 2005; Leverkus *et al.*, 2018b). Los incendios suponen, entre otras cosas, una oportunidad para replantear manejos pasados (Leverkus *et al.*, 2019a) y promover comunidades más resilientes (Pausas *et al.*, 2004), esto hace que sea necesario investigar el balance de las estrategias de manejo en cuanto a cómo favorecen estos aspectos positivos frente a los negativos de los incendios.

1.2 Dinámica post-incendio

El papel estructural de la madera muerta

La madera muerta representa un importante componente de los bosques (D'Amato *et al.*, 2011; Lassauce *et al.*, 2011). Se estima que a nivel mundial la cantidad de madera muerta puede contener 73 ± 6 Pg de carbono (Pan *et al.*, 2011). Incluyendo la madera muerta que permanece en pie junto con la que se encuentra en el suelo pueden representar entre un 10-20 % de la biomasa total en bosques boreales (Clark *et al.*, 2002; Harmon *et al.*, 1993; Krankina & Harmon, 1995) y hasta un 33 % en bosques tropicales (Clark *et al.*, 2002). La importancia ecológica de la madera muerta fue inicialmente reconocida en sistemas forestales boreales y templados sometidos a la explotación de productos maderables (Harmon *et al.*, 1986; Laudenslayer *et al.*, 2002). Su importante papel estructural y como hábitat de numerosas especies ha sido demostrado en numerosos tipos de bosque alrededor del planeta (Hämäläinen *et al.*, 2014; Harmon *et al.*, 1986; Krajick, 2001). Esto hace que la madera muerta sea actualmente reconocida como promotora de biodiversidad (Stokland *et al.*, 2012) y como un componente importante en los programas de manejo y monitoreo de bosques en Europa (Lassauce *et al.*, 2011).

La importancia de la madera muerta trasciende los estados en que se pueda encontrar un bosque. En particular, tras un incendio los ecosistemas presentan un estado profundamente transformado (Angers *et al.*, 2011), con un mosaico de escenarios entre los que se incluyen masas de árboles parcialmente vivos, muertos pero que aún permanecen en pie, troncos caídos y remanentes inalterados (Swanson *et al.*, 2011). Este tipo de paisajes conforman los denominados complejos de sucesión temprana, que se caracterizan por poseer condiciones únicas, determinadas por una alta productividad, cadenas alimenticias complejas, grandes flujos de nutrientes y una alta complejidad estructural y espacial (DellaSala *et al.*, 2014).

Las estructuras diversas, tanto las vivas como las inertes, que permanecen tras un incendio, son denominadas "legados biológicos" (Franklin & MacMahon, 2000; Swanson *et al.*, 2011). Dentro de estos legados biológicos, los árboles muertos pero que aún permanecen en pie, junto con los vivos que experimentan alguna demora en su mortalidad, representan uno de los legados estructurales más importantes (Harmon *et al.*, 1986; Russell *et al.*, 2006). Conocer el tiempo de permanencia de los legados estructurales y las causas que determinan su distribución espacial y temporal es de suma importancia debido a que son el punto de partida de la regeneración post-incendio (Marzano *et al.*, 2012). En particular, una representación exhaustiva del tiempo de permanencia de los árboles muertos en pie es esencial para comprender las reservas de madera muerta y para informar sobre la dinámica de transición entre la madera muerta en pie y la que se encuentra en el suelo (Harmon *et al.*, 2013; Russell *et al.*, 2015). Los árboles que permanecen en pie poseen una rica variedad de fauna y flora asociadas (Drapeau *et al.*, 2009; Hämäläinen *et al.*, 2014; Laudenslayer *et al.*, 2002). Dependiendo de la especie, los árboles quemados pueden permanecer erguidos durante años a décadas, aunque eventualmente su colapso es inevitable (Aakala *et al.*, 2008; Yatskov *et al.*, 2003).

El manejo post-incendio genera numerosas estructuras nuevas en el paisaje (p.ej., pilas de troncos, tocones y árboles caídos), pero también altera la cantidad y distribución espacial de los árboles en pie, que son usados como perchas por animales dispersores de semillas (Hebblewhite *et al.*, 2009; Herrando *et al.*, 2009; Leverkus & Castro, 2017). Estos árboles muertos pero que permanecen en pie permiten el establecimiento de conexiones entre diferentes paisajes o parches a través de la distribución de semillas (Castro *et al.*, 2012; Cavallero *et al.*, 2013). La tasa de caída de estos árboles muertos, que puede verse afectada por el manejo post-incendio, puede definir el rango temporal en que se cumpla la importante función ecológica que pueden desempeñar (Franklin *et al.*, 1987). El tiempo de residencia del arbolado muerto depende de factores relacionados con la causa de muerte, el tamaño y la especie de árbol, la velocidad de descomposición y el tipo de manejo (Aakala *et al.*, 2008; Garber *et al.*, 2005; Mitchell & Preisler, 1998; Vanderwel *et al.*, 2006).

El manejo post-incendio puede afectar al tamaño y a la distribución espacial de árboles que permanezcan en pie (Beschta *et al.*, 2004) y puede, por tanto, afectar a los procesos que determinan el cambio gradual en las condiciones ambientales lo largo de la sucesión (Kovács *et al.*, 2017; Lochhead & Comeau, 2012; Ma *et al.*, 2010).

Descomposición de la madera muerta

La descomposición de la madera es un proceso natural mediante el cual la compleja estructura de la madera es reducida a su forma mineral a través del tiempo (Swift, 1977). La liberación de los nutrientes retenidos dentro de la madera muerta (Ganjegunte *et al.*, 2004) aumenta la fertilidad del suelo y acelera los procesos microbiológicos tales como la inmovilización de nitrógeno y fósforo (Marañón-Jiménez & Castro, 2013).

La velocidad del proceso de descomposición puede verse afectado por la dinámica de caída del arbolado. El cambio de una estructura vertical a una horizontal permite que una gran cantidad de biomasa pase a formar parte del banco de madera muerta del suelo (Franklin *et al.*, 1987; Siitonen, 2001), lo que representa un depósito potencial de nutrientes que pueden contribuir a la regeneración de la vegetación (Harmon *et al.*, 2013). La diferencia entre una estructura vertical y horizontal de la madera muerta se da fundamentalmente en la tasa de descomposición y el tipo de hábitat que representa (Franklin *et al.*, 1987; Song *et al.*, 2017).

Cuando la madera muerta alcanza el suelo, su descomposición se acelera, promoviendo el retorno de los nutrientes contenidos en ella (Song *et al.*, 2017; Wei *et al.*, 1997; Merino *et al.*, 2005). Por ello, la tasa de descomposición puede tener importantes consecuencias para las propiedades del suelo tras un incendio (Marañón-Jiménez & Castro, 2013). Por otra parte, la madera muerta se convierte en uno de los hábitat menos conocidos pero de mayor biodiversidad en los bosques europeos (Marchetti, 2004; Seibold *et al.*, 2015; Siitonen, 2001) y del mundo (Lassauce *et al.*, 2011). Se estima que hasta un 25 % de todas las especies presentes en un bosque se encuentra asociadas a la madera en descomposición (Stokland *et al.*, 2012). Principalmente, artrópodos, moluscos y anélidos se benefician de la madera muerta debido a que ésta mantiene estables las condiciones de humedad de su entorno (Maser *et al.*, 1984; Ulyshen *et al.*, 2011).

El conocimiento de los factores que determinan la tasa de descomposición de la madera tras un incendio es, por lo tanto, relevante para comprender el tiempo de residencia de los troncos. Este tiempo de residencia, define la cantidad de tiempo que los bosques almacenan el carbono ya sea en sus tejidos vivos o muertos, lo que determina la condición de un ecosistema de funcionar como fuente o sumidero de carbono (Chave *et al.*, 2009; Keith *et al.*, 2009).

La descomposición de la madera depende de factores ambientales como la temperatura (Liu *et al.*, 2013) y la humedad (Herrmann & Bauhus, 2013). Entre los factores bióticos se encuentran la comunidad de organismos descomponedores (Mackensen *et al.*, 2003; Ulyshen, 2016, 2014), la especie de árbol del cual provino y el diámetro de la madera (Cornwell *et al.*, 2009).

El tamaño de los troncos puede determinar la identidad de las especies detritívoras que colonizan la madera en descomposición y estos pueden, a su vez, afectar los ensambles de especies de descomponedores. Por ejemplo, diversos grupos de artrópodos modifican el sustrato leñoso a través de la elaboración de canales y túneles que fraccionan la madera muerta. Entre estos grupos se encuentran la suprafamilia de Termotoidae, varias familias de coleópteros (Cerambycidae, Buprestidae, Tipulidae etc.) y algunos grupos de hormigas, tales como *Camponotus spp* (Ulyshen, 2016). El fraccionamiento de la madera aumenta el área de exposición para la colonización de los microorganismos (hongos en su gran mayoría). No obstante, muchos de los taxones asociados a los procesos de descomposición pueden actuar de manera antagónica, regulando la abundancia de descomponedores a través de la microbivoría y la depredación (Giller, 1995).

El fuego y la fauna edáfica

Los incendios consumen gran parte de la materia orgánica aérea (Brown & Smith, 2000), afectando tanto al suelo como a las comunidades que lo habitan (Certini, 2005). Sin embrago, su efecto sobre la biota dependerá del horizonte del suelo afectado, las características del incendio y la comunidad de organismos estudiada (Certini, 2005; Korobushkin *et al.*, 2017; Santín & Doerr, 2016).

El fuego puede afectar directamente a la fauna invertebrada que habita sobre el suelo al matar a una gran cantidad de individuos o aumentar su susceptibilidad a la depredación (McCullough *et al.*, 1998; New, 2014; Swengel, 2001). Sin embargo, la fauna posee distintos mecanismos que le permiten sobrevivir a las altas temperaturas alcanzadas durante un incendio (New, 2014). Estos mecanismos están principalmente relacionados con la movilidad de los individuos y la presencia de determinados refugios (Lawrence, 1966); por ejemplo, algunos grupos de hormigas pueden escapar de las llamas usando diversos tipos de refugios (Cane & Neff, 2011; Swengel, 2001). Sin embargo, el fuego puede afectar directamente a sus recursos o el modo en que los obtienen y de esta manera reducir drásticamente las poblaciones que hayan sobrevivido al incendio (Caut et al., 2014).

Para los organismos edáficos, las capas orgánicas del suelo representan una barrera natural frente a las altas temperaturas alcanzadas a nivel superficial, de manera que el efecto del fuego sobre las comunidades que habitan el suelo se encuentra más relacionados con su profundidad y el grado de consumo de la capa orgánica durante el incendio (Huebner *et al.*, 2012; Wikars & Schimmel, 2001). Este caso la movilidad de los invertebrados que habitan las capas orgánicas del suelo, depende del tamaño del cuerpo y de la capacidad de excavar a través del suelo, que difiere incluso entre organismos del mismo tamaño (Certini, 2005; Verma & Jayakumar, 2012). La fauna del suelo presenta una gran cantidad de rasgos y atributos que determinan la forma en cómo responden a los cambios producidos tras un incendio en especial aquellas que viven en un rango muy restringido de hábitat (Gongalsky *et al.*, 2012; Pressler *et al.*, 2019), por ejemplo las comunidades saprófagas pueden resultar entre las más comprometidas tras un incendio debido a condiciones hidroclimáticas desfavorables y falta de recursos adecuados entre los parches quemados (Korobushkin *et al.*, 2017).

La recuperación de la fauna tras un incendio se ve principalmente beneficiada por la creación de nuevos nichos, incluyendo la apertura de nuevos espacios (Cavallero *et al.*, 2013; Lawrence, 1966; Nappi *et al.*, 2004). La creación de nuevos recursos (en gran medida en la forma de madera muerta) provee refugio y alimento para una gran variedad de organismos, especialmente los de hábitos saproxílicos (Seibold *et al.*, 2015; Ulyshen, 2018). En cuanto a la fauna subterránea, la recuperación es variable para cada grupo taxonómico (Gongalsky & Persson, 2013; Korobushkin *et al.*, 2017). Donde, las condiciones microclimáticas y el aumento del recurso a través de la sucesión de la comunidad vegetal y el estado del suelo tras el incendio parecen ser indispensables para su recuperación (Bezkorovainaya *et al.*, 2007; Korobushkin *et al.*, 2017).

Los mecanismos que guían la recolonización de la fauna edáfica son poco conocidos, pero se ha sugerido que puede ocurrir a partir de individuos que han sobrevivido al fuego y a través de la colonización desde parches y corredores que no han sido alcanzados por las llamas (Zaitsev *et al.*, 2014). Sin embargo, las relaciones entre la estructura del hábitat por encima del suelo y el efecto sobre las comunidades que habitan por debajo de la superficie del suelo son inciertas y mucho menos estudiadas con relación a los organismos que habitan sobre la superficie del suelo (Decaëns, 2010; Veresoglou *et al.*, 2015).

El manejo post-incendio puede determinar una importante alteración del suelo (Wagenbrenner *et al.*, 2015). Estos cambios en las condiciones bióticas pueden influir sobre algunos de los factores que influyen en la diversidad de la fauna del suelo, como la humedad y la materia orgánica (Doblas-Miranda *et al.*, 2009). Por otra parte, el manejo post-incendio, determina no solo la abundancia de la madera sino también la distribución de este recurso, (Monsanto & Agee, 2008) produciendo efectos muy diferentes sobre la composición y abundancia de la fauna (Azeria *et al.*, 2012; Mateos *et al.*, 2011; Pons, 2015). No obstante, la gran cantidad estudios se enfocan en organismos que actúan en las capas más superficiales del suelo (Nielsen *et al.*, 2010; Veresoglou *et al.*, 2015), en cambio los factores que afectan la fauna subterránea en los bosques quemados, incluidos los factores relacionados con el manejo de la madera quemada, han sido menos estudiados (Zaitsev *et al.*, 2016).

1.3 Aspectos del manejo y sus consecuencias sobre la dinámica post-incendio

La estrategia más comun de manejo tras los incendios y otras perturbaciones alrededor del mundo es la extracción rápida de los restos maderables (Lindenmayer *et al.*, 2008; Müller *et al.*, 2019). Entre las labores comunes aparte de la extracción de la madera se encuentran la quema, el astillado y la trituración de ramas (Figura 1.1) y restos no aprovechables (DellaSala *et al.*, 2006; Lindenmayer & Noss, 2006). Estos procesos se encuentran mecanizados en la mayoría de los países industrializados, donde la producción implica un menor riesgo para los trabajadores y un ahorro en el tiempo de ejecución de las labores de extracción (Wagenbrenner *et al.*, 2015).

Las motivaciones que guían este tipo de manejo se centran en recuperar parte de la madera de los bosques afectados y facilitar otras actividades de restauración (McIver & Starr, 2001; Müller *et al.*, 2019; Sessions *et al.*, 2004). Sin embrago, en muchos países mediterráneos la explotación económica de la madera quemada no resulta rentable (por ejemplo Leverkus *et al.* (2012)). Además, en las últimas décadas se ha cuestionado la idoneidad de retirar la madera muerta desde el punto de vista ecológico, ya que puede resultar en un aumento de la erosión (Malvar *et al.*, 2017), afectar negativamente el ciclo de nutrientes y el secuestro de carbono (Brais *et al.*, 2000; Marañón-Jiménez *et al.*, 2011) y resultar aditivo a otras perturbaciones (Bradford *et al.*, 2012; Leverkus *et al.*, 2015b). Recientes meta-análisis a escala global indican que retirar la madera tras perturbaciones puede afectar negativamente a la biodiversidad (Thorn *et al.*, 2018) y a la provisión de servicios ecosistémicos (Leverkus *et al.*, 2019b). Sin embargo, una de las principales conclusiones de dichos meta-análisis es que existe una enorme heterogeneidad en la respuesta de distintas variables al manejo, de forma que no se pueden generalizar a escala global los efectos de retirar la madera sobre los ecosistemas.

Como resultado de los efectos del manejo sobre los diversos procesos ecológicos en la sucesión post-incendio, en especial cuando se modifica la cantidad y distribución de la madera muerta tiene el potencial de afectar a la regeneración natural y los servicios proveídos por los ecosistemas

***Figura 1.1: Manejo post-incendio de la madera muerta*:** Corte y desrramado de árboles (**izquierda**), extracción de troncos (**centro**) repoblación con pinos (**derecha**), en un lugar cercano al sitio de estudio. Fotos tomadas por el autor en febrero del 2015.

(Leverkus *et al.*, 2018b). Sin embargo, la extracción de la madera muerta continúa siendo utilizada como una práctica habitual de manejo que depende en gran medida del contexto en el que sea utilizada (Pons & Rost, 2017; Royo *et al.*, 2016; Schmiegelow *et al.*, 2006). De manera que, la elección del tipo de manejo que mejor se adapte a cada contexto, recaerá en nuestra capacidad para predecir sus efectos a largo plazo (Moreira *et al.*, 2012).

2. Objetivos de la tesis

Esta tesis abarca los procesos relacionados con la madera muerta tras un incendio. Me centro en los factores que afectan la velocidad de caída de los árboles, la descomposición de la madera y la diversidad de la fauna edáfica. Esta última fue estudiada en función del manejo de la madera quemada tras 10 años desde su implementación. El análisis de los diferentes aspectos de la presente tesis (Figura 2.1) permitirá reflejar los efectos de la gestión de los montes quemados y el estado de recuperación de las comunidades de macroartrópodos edáficos.

Objetivos específicos

La presente tesis está estructurada en 3 capítulos detallados a continuación:

Capítulo 1. *Cuantificar la tasa de descomposición de la madera muerta a través de un gradiente altitudinal.* Planteo como hipótesis que la tasa de caída dependerá tanto del gradiente altitudinal como del tratamiento post-incendio.

Capítulo 2. *Cuantificar la tasa de descomposición de la madera muerta a través de un gradiente altitudinal.* Aquí analizo una serie temporal para estimar la tasa de descomposición de la madera quemada a lo largo de 10 años tras el incendio. Planteo como hipótesis que el proceso de descomposición dependerá de la altitud sobre el nivel del mar y el diámetro de los troncos.

Capítulo 3. *Determinar el efecto del manejo de la madera quemada sobre la abundancia y diversidad de las comunidades de macroartrópodos edáficos.*Planteo como hipótesis que el tipo de manejo de la madera quemada afectará tanto a la abundancia como a la composición de las comunidades de macroartrópodos edáficos, que serán menos abundantes y diversos bajo suelos sin madera en descomposición.

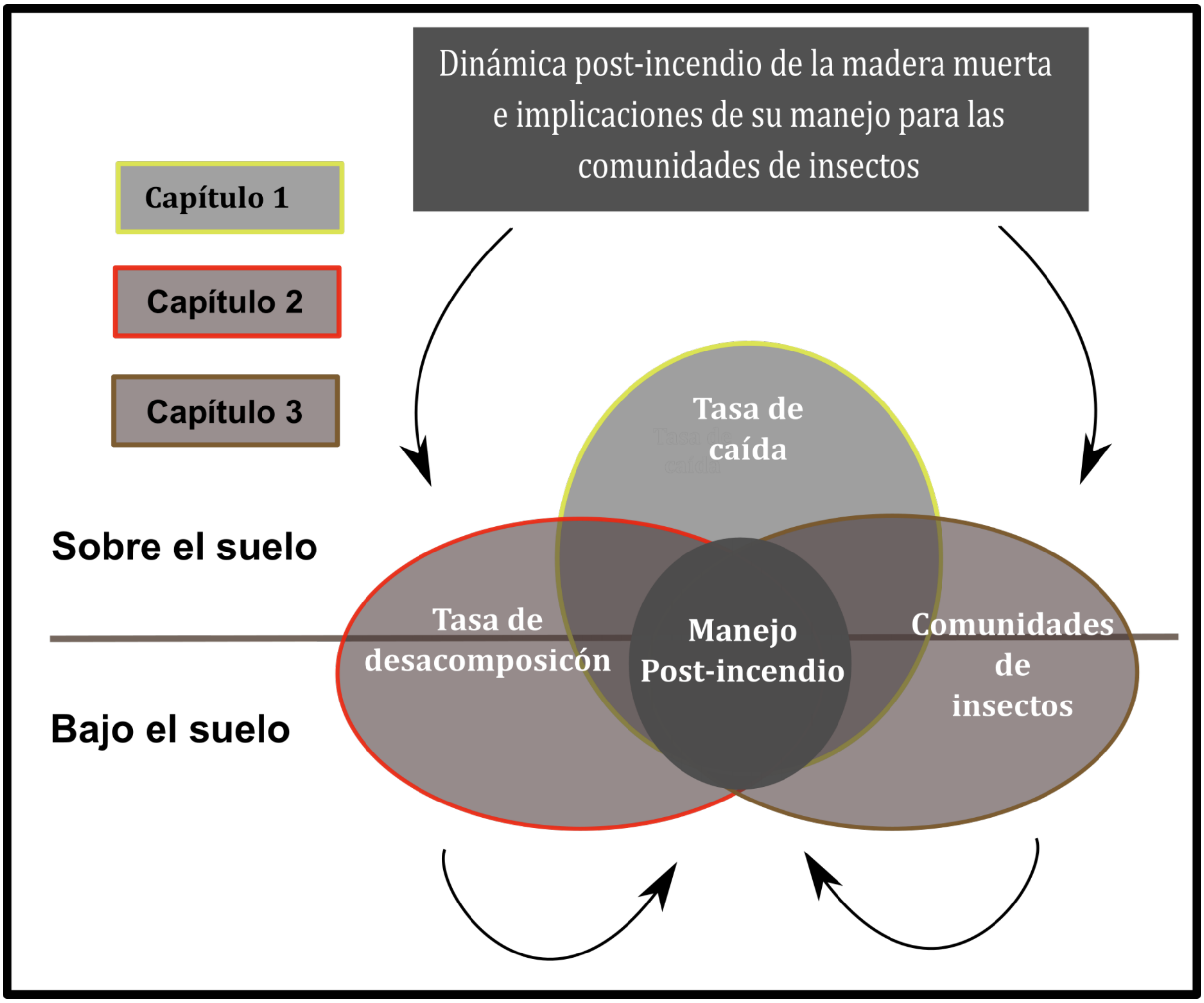


Figura 2.1: Esquema conceptual de los aspectos que se abarcan en la dinámica post-incendio de la madera muerta e implicaciones de su manejo para las comunidades de insectos.

3. Meteriales y métodos generales

3.1 Área de estudio

La presente tesis se enmarca dentro del complejo de parque natural y nacional de Sierra Nevada (suroeste de España). El clima en el área es de tipo mediterráneo con veranos cálidos y secos, inviernos suaves y húmedos, con precipitaciones concentradas en primavera y otoño. Corresponde a un típico ecosistema de montaña mediterránea, con caídas de nieve que se registran de manera persistentes durante los meses de noviembre y marzo, por encima de los 2000 metros de altura (Castro *et al.*, 2002).

La vegetación, se distribuye en función de sus requerimientos ecológicos y restricciones bioclimáticas, consiste de especies herbáceas, arbustiva como; *Ulex parviflorus*, *Adenocarpus decorticans*, *Juniperus oxycedrus*, *Crataegus monogyna*, *C. granatensis* entre otros, parches aislados de quercíneas; *Quercus ilex*, *Q. rotundifolia* y *Q. pyrenaica*, masas boscosas de diferentes especies de pinos autóctonos *(P. sylvestris)* y de repoblación *(Pinus halepensis, P. pinaster, P. nigra* y *P. sylvestris)* (Valle, 2003).

La mayor parte de los pinares son el resultado de una extensa labor de repoblación realizada casi 60 años atrás con el fin de aumentar la masa arbórea y de recuperar suelos degradados (Gómez-Aparicio *et al.*, 2009). Estas repoblaciones se realizaron utilizando terrazas, donde cada escalón se compone de una pendiente pronunciada de aproximadamente 1 m de altura y 3 m de ancho, siendo esta la práctica común en zonas de montañas con una marcada pendiente (Garrido Mesa, 2019; Leverkus *et al.*, 2012).

La alta competencia y una reducción en la entrada de semillas impuesta por la alta densidad de pinos (carca de 1000-1500 pies por hectárea tabla 3.1), resultó en una baja riqueza y diversidad de especies vegetales (Gómez-Aparicio *et al.*, 2009). Este tipo de sistemas caracterizados por una alta densidad de individuos coetáneos, representa alrededor del 80 %

de las masas boscosas presentes dentro del Parque Natural y Nacional de Sierra Nevada (Bonet *et al.*, 2009).

Tabla 3.1: Localización y características de las parcelas de estudio

	Parcelas		
	1	2	3
Coordenadas[1]	36° 57´ 12.1” N 03° 29´ 36.3” W	36° 58´ 11.9” N 03° 30´ 1.7” W	36° 58´ 6.5” N 03° 28´ 49” W
Altitud (m s.n.m.)[1]	1477	1698	2053
Pendiente (%)[2]	30.3	28.7	31.4
Densidad de pinos pre-incendio	1.480 ± 50	1.060 ± 70	1.050 ± 40
Superficie (ha)	17.7	23.9	31.7
Temperatura mínima diaria (°C)[3]	6.8 ± 0.2	5.6 ± 0.2	3.4 ± 0.2
Temperatura máxima diaria (°C)[3]	17.1 ± 0.2	16.2 ± 0.2	13.4 ± 0.2
Precipitación media anual. (mm)[3]	536 ± 41	550 ± 40	630 ± 42
Densidad del suelo (g cm $^{-3}$)[4]	1.25 ± 0.06	1.34 ± 0.07	1.15 ± 0.06

[1] Medidas en el centro de cada parcela

[2] Media de la pendientes de cada réplica (sub-parcelas)

[3] Datos obtenidos del Centro Andaluz de Medio Ambiente (CEAMA)

[4] Datos obtenidos de (Marañón-Jiménez *et al.*, 2013a))

Los trabajos de silvicultura en zonas del complejo de Sierra Nevada fueron el resultado de actuaciones que buscaban disminuir el riesgo de incendios en lugar de una finalidad ecológica, en especial la apertura de corta fuegos y líneas de defensa han marcado profundamente el paisaje en todo el entorno natural de Sierra Nevada (Garrido Mesa, 2019).

En septiembre del 2005, un incendio afectó un área total de 3420 hectáreas, de las cuales 1300, correspondían a plantaciones de pinos de entre 35 a 45 años de antigüedad (Castro *et al.*, 2010). Fue un incendio de copa que afectó a gran parte de la vegetación quemando hojas, ramas y calcinando los troncos de los árboles a través de un gradiente altitudinal de entre 1180-2460 m. (sobre el nivel del mar). No obstante, el fuego no afectó de igual manera a toda la masa forestal quedando remanentes boscosos inalterados o parcialmente afectados, como consecuencia de la topografía y dirección del viento durante el incendio.

3.2 Diseño experimental

Entre abril y junio del 2006 (7-9 meses tras el meses tras el incendio), la Consejería de Medio Ambiente de la Junta de Andalucía procedió a establecer tres parcelas de aproxidamente 25 hectáreas cada una. Cada parcela resultó homogénea en cuanto a la intensidad del incendio (alta), orientación (suroeste), pendiente (cerca de 30.1 %) y roca madre (micaesquistos del complejo nevado-filabride). Las especies de pinos quemados que permanecieron en cada parcela variaron a través de un gradiente de elevación y humedad (Tabla 3.1; Figura 3.1):

La parcela 1 se encuentra entre los 1420-1560 m. sobre el nivel de mar, estaba dominada por el pino resinero o marítimo (*Pinus pinaster*) junto con el pino laricio (*P. nigra*).

La parcela 2 se encuentra entre 1588-1775 m, estaba dominada por el pino laricio (*P. nigra*).

La parcela 3 se encuentra entre 1970-2123 m, estaba dominada por el pino albar (*P. sylvestris*).

El diseño experimental final corresponde a un diseño en bloques complemente aleatorizados (Quinn & Keough, 2002).

Tratamientos de la madera quemada

En cada una de las parcelas se establecieron tres réplicas que varían en la intensidad de manejo de la madera quemada (figura 3.2).

Extracción (Ex). Corte y desramado de los árboles y triturado de ramas y restos de menos grosor (procedimiento habitual). Los troncos fueron apilados manualmente (en grupos de 10-15) para su posterior extracción, sin embargo, este paso no pudo realizarse debido al arreglo espacial del diseño experimental.

Intervención intermedia (Ii). Corte del 90 % de los árboles, desramado y troceado del tronco en 2-3 trozas, quedando toda la biomasa in situ. Los restos de madera cubrían en torno al 40 % de la superficie del suelo (Castro *et al.*, 2011).

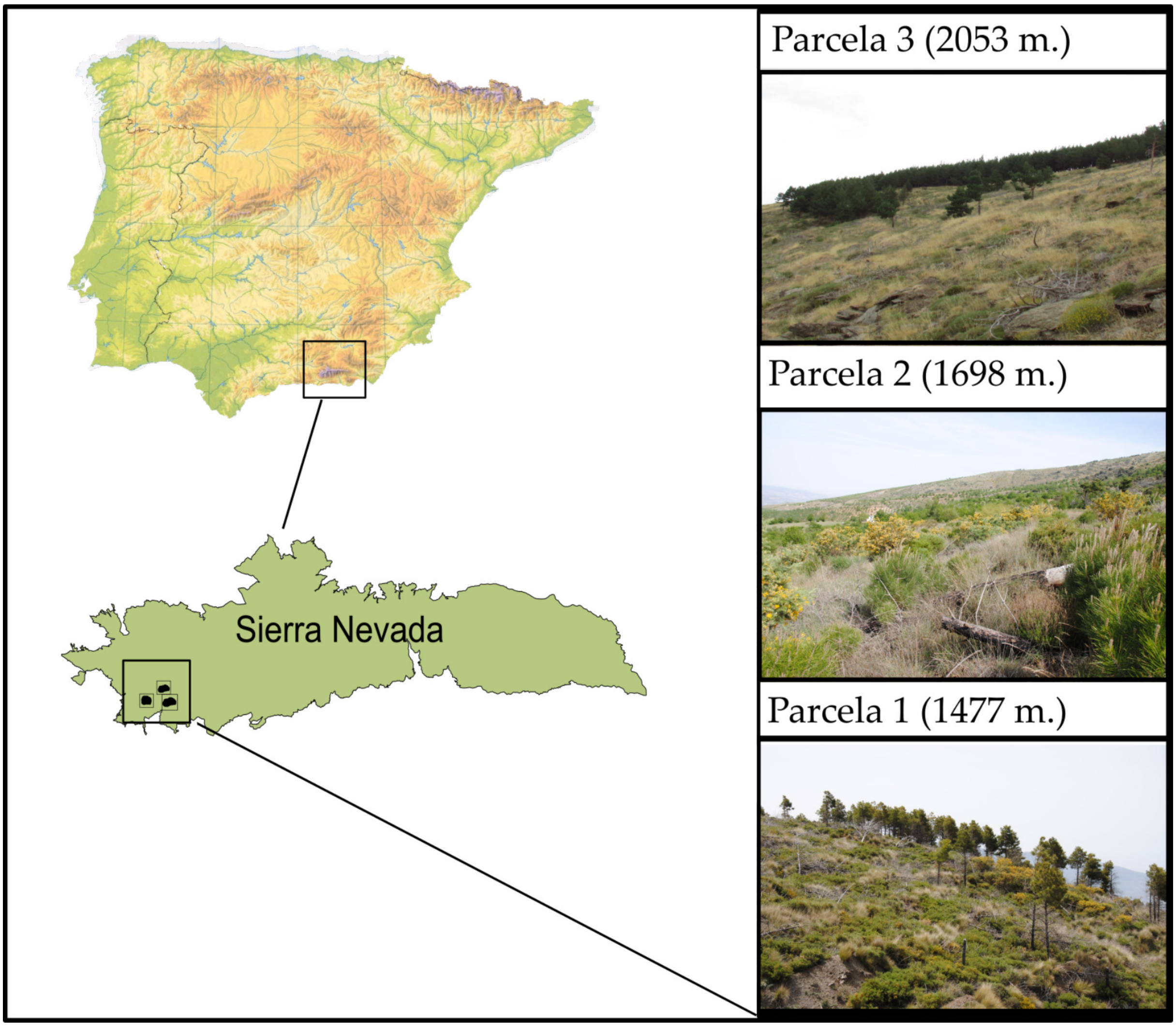


***Figura 3.1: Sitio de estudio*:** localización y detalle de las tres parcelas utilizadas en esta tesis.

No intervención (NI). En este tratamiento todos los árboles fueron dejados en pie, no se realizo intervención alguna.

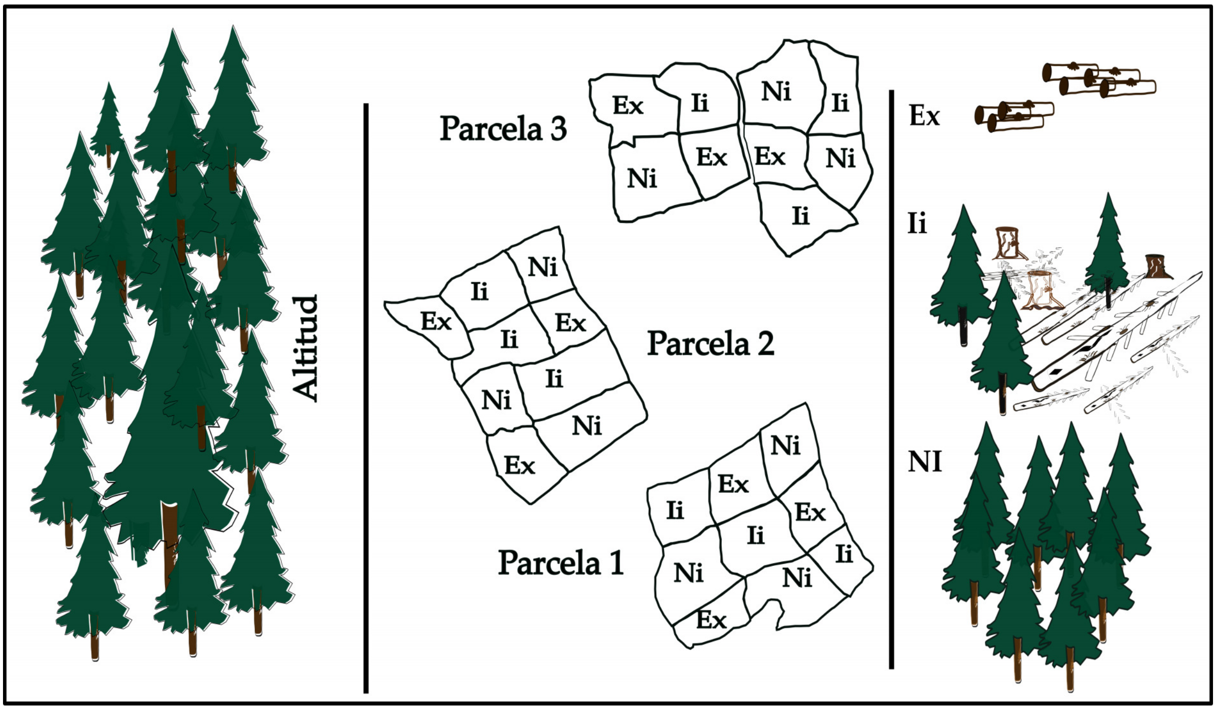


Figura 3.2: Diseño experimental: Se han establecido tres parcelas a lo largo de un gradiente altitudinal, con tres réplicas de cada tratamiento de la madera muerta: No intervención (NI), Extracción (SL), e Intervención intermedia (Ii).

Cambios en el sistema a partir del manejo y los tratamientos de la madera quemada

La comunidad vegetal dos años tras el incendio estuvo caracterizada por especies vegetales anuales y rebrotadoras. La cobertura de la vegetación perenne (fuese herbácea o leñosa) fue de 77 % en el tratamiento NI, 72 % en Ii y 64 % en Ex (Leverkus *et al.*, 2014).

Durante el 2010, la Consejería de Medio Ambiente de la Junta de Andalucía plantó alrededor de 10,800 plántulas de especies arbustivas y arbóreas (*Crategus monogyna*, *Berberis hispanica*, *Quercus pyrenaica* y *Q. ilex subsp. ballota*) cubriendo alrededor de 45 hectáreas distribuidas entre las parcelas 1, 2 y 3 (Leverkus *et al.*, 2012).

Selección de tratamientos y paracelas de acuerdo a los objetivos de cada capitulo

Para el desarrollo de esta tesis se han seleccionado los tratamientos y las parcelas más relevantes para los objetivos de cada capítulo, como se describe a continuación.

Para el capítulo 1, donde se analiza la tasa de caída de arbolado, se muestrearon los tratamientos donde había árboles quemados en pie (Ii y NI) en cada una de las tres parcelas. Dado que en el tratamiento de Intervención intermedia se realizó el corte sistemático de 9 árboles de cada 10, la diferencia en la cantidad de árboles en pie entre ambos tratamientos es de alrededor del 1000 %. Para cuantificar la tasa de caída de arbolado post-incendio se utilizó una sub-muestra de 100 árboles por réplica, que fueron marcados con una placa identificativa (Figura 3.3). Se obtuvieron medidas del diámetro basal y la altura a nivel del pecho que, aparte de la parcela y el tratamiento, se testaron como variables explicativas. Un árbol se consideró como caído cuando se encontraba al nivel suelo o parcialmente apoyado sobre otro árbol en un ángulo no mayor de 45º, si bien el 98 % de los árboles colapsaron al nivel de la base (Figura 3.3). El monitoreo de la caída de los árboles se realizó entre febrero y marzo de cada año, a partir del 2006 hasta el 2011, tiempo tras el cual el 100 % de los árboles había caído.

Para el capítulo 2, donde se estudia la tasa de descomposición de la madera, se utilizó el tratamiento de intervención intermedia dentro de cada una de las tres parcelas experimentales. Un total de 250 troncos fueron experimentalmente cortados y distribuidos aleatoriamente en el suelo unos 6 meses tras el incendio en cada una de las tres parcelas. Cada tronco provino de un árbol diferente, el cual fue cortado desde una altura aleatoria a lo largo del tronco. La descomposición fue medida como la pérdida de densidad de los troncos a través del tiempo. Una sub-muestra de alrededor de 50 troncos por parcela fue recolectada en 2016, completando una serie temporal bianual desde 2006 (Figura 3.4).

Para el capítulo 3, donde se estudió la macrofauna edáfica, se tuvieron en cuenta los tratamientos de Ex e Ii en las parcelas 1 y 3. Las diferencias entre ambos tratamientos son una cuestión fundamentalmente estructural a través del tiempo, relacionada con la presencia de árboles en pie (y su tasa de caída) y la abundancia y distribución espacial de madera en descomposición. El muestreo en el tratamiento intervención intermedia incluyó puntos bajo troncos en descomposición (Intervención intermedia - bajo tronco) y

Figura 3.3: Izquierda, detalle de árbol caído desde la base del tronco. ***Derecha***, placa de identificación. Fotos tomadas por el autor en enero del 2017.

Figura 3.4: Fotos tomadas por el autor en septiembre de 2016
Izquierda, detalle de troncos en descomposición. **Derecha**, discos utilizados para medir la descomposición. Fotos tomadas por el autor en febrero del 2016.

puntos de muestreo en áreas de suelo desprovistas de restos de madera (Intervención intermedia-fuera de tronco). El diseño el capítulo 3 cuenta por tanto con dos tratamientos: Ex e Ii, y con tres 3 sub-tratamientos: Ex - suelo sin tronco, Ii - bajo tronco e Ii - fuera de tronco (Figura 3.5). Más detalles procedimentales relacionados con esta tesis se incluyen en cada capítulo.

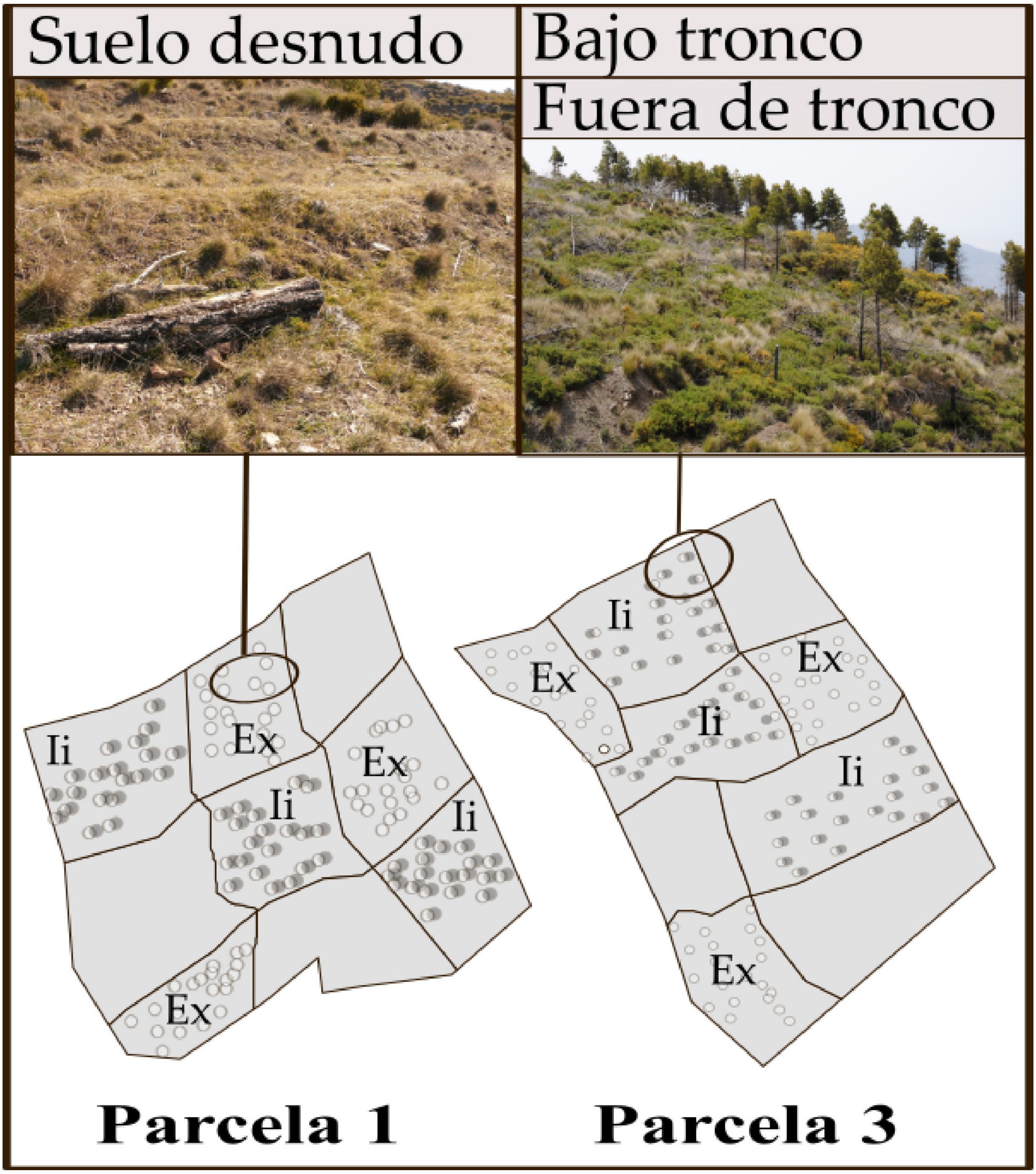


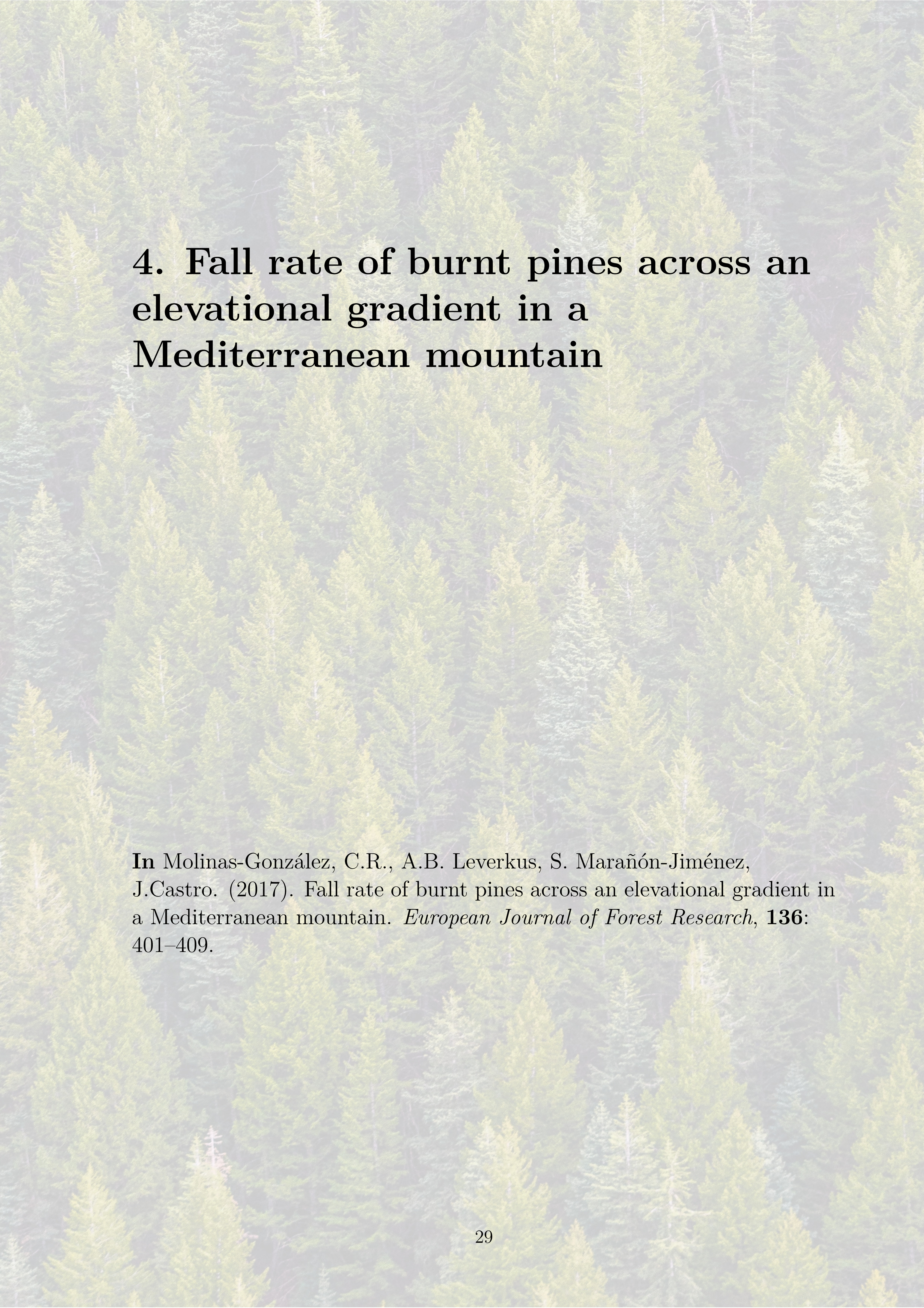
Figura 3.5: ***Detalle de los sub-tratamientos (microhabitats)***: Incluyendo los puntos de muestreo bajo troncos en descomposición ("intervención intermedia-bajo tronco"), y puntos de muestreo en áreas de suelo desprovistas de restos de madera ("extracción-fuera de tronco") y (extracción-suelo desnudo).

Part II

Capítulos principales | Main chapters

If the biota, in the course of aeons, has built something we like but do not understand, then who but a fool would discard seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent thinkering.

Aldo Leopold



4. Fall rate of burnt pines across an elevational gradient in a Mediterranean mountain

In Molinas-González, C.R., A.B. Leverkus, S. Marañón-Jiménez, J.Castro. (2017). Fall rate of burnt pines across an elevational gradient in a Mediterranean mountain. *European Journal of Forest Research*, **136**: 401–409.

Abstract

Burnt wood remaining after a wildfire is a biological legacy with important implications for habitat structure, ecosystem regeneration, and post-fire management. Knowledge of the time required for snags to fall is thus a key aspect for planning forest restoration. In this study, we analyze the fall rate of burnt trees in a Mediterranean pine reforestation. Three plots of 18–32 ha were established after a fire across an elevational gradient spanning from 1400 to 2100 m a.s.l., and snag fall rate was measured on a yearly basis using an experimental setup that considered two levels of a thinning treatment: unthinned (where no post-fire management was conducted and all the snags were left standing after the fire) and thinned (where 90% of the trees were cut after the fire and left on the ground). All the snags remained standing during the first and second winter, and thereafter, they collapsed quickly until reaching 100% after 5.5 years. Snags in low density stands resulting from thinning fell faster than in unthinned stands, but the differences were minor. There was a negative effect of tree diameter on the rate of collapse, especially in the unthinned treatment, but the effect of diameter was minor too. There was no effect of the elevational gradient on fall rate despite patent differences in climatic conditions and pine species across plots. The results support the contention that post-fire fall rate in dense pine plantations in Mediterranean mountains can occur quickly after the second winter and may show little variation across environmental gradients.

4.1 Introduction

Wildfire is a common disturbance in many ecosystems of the world (Rowell & Moore, 2000; Keeley *et al.*, 2012). After a fire of medium to high intensity, snags—i.e., standing burnt trees—usually remain standing for some time and create a landscape with a complex habitat struc- ture along with downed wood (DeLong *et al.*, 2008; Swanson *et al.*, 2011). This habitat is the starting point for post-fire regeneration, whether natural or assisted. Burnt trees create habitat heterogeneity through their different types, sizes, abundances, and fall or decay rates (Franklin & MacMahon, 2000; Lindenmayer *et al.*, 2008). Therefore, they constitute a biological legacy from the past forest that persists during secondary succession whose presence and characteristics may affect successional trajectories and, hence, future community composition (Macdonald, 2007; Lindenmayer *et al.*, 2008; Leverkus *et al.*, 2014).

Understanding the rate of tree fall and the causes determining its spatial and temporal patterns is of great interest for several ecological and practical/management reasons. First, burnt trees create habitat heterogeneity which, in turn, may affect key parameters for forest restoration and natural regeneration such as nutrient availability (Marañón-Jiménez *et al.*, 2013a), microclimatic conditions (Castro *et al.*, 2011; Marzano *et al.*, 2013), seed dispersal (Rost *et al.*, 2009; Castro *et al.*, 2012; Cavallero *et al.*, 2013), or seed predation and herbivore damage on vegetation (Hebblewhite *et al.*, 2009; Castro, 2013; Leverkus *et al.*, 2013). Second, standing burnt trees are an important component of the habitat of numerous species of lichens, bryophytes, mammals, cavity-nesting birds, and several bark- and wood-inhabiting beetles (Bull *et al.*, 1997; Chamber & Mast, 2005; Bradbury, 2006; Hutto, 2006), whose conservation or management requires accurate pre- dictions of the residence time of snags. Third, since fallen wood decomposes faster than standing snags, tree fall rate can affect the decay rate and therefore define the speed of nutrient cycling and the rate of nutrient uptake by plants (Marañón-Jiménez & Castro, 2013; Heikkala *et al.*, 2014). Fourth, the amount of burnt biomass and the proportion of standing or downed trees may determine the ease for subsequent management actions such as reforestation, with implications for management costs (Kirby *et al.*, 1998; Leverkus *et al.*, 2012). Finally, standing dead trees may also compromise the safety of recreational or management activities (Wagener, 1963; Mitchell & Preisler, 1998). In summary, there are many implications resulting from the abundance and condition of burnt wood, and post-fire management requires proper understanding of the timing and potential modifiers of snag collapse.

Snag fall rate has been related to several factors such as decay rate (Aakala *et al.*, 2008), tree species (Mitchell & Preisler, 1998; Everett *et al.*, 1999; Heikkala *et al.*, 2014), and silvicultural treatments (Mitchell & Preisler, 1998; Huggard, 1999; Garber *et al.*, 2005), and nearly all studies have obtained positive relationships between tree diameter and the resistance to collapse (Maser *et al.*, 1984; Vanderwel *et al.*, 2006; Parish *et al.*, 2010). However, snag dynamics have mostly been studied in North American coniferous forests, whereas studies in other biomes and forest types are scant. In addition, there is a lack of studies performed under controlled experimental conditions, in particular including replicated and properly randomized post-fire management regimes. Given the large set of biotic and abiotic variables that may affect snag fall rate, the use of experimental designs is particularly needed in order to draw useful, predictive conclusions for post-fire management.

In this study, we seek to determine the effect of elevation and stand density on the pattern and pace of post-fire snag fall in a burnt Mediterranean pine reforestation. Pines were massively planted in the twentieth century for different purposes, yet scant recent management of these plantations has often resulted in large, dense, and homogeneous stands with a high fire risk . After the 2005 Lanjarón fire, three experimental plots were created across an elevational gradient spanning ca. 800 m, and stand density was manipulated after the fire through thinning, which created two treatments replicated three times within each elevational level. Burnt trees were thereafter monitored until all had collapsed. Our working hypotheses were that snag fall rate would be affected by a number of factors, namely: (1) the elevational gradient, which generates gradients in parameters that may affect snag residence time such as climatic conditions and pine species; (2) the thinning treatments, because thinning would likely increase susceptibility to wind; and (3) tree size, as larger diameters tend to increase the resistance of snags. Overall, we seek to determine the main factors affecting the residence time of snags in a Mediterranean forest, which underlies their capacity to create structural habitat complexity and represents a relevant consideration for post-fire management decisions.

4.2 Methods

Study site and experimental design

The study was conducted in the Sierra Nevada Natural and National Park (SE Spain), in an area that burned in September 2005 (the Lanjarón fire). The fire burned around 1,300 ha of 35 to 45 year-old reforested pine stands on a SW-oriented mountainside. It was a high-intensity crown fire that consumed all the leaves, twigs and litter and charred the bark of the trunks (Marañón-Jiménez *et al.*, 2013a). Terraces occupied all the surface of the study area, and the burnt pines were initially planted on approximately 3 m wide terrace beds (Leverkus *et al.*, 2012). The pine species were distributed along an elevational/moisture gradient according to their ecological requirements, and included *P. pinaster*, *P. nigra* and *P. sylvestris* (in order of increasing elevation; Table 4.1). The three species are native in the south of the Iberian Peninsula, yet those of the study area constitute a plantation made in the second half of the XXth century. Climate in the area is Mediterranean, characterized by precipitation falling mostly during autumn and winter and by a hot, dry summer. Annual precipitation increases with elevation, whereas temperature follows the opposite trend (Table 4.1). Initial pre-fire pine density differed among plots but was high in all cases (> 1000 trees ha^{-1}; Table 4.1). Snowfall occurs between November and March, persisting up to 3 months above 2000 m a.s.l.

Between March and May 2006 (around 7 months after the fire) three plots of 18-32 ha were established at three different elevations (Figure 4.1). The plots had a similar orientation, slope, aspect (SW), and soil type (Haplic phaeozems; for details on soils see Marañón-Jiménez *et al.*, 2013a), but differed in elevation and related variables such as climate and pine species (Table 4.1). Within each plot, six subplots were established, which constituted three replicates of two post-fire thinning treatments that differed in the degree of intervention and in final stand density: (1) Thinned (T), where ca. 90% of the snags were cut, the main branches were lopped off, the boles were cut in pieces of 2–3 m length, and all the wood was left spread over the ground. The remaining 10% of the snags were left standing

Table 4.1: Location and characteristics of the study plots

	Plot		
	1	2	3
Coordinates[a]	36° 57´ 12.1” N 03° 29´ 36.3” W	36° 58´ 11.9” N 03° 30´ 1.7” W	36° 58´ 6.5” N 03° 28´ 49.1” W
Elevation (a.s.l.)[a]	1477	1698	2053
Slope (%) [b]	30.3	28.7	31.4
Plot area (ha)	17.7	23.9	31.7
Subplot area (ha)[c]	2.07 ± 0.20	2.77 ± 0.24	3.86 ± 0.37
Mean daily min. temp. (°C)[d]	6.8 ± 0.2	5.6 ± 0.2	3.4 ± 0.2
Mean daily max. temp. (°C)[d]	17.1 ± 0.2	16.2 ± 0.2	13.4 ± 0.2
Mean ann. precip. (mm)[d]	536 ± 41	550 ± 40	630 ± 42
Soil density (g cm^{-3}) [e]	1.25 ± 0.06	1.34 ± 0.07	1.15 ± 0.06
Dominant species	*Pinus pinaster/ P. nigra*	*Pinus nigra*	*Pinus sylvestris*
Pre-Treatment tree density (individuals ha^{-1})	1477 ± 46	1064 ± 67	1051 ± 42
Tree height (m)	6.3 ± 0.1	6.6 ± 0.1	6.2 ± 0.1
Trunk basal diameter (cm)	21.62 ± 7.2	21.33 ± 5	19.78 ± 6.5

[a] Measured at the centroid of each plot
[b] Average of the slope of the replicates (subplots)
[c] No difference in subplot size across treatments; Kruskal Wallis test (X^2= 0.24; df=1; P=0.63). Values are mean ± 1 SE of the mean.
[d] Data obtained from interpolated maps of Sierra Nevada (1981-2010) generated at the Centro Andaluz de Medio Ambiente (CEAMA)
[e] Data from Marañón-Jiménez et al. (2013); for more soil properties refer to the cited article.

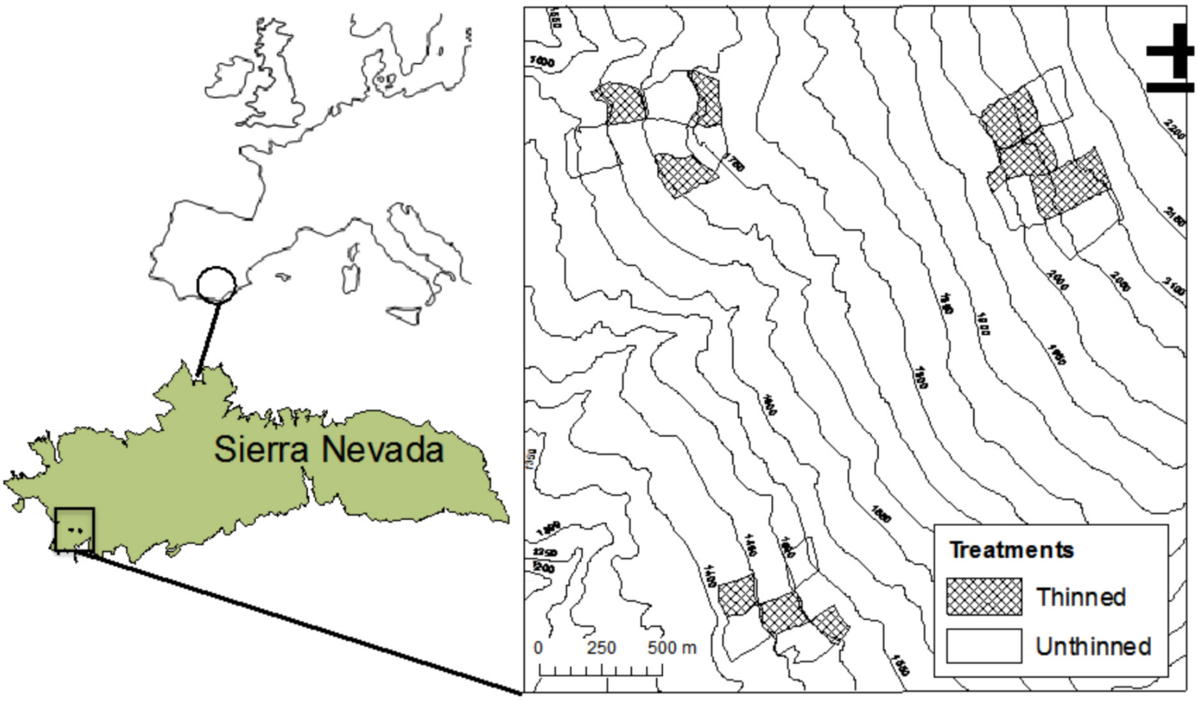


Figure 4.1: Map of the study site after the Lanjarón fire in Sierra Nevada (Spain). For further details, see Table 4.1. The solid lines indicate 50 m contour lines.

with the initial purpose of providing perches for birds, and they were regularly distributed across the whole surface of the subplots (i.e. the forestry staff selected approximately every tenth tree to remain standing). The final density of standing snags depended on the initial tree density, and it ranged between 100 and 140 trees ha^{-1}. (2) Unthinned (U), where all the snags were left standing and no further action was taken. Snag density in this treatment thus represented the initial tree density, and it ranged between 1000 and 1450 trees ha^{-1} (Table 4.1). Previous to management, tree density did not significantly vary between treatments (Kruskal-Wallis test; $P = 0.29$), nor did tree dbh ($P = 0.78$). The experiment thus consisted of a generalized randomized block design (Quinn & Keough, 2002), where the three blocks (plots) were defined by elevation, and each plot contained three replicates (subplots) of each of two thinning treatments. Pine species varied across blocks, which is a normal situation in reforested pine stands across marked elevational gradients. The design thus does not allow separating the contribution of elevation and pine species to the effect of block on fall rate, although the replication within each block allows testing the effects of the other factors within and across elevational levels. All the burnt trees that remained in the area surrounding the study plots were cut and removed (salvage logged).

Snag monitoring

After treatment implementation (between March and May 2006), we randomly selected 100 standing snags per subplot (thus totaling 1800) and tagged them with a metal plaque. We measured snag basal diameter for each of them (averaging two perpendicular measurements made with a large caliper), and snag height for a subset of 20-30 randomly chosen pines per subplot. We monitored the fall rate of the snags between February and March every year until 2011, by when all had collapsed. This corresponds to the 2006 to 2011 sampling periods hereafter. At each sampling period we ascribed the state of the snag as standing or fallen. Trees considered fallen could be either totally touching the ground or supported by neighboring snags, but clearly bent in all cases with an angle above 45℃. The position at which each snag broke (i.e. from the base of the stump or higher along the trunk) was also noted.

4.3 Statistical analyses

All the following analyses were performed in R version 3.1.1 (R Core Team, 2016). To test for collinearity between our explanatory variables, we analyzed the effect of Thinning (a categorical factor with two levels) and Elevation (a categorical factor with three levels) on average snag diameter at subplot level with ANOVA, including both factors and the interaction between them as explanatory variables. Prior to the analysis the data were log-transformed.

We assessed the effect of the thinning treatment on the proportion of snags that remained standing in each particular year with a Kaplan-Meier survival function. The survivors function of the survival package (Therneau, 2014) estimated the probability that a tree remained standing after each year, and 95% confidence intervals provided a measure of the differences in this probability between the thinning treatments for each consecutive year.

We modeled snag retention time with linear mixed-effects models. We first developed a full model, specifying Thinning, Elevation, and Snag basal diameter, as well as all the possible interactions between these factors, as fixed effects. As a random effect we specified subplot (a categorical factor with 18 levels). To determine the significance of the terms included in the full model, we used stepwise elimination and likelihood ratio tests (Pinheiro & Bates, 2000; Crawley, 2013). The significance of a term was considered at $\alpha = 0.05$, and data were square root-transformed prior to analysis. As the range of available snag diameters differed across the two thinning treatments (see Results), for this analysis we considered only those snags whose diameter fell within the range of diameters available in both treatments (i.e. from 12.7 to 33.7 cm). This resulted in the use of 778 and 840 snags in the Unthinned and Thinned treatments, respectively, in the statistical procedures (see Supplementary information 4.3 for the number of individuals per replicate). The same modeling procedure was also performed for the snags of each plot separately (Supplementary information 4.4). Mixed effects models were performed with the lme function from the nlme package (Pinheiro *et al.*, 2014).

4.4 Results

Snag basal diameter across elevations and thinning treatments

Snag diameter differed significantly among elevations (x^2 = 29.5; df= 2; P < 0.01), with an overall value of 21.66 ± 7.24 cm for Plot 1, 21.33 ± 5.08 cm for Plot 2, and 19.78 ± 6.6 cm for Plot 3 (values are mean ± 1 SE of the mean throughout the paper). Snag diameter also differed among treatments (x^2 = 695.9; df=1; P<0.001), with an average of 17.73 ± 4.75 cm in the Unthinned treatment and 24.12 ± 6.28 cm in the Thinned treatment. However, the effect of Thinning varied across plots, which gave rise to a significant Elevation x Thinning interaction (x^2 = 23.6 df=2; P<0.001; Figure 4.2). Thinning had an effect size of 1.45 in Plots 1 and 3, whereas in Plot 2 the diameters of trees in the Thinned treatment were only 1.20 times as large as in the Unthinned treatment. Thus, although the effect sizes differed, the direction of the Thinning effect was still the same regardless of the plot. The differences in diameter between treatments were likely the result of decisions of workers, who nonrandomly selected smaller trunks for cutting in the Thinned treatment (despite cutting more or less every tenth snag in a regular pattern). As this outcome generated collinearity between the Thinning treatment and snag diameter, below we express the results of snag fall rate with consideration of this issue and avoiding the provision of average effects of the Thinning treatment.

Snag fall rate

The cumulative proportion of collapsed snags averaged 0% in 2006 and 2007, 13.3% in 2008, 84.6% in 2009, 98.2% in 2010, and 100% by the end of the study period in 2011 (thus 5.5 years after the fire). There were significant differences across treatments in these proportions in 2008 and 2009 according to the Kaplan-Meier model (Figure 4.3), although the differences were small and this model did not consider the effect of snag diameter (see below). The largest number of snags collapsed between the 2008 and 2009 assessments (Figure 4.2). Overall, trees broke off at the stump in 98% of the cases (for a photo see experimental designe 3.3), whereas 2% of the snags were broken at a higher position of the trunk.

The mixed-effects model showed significant main effects of Elevation and Thinning (Table 4.2): average snag retention time was higher in Plot

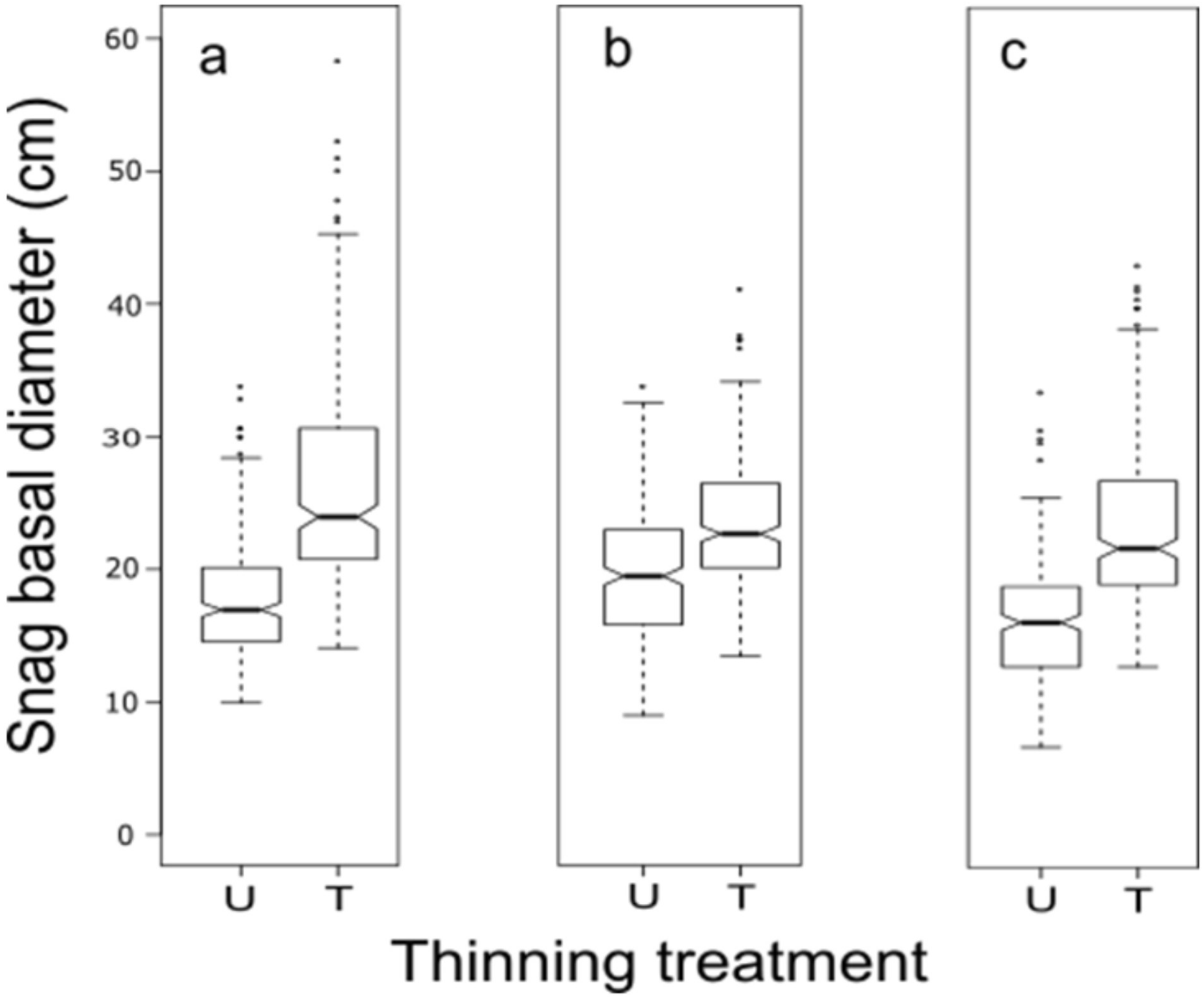


***Figure 4.2: Snag basal diameter across the two post-fire thinning treat- ments: Unthinned (U) and thinned (T), and across elevations, after the Lanjarón wildfire*: a** Plot 1, **b** Plot 2, **c** Plot 3. The lines in bold represent medians, and the boxes indicate the first and third quartiles of the data. Whiskers are either the minimum/maximum values or 1.5 times the interquartile range of the data, in which case outliers are shown as points.

2 (676.6 ± 41.9 days) than in either Plot 1 (577.7 ± 9.8 days) or Plot 3 (597.4 ± 36.2 days), and it was also greater in Unthinned than in Thinned plots (Figure 4.4). Snag basal diameter had an overall positive effect on retention time, but this effect was modulated by interactions with Elevation and Thinning (Table 4.2). While the diameter effect was pronounced in the Unthinned treatment, it was close to inexistent in the Thinned treatment (Figure 4.4). Similarly, the model coefficients for the slope of the diameter effect were greater for Plot 2 (0.51) than for either Plot 1 (0.31) or Plot 3 (0.26). Similar effects of Thinning and Diameter occurred within each plot (Supplementary information 4.5).

Table 4.2: Effects of snag diameter, the thinning treatment, and elevation on snag retention time as estimated with linear mixed models

Terms excluded from the model			Terms kept in the model			
Term	L.Ratio	*P value*	Term	df	F	*P value*
Diameter x thining x elevation	0.95	0.62	Diameter	1, 1596	65.84	<0.001
Thinning x elevation	3.64	0.16	Thinning	1, 14	8.66	<0.05
			Elevation	2, 14	4.48	<0.05
			Diameter x thinning	1, 1596	33.72	<0.001
			Diameter x elevation	2, 1596	10.40	<0.001

4.5 Discussion

In this study the burnt pines of a Mediterranean reforestation fell quickly, with most of the snags having collapsed 3.5 years after the fire. Snags with larger diameter remained standing for longer at sites with high snag densities, and snags at sites with low densities due to post-fire thinning collapsed faster irrespective of their size. However, these effects were small, and 100% of the snags had collapsed 5.5 years after the fire. Our results provide insights for the post-fire management of Mediterranean pine stands, with the advantage of having used a carefully-designed experimental approach.Tree fall after the Lanjarón fire was quite fast compared to other studies (Harrington, 1996; Chamber & Mast, 2005; Russell *et al.*, 2006; Ritchie *et al.*, 2013), and we attribute this to several mutually non-exclusive factors.

First, the cause of mortality, fire, generally makes snags less persistent and more susceptible to wind when compared to other disturbances such as insect outbreaks (Morrison & Raphael, 1993). Second, high pre-fire stand

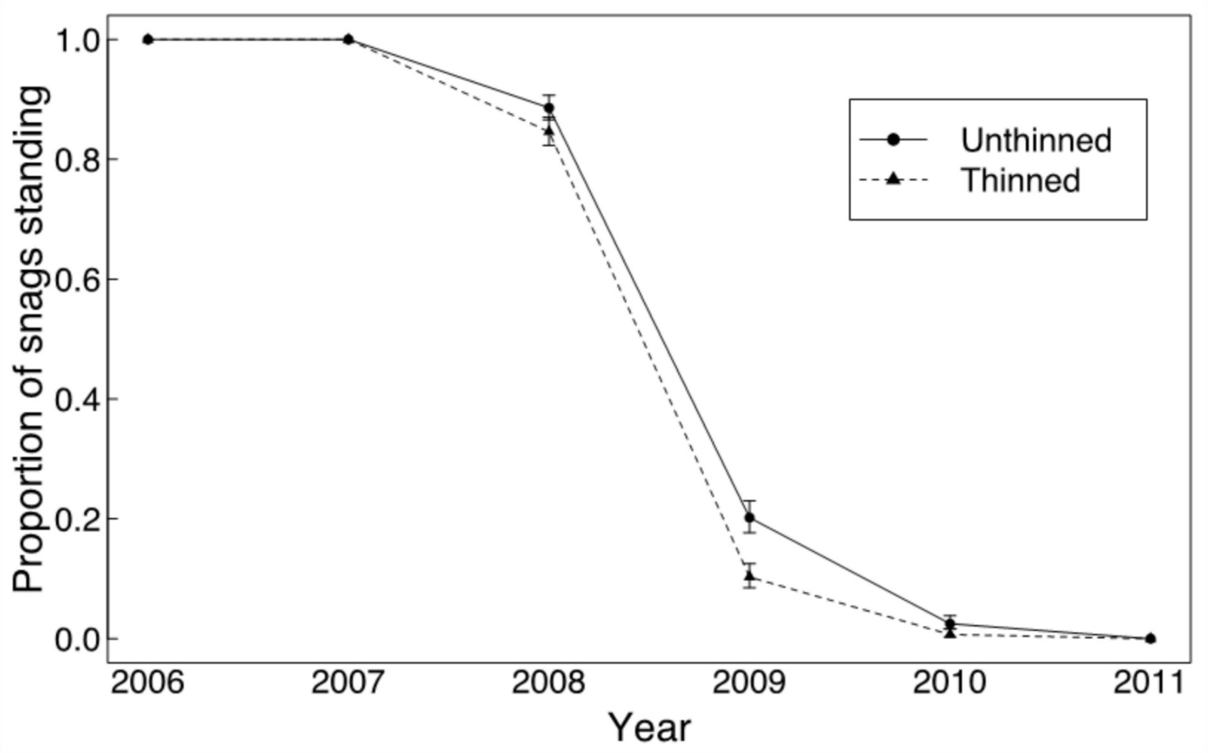


Figure 4.3: *Fall rate of the snags according* to the Kaplan-Meier model across years and thinning treatments. Error bars indicate the 95% confidence interval of the proportion of snags standing each year, and significant effects of thinning arose in years for which the bars do not overlap.

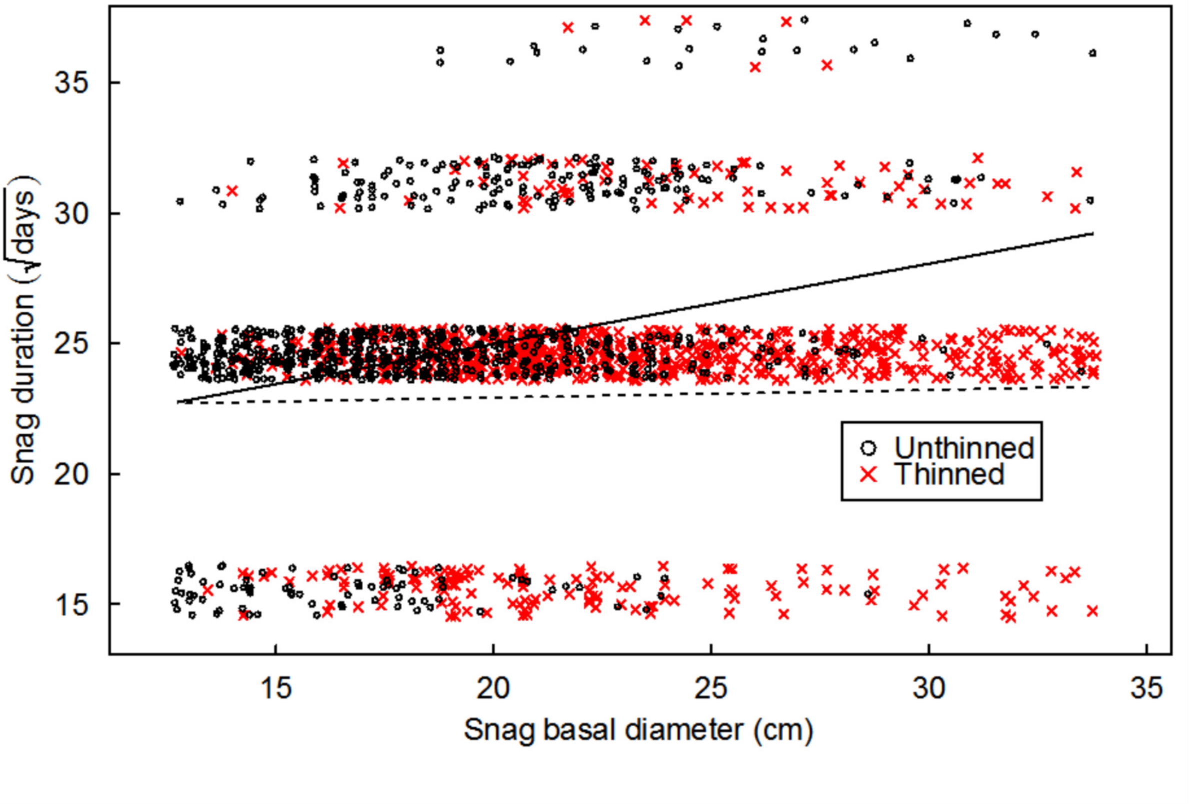


Figure 4.4: *Effects of snag diameter on snag duration for each of the thinning treatments.* The lines are best-fit lines from the linear mixed-effects model: the solid line is for the Unthinned treatment, while the dashed line is for the Thinned treatment. The points are jittered on both axes to reduce overlapping.

densities led to a high fire intensity and severity, which may have accelerated fall rates due to the quick death of the trees (Ritchie *et al.*, 2013). Third, Pinus species generally show short snag fall times as compared to other species such as *Abies spp.* (Landram *et al.*, 2002; Ritchie *et al.*, 2013). And fourth, the study plots were located on an exposed mountain slope with strong winds occurring in pulses during the autumn and winter that likely accelerated the collapse of the snags (see below). Although our results showed little effect of the analyzed factors on fall rate, some patterns did emerge. First, greater snag diameter increased retention time, which is consistent with the general findings reported in other studies (Dahms, 1949; Morrison & Raphael, 1993; Mitchell & Preisler, 1998; Russell *et al.*, 2006).

This positive effect of the diameter on snag persistence may be related to the greater stability provided by the higher proportion of heartwood as compared to sapwood in larger trees, which provides greater resistance to decay (Russell *et al.*, 2006; Smith *et al.*, 2009). Additionally, smaller snags tend to be rapidly colonized by decay fungi (Vanderwel *et al.*, 2006), resulting in a loss of bole strength with increased likelihood of falling (Harrington, 1996). While the magnitude of the snag diameter effect on fall rates was small in this study, it would likely be amplified in cases with a more heterogeneous forestage structure, as our study only encompassed snags with base diameters of 12.7 to 33.7 cm. As a second pattern, the thinning treatment affected the rate at which snags collapsed and also modulated the effect of snag diameter, likely due to the effect of thinning on snag density. In general, snags within areas of higher snag density (i.e. in the unthinned treatment) remained standing for longer than in the low-density thinned treatment.

Similar results of longer snag retention time in denser stands have been reported previously (e.g. Mitchell & Preisler, 1998; Russell & Weiskittel, 2012) and likely appear because higher snag densities act as wind shields that delay the collapse of snags located away from the border of the stand (Vanderwel *et al.*, 2006). This is further supported by the fact that the effect of trunk basal diameter on snag duration, although positive for both thinning treatments, was much weaker in thinned subplots: in a situation where there was no protection provided by neighboring snags, the resistance conferred by larger snag diameter diminished. In fact, maximum peak wind speed registered in 2010 at our study area, measured in a micrometeorological station at 2200 m a.s.l., reached 177 m s^{-1} within the unthinned treatment and 376 m s-1 in the surrounding salvage-logged matrix (Serrano-Ortiz *et al.*, 2011), so that the dense stands buffered the strength of peak windy events (Chamber & Mast, 2005; Edworthy *et al.*, 2012).

Finally, we found only small effects of elevation on fall rate despite the variation in climatic conditions and species across plots. We had hypothesized higher fall rates at higher elevation due to differences in rainfall, snow load, and wind speed. However, the slightly greater snag retention time in Plot 2 than in the other plots (ca. 100 days), and the greater effect of the thinning treatment on retention time in Plot 2, do not correspond to any clear elevational trend. Indeed, if any elevation-related effects existed, they may either have been offset by the quick fall of the snags, or cancelled-out by counteracting effects, as more than one factor varied across the plots. For example, factors such as the different wood density and concentration of lignin in the heartwood of the different pine species (de Aza *et al.*, 2011) may have resulted in different decay rates across plots. Further, Mitchell & Preisler (1998) proposed that the effects of lower decay rate resulting from lower temperature might counteract those of higher wind speed and snow load at higher elevation. Further studies controlling factors such as species are required to assess the effect of elevation on snag fall rate, but a key point here is that tree species (pines in our case) generally change across sharp elevational gradients, so that maintaining this factor constant is often impossible and, in any case, does not correspond to most real-world scenarios. Thus, our results provide strong support from a management point of view to assume that fall rate in dense pine stands may be similar across elevational gradients, irrespective of the underlying mechanisms that drive the collapse of snags.

4.6 Conslusion

In conclusion, our results show that the collapse of the snags of a burnt pine reforestation in a Mediterranean mountain was fast and little affected by snag density, size or elevational location. Although differences related to climatic and species-specific characteristics might be expected, it is likely that counteracting factors, together with the overall short time required for snag fall, eliminated potential differences across elevations. This suggests that land managers may have consistent predictions related to snag fall rate after fire in pine reforestations, and thus may plan activities accordingly. From an ecological perspective, burnt wood, whether standing or after its collapse, is a biological legacy with important implications for ecosystem structure and functioning. Dead wood provides habitat and/or resources for a wide set of taxa of lichens, fungi, plants, and animals , and it promotes plant natural regeneration through the enhancement of soil fertility and the increase in the spatial and temporal heterogeneity in the microhabitat conditions that affect plant recruitment. Local forest services may seek to remove the burnt wood in order to facilitate reforestation in areas with low potential for natural regeneration, to prevent visitor accidents caused by falling trunks near roads and trails, or for other management targets. However, given the fast rate of snag collapse observed in this study and the generally observed positive role of burnt wood on natural regeneration, we propose that policies of total or partial snag retention be implemented in the post-fire management of Mediterranean pine forests.

4.7 Supplementary information

Number of snags for statistical procedures

Table 4.3: Number of snags used in the mixed models; the numbers arise from the elimination of the snags whose diameter fell outside the range of diameters available in both thinning treatments. The number of snags that were monitored was 100 per replicate

Plot	Replicate	Unthinned	Thinned
1	1	95	83
	2	95	100
	3	84	89
2	1	80	98
	2	99	99
	3	96	97
3	1	87	95
	2	97	82
	3	45	97

Snag retention time per plot

Methods We repeated the linear mixed-effects models described in the section on Statistical analyses for each plot individually. For this we considered the effects of the thinning treatment, snag basal diameter, and the interaction between these two variables as fixed effects, and subplot (a factor with 6 levels) as a random effect. Again, we restricted the analysis to the snags whose basal diameter fell within the range available in both treatments within the plot. These were: 14.0-33.7 cm in Plot 1, 13.4-33.7 cm in Plot 2, and 12.7-33.4 cm in Plot 3.

Results Snag basal diameter and Thinning generated similar trends within each plot as for the entire experiment: diameter had a positive effect on snag duration, but this effect was greater in the Unthinned treatment than in the Thinned treatment; snag duration was greatest in the Unthinned treatment for any diameter considered (Figure 4.5). The effects that were significant when analyzing the data of each plot individually were: Diameter in Plot 1; Thinning, Diameter and the Thinning x Diame-

Table 4.4: Effects of snag basal diameter, the thinning treatment, and the diameter x thinning interaction on snag retention time as estimated with linear mixed models.

	Plot 1			Plot 2			Plot 3		
Factor	df	F	p	df	F	p	df	F	p
Thinning [T] 1	1,4	2.08	0.22	1,4	7.87	<.05	1, 4	4.53	0.10
Diameter [D] 1	1,507	9.07	<0.01	1,556	55.86	<.0001	1, 494	1.96	0.16
T x D 1	1,507	2.58	0.11	1,556	12.00	<.001	1, 494	7.47	<0.01

ter interaction in Plot 2; and the Thinning x Diameter interaction in Plot 3 (Table 4.3).

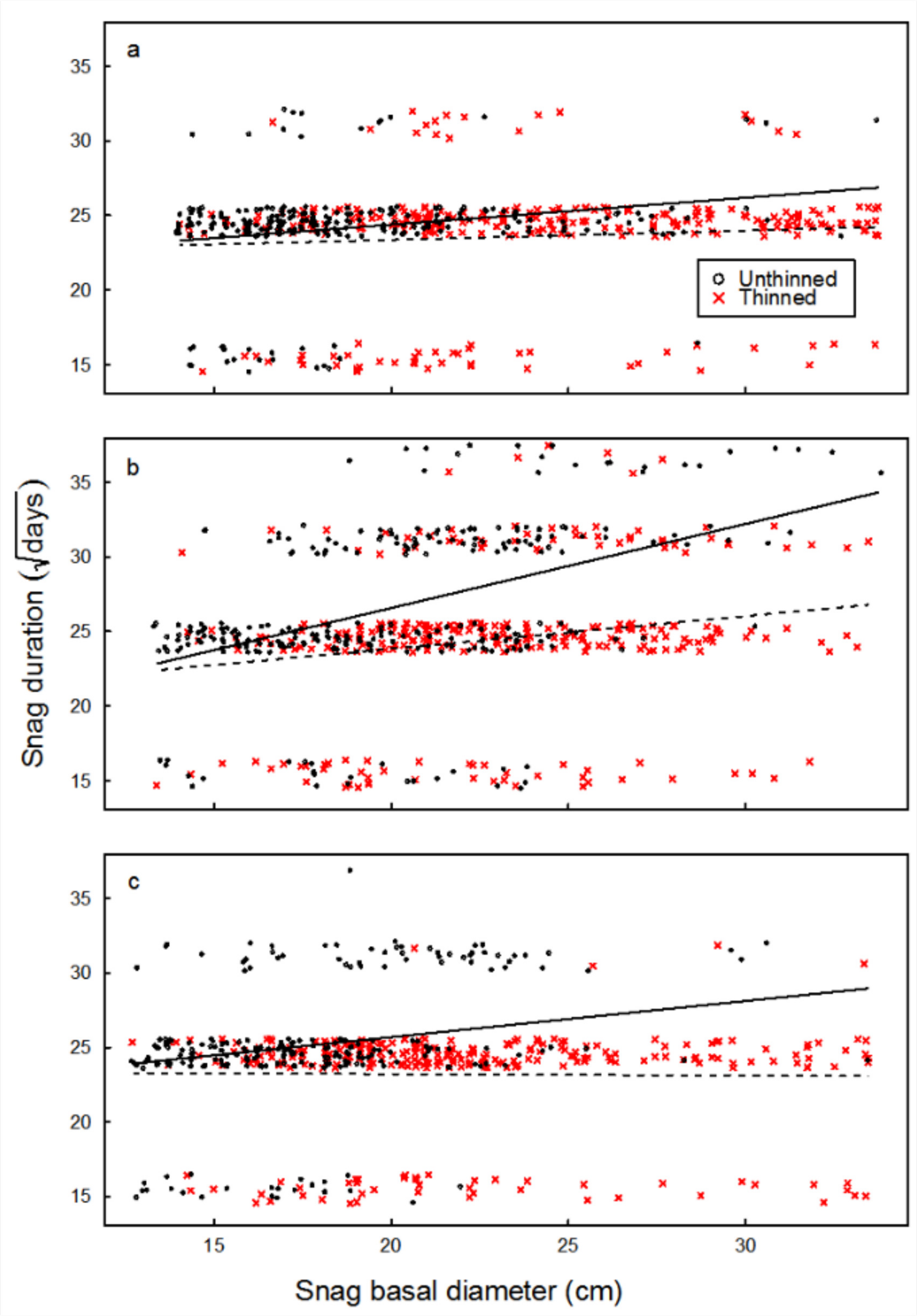
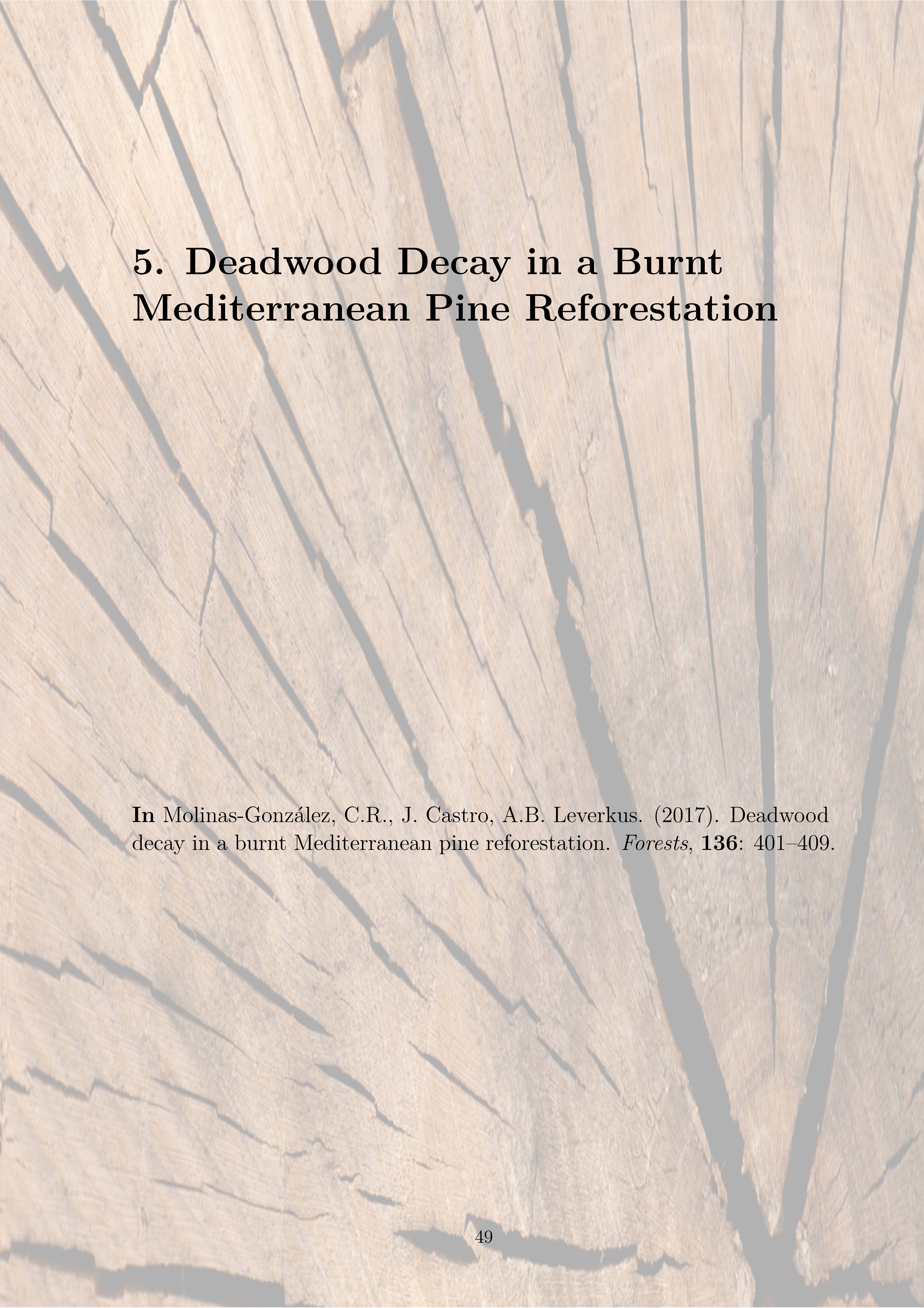


Figure 4.5: Effects of snag diameter on snag duration for each of the thinning treatments in **a**) Plot 1, **b**) Plot 2, and **c**) Plot 3. The lines are best-fit lines from the linear mixed-effects models: the solid line is for the Unthinned treatment, while the dashed line is for the Thinned treatment. The points are jittered on both axes to reduce overlapping.



5. Deadwood Decay in a Burnt Mediterranean Pine Reforestation

In Molinas-González, C.R., J. Castro, A.B. Leverkus. (2017). Deadwood decay in a burnt Mediterranean pine reforestation. *Forests*, **136**: 401–409.

Abstract

Dead wood remaining after wildfires represents a biological legacy for forest regeneration, and its decay is both cause and consequence of a large set of ecological processes. However, the rate of wood decomposition after fires is still poorly understood, particularly for Mediterranean-type ecosystems. In this study, we analyzed deadwood decomposition following a wildfire in a Mediterranean pine plantation in the Sierra Nevada Natural and National Park (southeast Spain). Three plots were established over an elevational/species gradient spanning from 1477 to 2053 m above sea level, in which burnt logs of three species of pines were experimentally laid out and wood densities were estimated five times over ten years. The logs lost an overall 23% of their density, although this value ranged from an average 11% at the highest-elevation plot (dominated by *Pinus sylvestris*) to 32% at an intermediate elevation (with *P. nigra*). Contrary to studies in other climates, large-diameter logs decomposed faster than small-diameter logs. Our results provide one of the longest time series for wood decomposition in Mediterranean ecosystems and suggest that this process provides spatial variability in the post-fire ecosystem at the scale of stands due to variable speeds of decay. Common management practices such as salvage logging diminish burnt wood and influence the rich ecological processes related to its decay.

5.1 Introduction

Deadwood decomposition is a key process for ecosystem functioning and structure. Throughout the time of decomposition, decaying wood provides shelter and habitat for a large number of organisms (Harmon *et al.*, 1986; Franklin *et al.*, 1987; Chamber & Mast, 2005; Stokland *et al.*, 2012), guarantees nutrient availability and turnover (Swift, 1977; Ganjegunte *et al.*, 2004; Palviainen *et al.*, 2004), defines carbon residence time and sequestration (Russell *et al.*, 2014; Cornwell *et al.*, 2009), enhances soil moisture (Means *et al.*, 1992), and determines the vertical and horizontal physical structure of the habitat as snags or fallen logs (Schiegg, 2000; Vodka *et al.*, 2009; Angelstam *et al.*, 2003; Lassauce *et al.*, 2011). All these processes, both singly and in synergic combination, deeply influence other ecosystem processes, ranging from the performance of individual plants to landscape-scale biodiversity and even biogeochemical cycles (Rajandu *et al.*, 2009; Marzano *et al.*, 2013; Leverkus *et al.*, 2014; Chmura *et al.*, 2016; Cadieux & Drapeau, 2017; Serrano-Ortiz *et al.*, 2011). Knowledge of the factors that determine the rate of wood decomposition is therefore relevant for understanding the residence time of logs, with broad implications for numerous ecosystem functions and services (Serrano-Ortiz *et al.*, 2011; Shorohova & Kapitsa, 2014; Russell *et al.*, 2015).

The rate of wood decomposition is also of paramount importance for forest management and planning, particularly after severe disturbances that create large amounts of dead wood, such as fires, pest outbreaks, or windstorms (Harmon *et al.*, 1986; Olajuyigbe *et al.*, 2011). Particularly in the case of burnt forests, the rapid loss of economic value of the wood due to decomposition and the difficulties that it imposes for transit and management are often-claimed arguments for the quick implementation of post-fire management (Passovoy & Fulé, 2006; Lindenmayer *et al.*, 2008; Castro *et al.*, 2010; Ritchie *et al.*, 2013). In this sense, extensive post-fire salvage logging—i.e., the removal of the logs, usually accompanied with the in situ elimination of the rest of coarse woody debris—is a widely implemented post-fire management action that seeks to recover part of the capital of the forest as well as to prepare the terrain for post-fire restoration (Lindenmayer *et al.*, 2008; Castro *et al.*, 2010). However, post-fire salvage logging may impact ecosystem functioning and the capacity for natural regeneration through a variety of processes, such as reducing nutrient and moisture availability, decreasing the necessary substrate for saproxylic organisms, diminishing advance regeneration, or increasing soil erosion, among others (Lindenmayer *et al.*, 2008; Donato *et al.*, 2006; Castro *et al.*, 2011; Marañón-Jiménez *et al.*, 2013a; Thorn *et al.*, 2018). Understanding the rate of wood decomposition after a fire is thus of great relevance to properly balance the economic benefit of quick salvage operations against the potential benefits for conservation and natural regeneration of nonintervention approaches. However, studies on wood decomposition are scarce and mostly concentrated in certain types of ecosystems such as boreal forests (Sippola *et al.*, 1998; Rock *et al.*, 2008). In particular, studies in Mediterranean-type ecosystems are very scarce (Rock *et al.*, 2008), except for some that have focused on the decomposition of standing snags (Lombardi *et al.*, 2008, 2013).

Wood decomposition is affected by abiotic and biotic factors, as well as the interactions and feedbacks between them. The speed of decomposition depends on moisture and temperature (Harmon *et al.*, 1986; Russell *et al.*, 2015; Liu *et al.*, 2013; Herrmann & Bauhus, 2013), and hence it can be expected to vary across environmental gradients where these factors gradually change, such as elevational or latitudinal gradients (Harmon *et al.*, 1986; Shorohova & Kapitsa, 2014; Fravolini *et al.*, 2016). Decomposition rates may also be affected by species identity and log diameter, as these factors determine the proportion between heartwood and sapwood (Cornwell *et al.*, 2009), and heartwood resists decay for longer than sapwood (de Aza *et al.*, 2011).Trunk diameter can also determine the identity of detritivorous species that colonize the log, and these may, in turn, affect the species assemblages of decomposers (Swift, 1977; Boddy, 2001; Ulyshen, 2016). In short, decomposition is a complex process whose understanding requires proper control of the starting conditions and stand characteristics.

In this study, we seek to determine the rate of wood decomposition in a burnt pine reforestation under Mediterranean conditions. Three experimental plots were distributed across an elevational gradient spanning some 800 m, and logs with a standardized length but variable diameter were marked, spread on the ground, and sampled over 10 years. Given the marked differences in climatic conditions and the change in species across the elevational gradient, we hypothesized that decomposition rate would vary across elevations (hypothesis 1). Furthermore, the proportion of hartwood to sapwood tends to increase with log diameter (Yang & Hazenberg, 1991), so we hypothesized that decomposition would be faster in logs with smaller diameters (hypothesis 2). Given the large amount of conditions that may affect decomposition rates and their variability across time, we expected potential interactions between elevation and diameter to affect decomposition rates (hypothesis 3). Overall, we expect this study to contribute to the understanding of the speed of wood decomposition in Mediterranean-type ecosystems, which should ultimately provide input to make informed post-fire decision-making.

5.2 Methods

Study Site

The study was conducted in the Sierra Nevada Natural and National Park (southeast Spain), in an area that burned in September 2005 (the Lanjarón fire). The fire burned around 1300 ha of 35 to 45 year-old reforested pine stands on a southwest-oriented mountainside. It was a high-intensity crown fire that consumed all the leaves, twigs, and litter and charred the bark of the trunks (Marañón-Jiménez *et al.*, 2013a). After the fire, the Forest Service established three plots across an elevational gradient within the context of a long-term research program devoted to study the effect of salvage logging with respect to other post-fire burnt wood management alternatives on ecosystem restoration and regeneration ((Leverkus *et al.*, 2014; Castro *et al.*, 2010; Leverkus *et al.*, 2012); Table 5.1). The three plots were similar in terms of pre-fire tree density (1000–1500 trees ha^{1}), fire intensity (high), bedrock (micaschist), aspect (southwest), soil type (haplic phaeozems), and other soil characteristics ((Marañón-Jiménez *et al.*, 2013a; Leverkus *et al.*, 2015a); Table 5.1). However, the plots differed in climatic conditions, as expected from the increasing elevational gradient: mean rainfall increased and temperature decreased with elevation. This influenced the species of pine that had been planted at each site (Table 5.1). For this study, we made use of areas in which 90% of the burnt trees were felled, the trunks were separated from their main branches and cut in pieces of ca. 2 m, and all the wood was left on the ground (Molinas-González *et al.*, 2017b). The climate is Mediterranean, with rainfall concentrated in spring and autumn, alternating with hot, dry summers. Snow is common during the winter, persisting up to 2 months at the highest elevation.

Sampling Design

Six months after the fire (March to April 2006), 50 sampling points were randomly established within an area of 2 ha at each elevation to monitor wood decomposition.

The sampling points were sufficiently away from standing trees so as to avoid their collapse over the point. At each of the sampling points, five logs were cut with a chainsaw to a standardized length of 75 cm (experimental logs, hereafter) and spread over an area of ca. 1 × 1 m, resulting in 250 experimental logs per elevation (Figure 5.1).

Table 5.1: Location and characteristics of the study plots.

	Plot		
	1	**2**	**3**
Coordinates[1]	36° 57´ 12.1” N 03° 29´ 36.3” W	36° 58´ 11.9” N 03° 30´ 1.7”	36° 58´ 6.5” N 03° 28´ 49.1” W
Elevation (m above sea level)[1]	1477	1698	2053
Mean daily minimum temp. (°C)[2]	6.8 ± 0.2	5.6 ± 0.2	3.4 ± 0.2
Mean daily maximum temp. (°C)[2]	17.1 ± 0.2	16.2 ± 0.2	13.4 ± 0.2
Mean ann. precip. (mm)[2]	536 ± 41	550 ± 40	630 ± 42
Dominant species	*Pinus pinaster*	*P. nigra*	*P. sylvestris*
Mean log diameter (cm)[3]	12.6 ± 0.4	12.8 ± 0.3	10.0 ± 0.2

[1] Measured at the centroid of each plot

[2] Data obtained from interpolated maps of Sierra Nevada (1981–2010) generated at the Centro Andaluz de Medio Ambiente (CEAMA).

[3] Estimated from the logs that were used in this study, mean ± 1 SE.

All the logs had the bark charred to a similar extent as a result of the even-aged and even-spaced nature of the stands, and they were only superficially affected by the fire (Figure 5.1). The experimental logs belonged to *Pinus pinaster* in plot 1 (lower elevation), *P. nigra* in plot 2 (intermediate elevation), and *P. sylvestris* in plot 3 (higher elevation), which were the main pine species at each elevation according to their climatic requirements. This variation in species is a normal situation in reforested (and natural) pine stands across marked elevational gradients. Although such sampling design does not allow the effect of pine species and elevation on decay rates to be separated, it does provide the opportunity to measure wood decomposition under three realistic forest scenarios. Each experimental log came from a different tree and was cut from a random height

Figure 5.1: *Wood samples used in the study.* ***Left:*** standardized 75 cm length experimental logs that were spread through the three elevations (plots) since the beginning of the experiment (March–April 2006); a metal tag can be observed in one of the logs. ***Center:*** Wood disc from an experimental log after some years (two in this case) of decomposition. ***Right:*** a highly decomposed wood disc after 10 years; when discs showed a high degree of fragmentation, as in this case, we used the two longest available arcs of the circle to find the perpendicular bisectors and the center of the disk at their intersection, from which the diameter was measured.

along the tree trunk. Therefore, the logs constitute a representative sample of trunk characteristics in the study site in terms of diameter and sectional origin along the trunks. At the same time, we cut one wood disc of 6–8 cm height from each of 50 logs that were randomly selected at each elevation (initial discs, hereafter). These discs were brought to the laboratory, and their volume was estimated after measuring two perpendicular diameters from both sides and four heights. The discs were then oven-dried at 40℃ to constant weight. The initial density of the wood was estimated from the known volume and weight of these discs, which did not present any sign of decay.

Wood Decomposition

Wood decomposition was estimated by cutting one random subsample of each of 20 randomly-chosen experimental logs per elevation in June 2008, 2010, 2014, and 2016, thus at 2, 4, 8, and 10 years after the experimental setup. The experimental logs were brought to the laboratory, and afterwards a disc of 6–8 cm length was obtained from the central part of each log by using a manual saw. Log dimensions and dry mass were measured as indicated above for the initial discs. As decay progresses, dead wood pieces become more elliptical. This is why we used the conic-parabolic formula proposed by Fraver *et al.* (2007) to estimate the volume of the logs. Wood density (gcm^3) was then calculated by dividing wood dry weight by its volume for each disc sample.

Statistical Analyses

We analyzed wood density with mixed models in R version 3.3.1 (R Core Team, 2016), with the "nlme" package (Pinheiro *et al.*, 2016). We initially fitted a model with Plot (a categorical factor with three levels), Year, and Log Diameter, as well as all the possible interactions between these factors, as fixed effects, and we included plot as a random effect to account for pseudoreplication (Crawley, 2013). The response variable was wood density. Model simplification was carried out by sequentially eliminating interaction terms from the model and performing likelihood ratio tests (LRTs) to assess their significance (Crawley, 2013). Heteroscedasticity was assessed with the varIdent function, with the use of LRTs (Pinheiro & Bates, 2000). Assumption checking through plotting of residuals and random effects was carried out as suggested by Pinheiro & Bates (2000).

As our response variable was wood density measured at a specific point in time but we were interested in assessing the factors that changed the speed at which density was reduced, in the Results we mainly focus on the factors that changed the effect of Year on wood density (i.e., we interpreted an interaction between Year and another factor as an effect of that factor on the speed of decomposition).

5.3 Results

Wood density showed an initial decline from an average of 0.482 ± 0.004 g cm^3 (mean ± 1 standard error (SE)) in 2006 to 0.420 ± 0.007 g cm^3 in 2008. Density then increased slightly until 0.445 ± 0.007 g cm^3 in 2010, and then dropped again to 0.415 ± 0.008 g cm^3 in 2014 and 0.370 ± 0.013 g cm^3 in 2016 (all plots pooled). Our results show that wood density was affected by three interactions between the studied factors. First, there was an effect of plot on wood decomposition rates (i.e., Plot × Year interaction affecting wood density; Table 5.2): the wood decomposed slower at

Table 5.2: Results from linear mixed effects models on the effect of year, log diameter, and plot (defined by the elevation/species gradient) on wood density.

Term Removed from Model	Likelihood Ratio	P-Value
Year × Diameter × Plot [1]	1.63	0.44
Year × Diameter[2]	8.26	<0.01
Year × Plot [2]	6.48	<0.05
Diameter × Plot [2]	10.78	<0.01

[1] Tested by removal from the model containing all possible interactions among factors.
[2] Tested by removal from the model containing all two-way interactions between the factors.

the highest-elevation plot than at the other plots (Figure 5.2). Second, the temporal change in wood density was also modified by the size of the log (i.e., significant Year × Diameter interaction; Table 5.2): larger logs decomposed faster than smaller logs (Figure 5.3). Third, there was a Diameter × Plot interaction, indicating different effects of log diameter on wood density across plots when years are pooled (Table 5.2). The Year × Diameter × Plot interaction was not significant, indicating that diameter and plot affected the speed of decomposition independently. Note that the Plot factor includes differences in elevation and species.

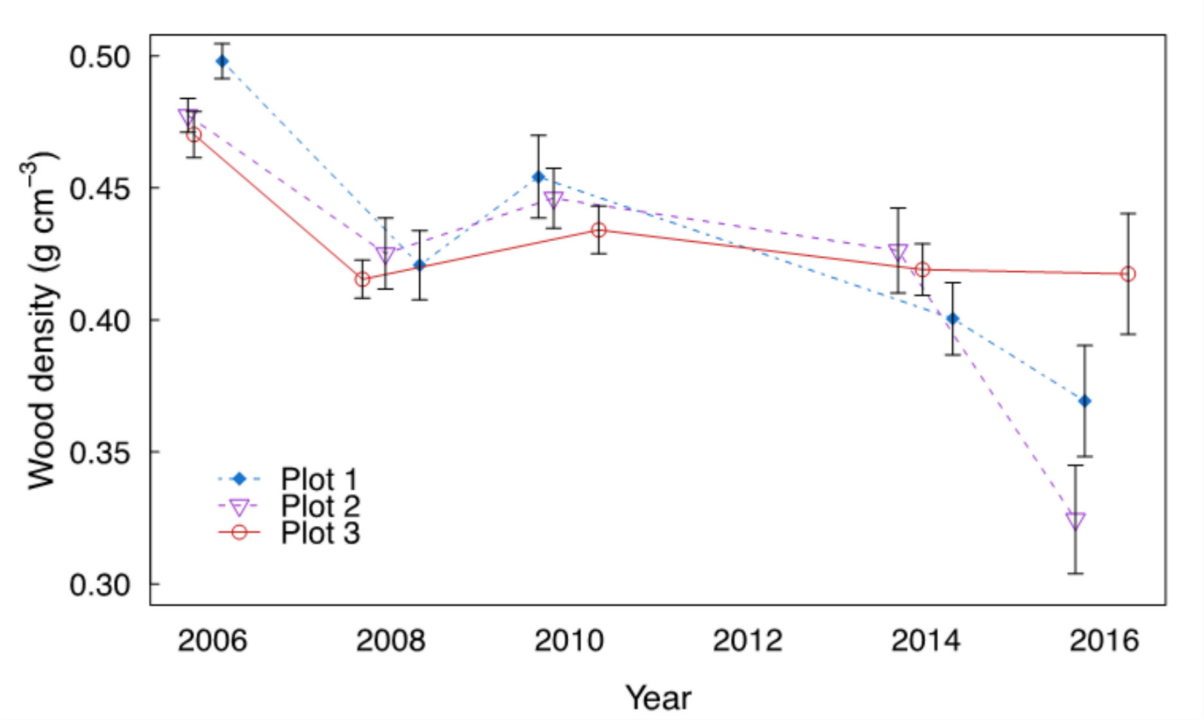


Figure 5.2: *Temporal changes in wood density across the three study elevations (plots).* Plot 1 was located at an elevation of 1477 m, Plot 2 at 1698 m, and Plot 3 at 2053 m (note that tree species varied across elevations too; Table 5.1). Plot did not significantly affect wood density in 2016 according to ANCOVA ($F_{2,66} = 0.74$, $p = 0.48$), but log diameter did (see Figure 5.3). Error bars indicate ± 1 SE of the mean.

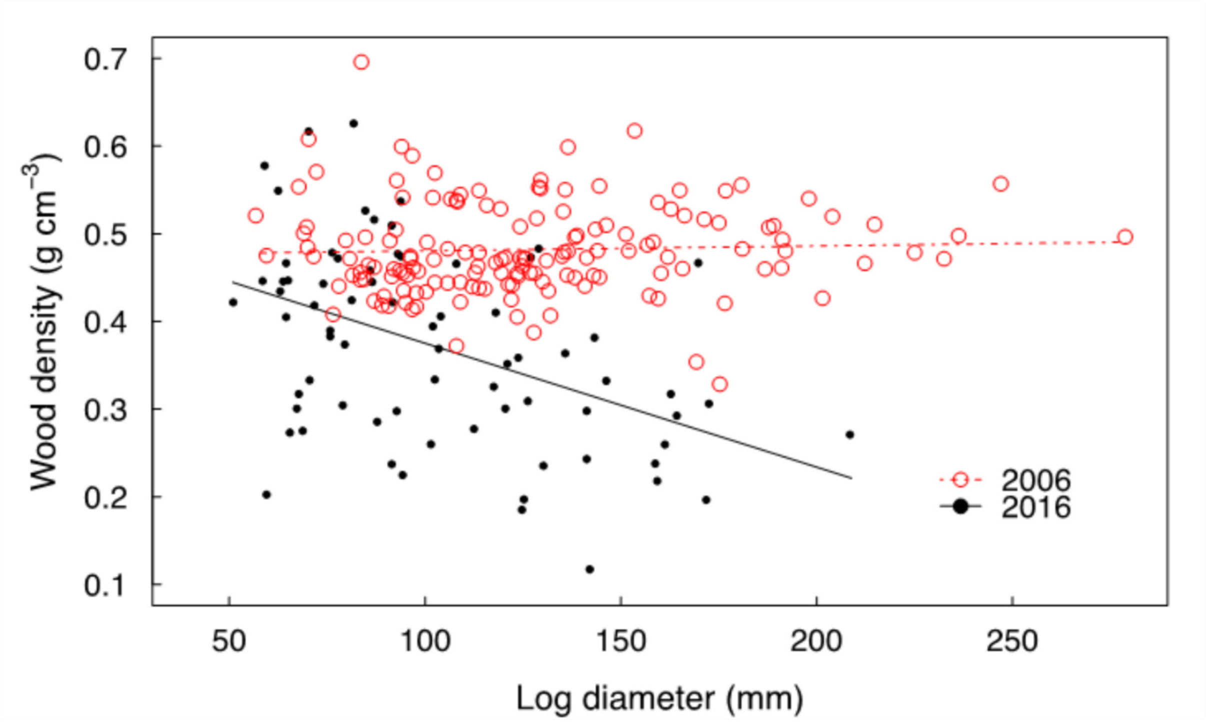


Figure 5.3: *Effect of log diameter on wood decomposition.* The density of wood was independent of diameter in 2006 (ANCOVA; $F_{1,70} = 0.28$, $p = 0.6$). In 2016, the average density was lower than in 2006 for all the ranges of diameters considered in the study and negatively affected by log diameter (ANCOVA; $F_{1,70} = 18.4$, $p < 0.001$), indicating that larger-diameter logs decomposed faster than smaller logs. The figure shows the measured values of each log and simple linear regression lines for each year.

5.4 Discussion

We found that the burnt wood lost nearly one-fourth of its mass after 10 years of decomposition. The rate of decomposition was lowest at the greatest elevation and for small-diameter logs. The differences across elevations might be related to several interacting factors that we cannot rule out, such as differences in climatic conditions and species, or even to an indirect effect of log diameters, which were lowest at the highest elevation (Table 5.1). This is, in any case, a normal situation under natural conditions, where variability in forest conditions across elevational gradients exists even within even-aged stands. Overall, our study provides novel results concerning burnt wood decomposition in Mediterranean mountains, and it represents one of the longest wood decomposition time-series available for a Mediterranean-type ecosystem.

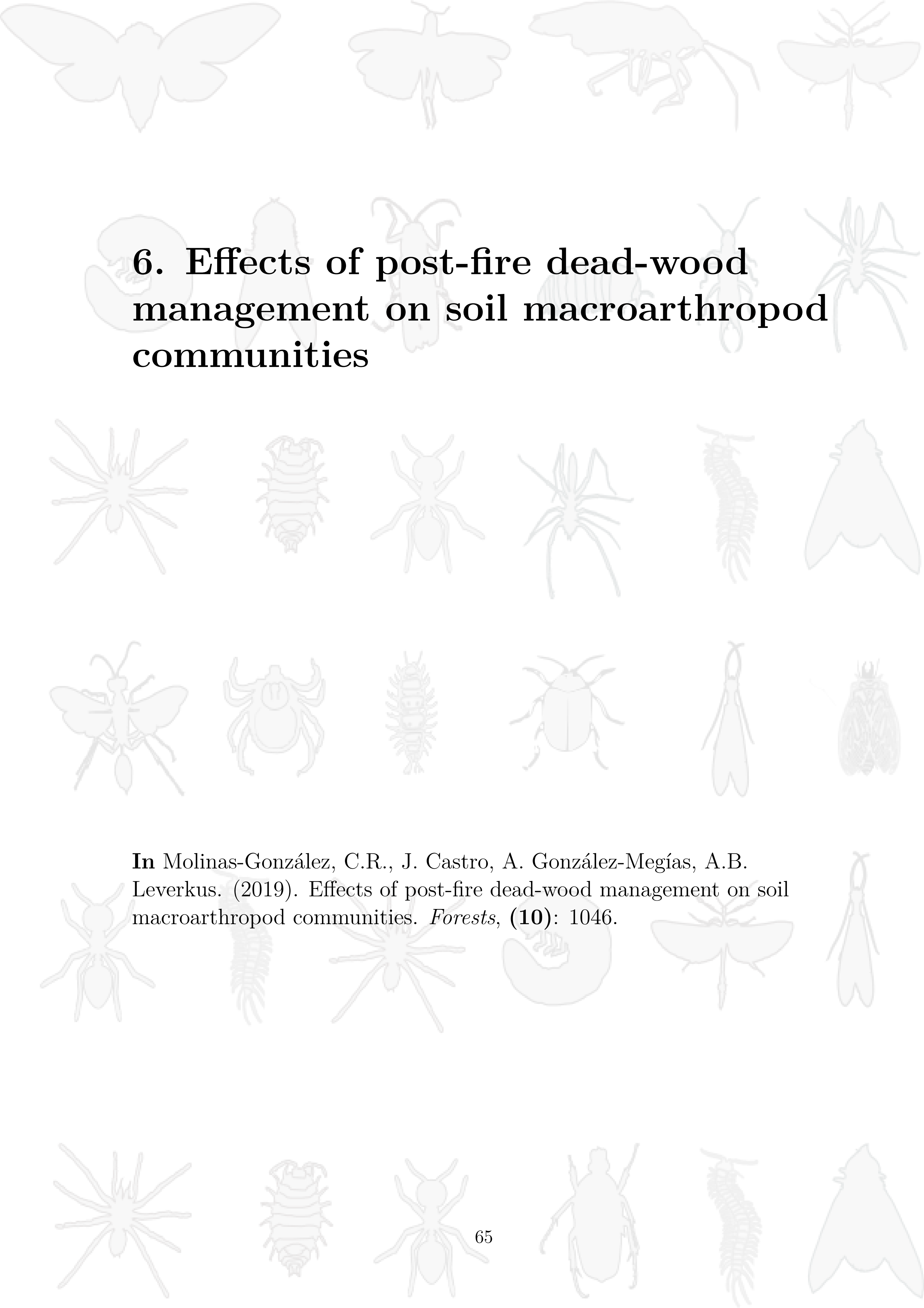
Despite the overall decline in wood density, the rate of this process changed over time and even reversed from the second to the fourth year. This has also been observed in previous studies of wood decomposition (e.g., Foster & Lang, 1982), and it might be related to the often-reported peak in colonization and nutrient immobilization by detritivorous organisms and decomposers in substrates with high carbon to nutrient ratios at the initial stages of decomposition (Stokland *et al.*, 2012; Coleman *et al.*, 2004). On the other hand, our final values of wood density loss are clearly lower than those reported for other ecosystem types with higher rainfall. For example, Olajuyigbe *et al.* (2011) found 50% of decomposition for *Picea sitchensis* after 12 years in Ireland, Mackensen & Bauhus (2003) found a 71% decomposition for *Pinus radiata* after 10 years in southeastern Australia, Brown *et al.* (1996) reported 25% of decomposition for *Pinus pinaster* after 5 years in places of Western Australia with average rainfall around 1000 L m^{-2} $year^{-1}$, and Yang and colleagues Yang *et al.* (2010) found density losses greater than 50% after 9 years for three species in an old-growth tropical forest. The lower decomposition rate in our study might be explained by the uncoupling between moisture and temperature during the characteristic summer drought in Mediterranean-type ecosystems (Aschmann, 1973). Still, the wood lost up to 26% and 32% of its mass in plots 1 and 2 (lowest and intermediate elevations, respectively) after 10 years, which supports that decomposition, despite being slower than in other temperate ecosystems, remains fast enough to ensure nutrient turnover, increase soil fertility, and reduce the fuel potential of the burnt logs (Passovoy & Fulé, 2006; Marañón-Jiménez & Castro, 2013; Marañón-Jiménez *et al.*, 2013a). Although the logs laid out for this study likely decomposed faster than the remaining wood due to their direct contact with the soil, the decomposition of the standing snags was likely not much slower, as all of them had collapsed and were mostly touching the ground 5.5 years after the fire (Molinas-González *et al.*, 2017b).

The results also show an effect of log diameter on the speed of decomposition. The effect reported for the diameter in the literature is variable. For instance, several studies found no relationship between diameter and decay rate (Foster & Lang, 1982; Laiho & Prescott, 1999; Mackensen *et al.*, 2003), and other studies found that decomposition rate declined with increasing log diameter because of reduced surface-to-volume ratios (Mackensen *et al.*, 2003; Jonsell *et al.*, 2007; Weedon *et al.*, 2009). Interestingly, our results show the opposite trend. Although we did not study the mechanism behind this diameter effect, we consider that it was likely mediated by an effect of diameter on the deadwood-inhabiting organisms involved in the decay process. In particular, we observed larger holes produced by the larvae of xylophagous insects in the thicker logs (Figure 5.1). In fact, it is well known that the larvae of larger species tend to inhabit logs of greater diameter (Ulyshen, 2016). The galleries they create increase bole fragmentation and respiration and can be used by other detritivorous organisms and decomposers that further accelerate decay (Stokland *et al.*, 2012; Kitchell *et al.*, 1979). Logs with a larger diameter also retain more humidity, which is especially beneficial for the colonization of microbial fungi during drought periods (Stokland *et al.*, 2012; Harvey *et al.*, 1978) and thus accelerates decomposition (Erickson *et al.*, 1985). Another explanation lies in the phenomenon known as “case-hardening”, which refers to solar radiation heating and hardening the outer wood layers (Kimmey & Furnis, 1943; Yatskov *et al.*, 2003), so that a larger surface-to-volume ratio would induce a greater loss of moisture rather than enhanced decomposer colonization (Erickson *et al.*, 1985). Under Mediterranean climate, characterized by a long, hot, and dry summer, the retention of moisture inside large logs may represent an important factor speeding up wood decomposition. Our results thus support that log size may accelerate decay under Mediterranean climate, and they highlight the need to carefully control log diameter to correctly interpret the speed of decay across environmental gradients.

Salvage logging is a common silvicultural practice after fires in Mediterranean pine reforestations, as well as other parts of the world (Lindenmayer *et al.*, 2008; Castro *et al.*, 2010, 2011). The most obvious consequence of this approach is the subsequent large-scale absence of decomposing wood. While ecosystems and the species that constitute them are resilient to historical disturbance regimes, this resilience hinges on the existence of material legacies of the previous ecosystem that set the scene for regeneration; changes in the post-disturbance environmental conditions compared to those under which the ecosystem historically regenerated can seriously undermine resilience (Johnstone *et al.*, 2016). The present study documents relatively fast and heterogeneous decay rates in burned pine plantations under Mediterranean-type conditions, a process that involves myriads of species ranging from fungi to mammals and that virtually disappears after post-fire logging. The final decision concerning burnt wood should ultimately depend on the balance between the economic value of the wood, the cost of wood removal, the risks posed by the presence of decaying logs, and the ecological processes that dominate post-fire ecosystems under different management scenarios.

5.5 Conclusion

Our study shows that burnt wood decay in Mediterranean mountains is slower than in other temperate ecosystems, but still fast enough to be considered a process that may support nutrient cycling and ecosystem regeneration. Wood decay changed across an altitudinal gradient, a fact that is likely linked to changes in both abiotic (climatic conditions) and biotic (wood characteristics, decomposer and detritivorous communities) factors. Overall, we conclude that burnt wood is a biological legacy that should be partially or totally kept in situ after fires.



6. Effects of post-fire dead-wood management on soil macroarthropod communities

In Molinas-González, C.R., J. Castro, A. González-Megías, A.B. Leverkus. (2019). Effects of post-fire dead-wood management on soil macroarthropod communities. *Forests*, **(10)**: 1046.

Abstract

Dead wood comprises a vast amount of biological legacies that set the scene for ecological regeneration after wildfires, yet its removal is the most frequent management strategy worldwide. Soil-dwelling organisms are conspicuous, and they provide essential ecosystem functions, but their possible affection by different post-fire management strategies has so far been neglected. We analyzed the abundance, richness, and composition of belowground macroarthropod communities under two contrasting dead-wood management regimes after a large wildfire in the Sierra Nevada Natural and National Park (Southeast Spain). Two plots at different elevation were established, each containing three replicates of two experimental treatments: partial cut, where trees were cut and their branches lopped off and left over the ground, and salvage logging, where all the trees were cut, logs were piled, branches were mechanically masticated, and slash was spread on the ground. Ten years after the application of the treatments, soil cores were extracted from two types of microhabitat created by these treatments: bare-soil (in both treatments) and under-logs (in the partial cut treatment only). Soil macroarthropod assemblages were dominated by Hemiptera and Hymenoptera (mostly ants) and were more abundant and richer in the lowest plot. The differences between dead-wood treatments were most evident at the scale of management interventions: abundance and richness were lowest after salvage logging, even under similar microhabitats (bare-soil). However, there were no significant differences between microhabitat types on abundance and richness within the partial cut treatment. Higher abundance and richness in the partial cut treatment likely resulted from higher resource availability and higher plant diversity after natural regeneration. Our results suggest that belowground macroarthropod communities are sensitive to the manipulation of dead-wood legacies and that management through salvage logging could reduce soil macroarthropod recuperation compared to other treatments with less intense management even a decade after application.

6.1 Introduction

Soil fauna comprises an enormous amount of forest biomass (Bardgett & van der Putten, 2014). In forests, soil fauna can amount to millions of individuals of hundreds of species per square meter (André *et al.*, 2002; Bardgett & van der Putten, 2014), encompassing an array of taxa and functional groups (Coleman *et al.*, 2004; Jones *et al.*, 1994). Recently, belowground diversity has attracted special attention due to its importance for ecosystem functions (e.g., decomposition, mineralization and nutrient cycling (Bardgett & van der Putten, 2014; Wall *et al.*, 2010)) and ecosystem services (e.g., pathogen control and soil fertility (Wall *et al.*, 2015)) and the low amount of existing knowledge compared to aboveground fauna (Veresoglou *et al.*, 2015). As a result, understanding the drivers of soil fauna distribution and diversity represents a priority in soil ecological research (Eisenhauer *et al.*, 2017) and biodiversity conservation (Decaëns *et al.*, 2006).

A major current concern in ecological conservation globally is the increase in the frequency of large disturbance events such as wildfires (Seidl *et al.*, 2017). Fire affects soil insects and other invertebrates by killing individuals directly (McCullough *et al.*, 1998; Swengel, 2001), increasing their susceptibility to predation (Warren et al., 1987), and/or reducing the quantity and quality of food (Coleman *et al.*, 2004; New, 2014). However, some belowground organisms, such as ant communities and mining bees, are often able to survive because underground nesting protects adult individuals, larvae, eggs, and some of their resources, from the flames (Cane & Neff, 2011; Gongalsky *et al.*, 2012; Swengel, 2001). Several soil faunal taxa even increase in abundance during the few years after a fire (Mateos *et al.*, 2011; Moretti *et al.*, 2014) as a result of attraction by smoke (Swengel, 2001), stimulation of emergence of adults due to increases in soil temperature (New, 2014) and, particularly, large pulses in the supply of dead wood (Moretti *et al.*, 2014; Thorn *et al.*, 2014). An estimated 20–25% of all forest species are saproxylic, and many of them contribute to soil biota by having at least some life stage belowground (Stokland *et al.*, 2012). However, while there is a rich body of scientific literature on the effects of fire on arthropods (New, 2014; Swengel, 2001), most of it focuses on aboveground species (Veresoglou *et al.*, 2015), and the factors that affect belowground fauna in burnt forests –including factors related to the management of burnt wood– have generally been neglected (Zaitsev *et al.*, 2016).Further, the effects of post-fire management on belowground organisms have received very little attention.

Around the world, managing burnt forests frequently involves the removal of large trunks, often including a considerable elimination of smaller woody material by chipping, mastication, or burning. This practice is called salvage logging (Lindenmayer *et al.*, 2008; Müller *et al.*, 2019). Salvage logging has generated strong controversy in recent decades because it alters the ecological conditions for secondary succession (Hernández-Hernández *et al.*, 2017; Leverkus *et al.*, 2018a; Leverkus & Castro, 2017; Lindenmayer *et al.*, 2017; Thorn *et al.*, 2018). Less aggressive post-fire interventions, such as partial retention and the cutting of trees without their extraction, have been suggested as alternatives to avoid compromising ecosystem recovery (e.g. Castro *et al.*, 2011; Ritchie & Knapp, 2014).The key differences between salvage logging and such alternatives lie in a) the greater mechanical disturbance of logging operations and b) the greater reduction in the amount of dead wood under the salvage-logging regime. These differences can affect soil fauna through several non-mutually exclusive mechanisms, including changes in abiotic conditions such as solar radiation at ground level, and resulting changes in the biotic environment (Pons, 2015; Toivio *et al.*, 2017; Wagenbrenner *et al.*, 2015). In fact, some of the main factors that influence soil faunal diversity, such as soil humidity and organic matter (Doblas-Miranda *et al.*, 2009), are strongly linked to the abundance of dead wood (Castro *et al.*, 2011; Marañón-Jiménez *et al.*, 2011; Siitonen, 2001). The management of burnt wood may thus bring about changes in the abundance and composition of post-fire soil communities, with subsequent alterations in the functions that they perform. However, despite the known effects of salvage logging on many aboveground communities (Thorn *et al.*, 2018) and some evidence pointing out that harvesting undisturbed forest compromises the recuperation of belowground insects (Edmonds *et al.*, 2000; Marra & Edmonds, 1998; Siira-Pietikäinen & Haimi, 2009), the effects of different post-fire management treatments on belowground fauna remain poorly known.

To assess the differences in belowground arthropod communities across different dead-wood management treatments, we took soil cores 11 years after a wildfire in southeastern Spain (10.5 years after dead-wood management). We sampled a post-fire management experiment that was replicated within and between two plots located at different elevation (at approximately 1500 and 2000 m a.s.l.). Treatments comprised salvage logging (cutting all trees) and partial cut (90% of trees were cut and the branches lopped off); within the latter, we sampled soils underneath logs and away from logs. We aimed to analyze the differences between management treatments and the microhabitats therein and to assess whether changes in ecological conditions due to elevation –a key factor affecting macroarthropod abundance and composition(McCain & Grytnes, 2010)– modified the response of macroarthropod communities to management. We hypothesized that: (1) the salvage logging treatment would host the lowest richness and abundance of soil fauna due to the reduction in dead-wood resources at the stand scale, (2) soils in the partial cut treatment would contain more diverse communities than in the salvage logging treatment even under similar microhabitat conditions due to a greater stand-scale species pool, and (3) within the partial cut treatment, the soils sampled beneath lying logs would contain richer soil faunal communities than those in the same stand-scale treatment but away from logs.

6.2 Materials and Methods

Study area

The study was conducted in the Sierra Nevada National and Natural Park (SE Spain), in an area affected by a wildfire that burned 3,400 ha of shrublands and pine stands in September 2005 (Leverkus *et al.*, 2012). Two plots were established six months after the fire (Table 6.1), one at 1477 m a.s.l. (Low Plot, hereafter), and one at 2053 m a.s.l. (High Plot, hereafter). The plots were similar in terms of bedrock (micaschist), orientation (SW), soil type (haplic phaeozems) and fire severity (high according to the local forest service; the fire consumed all the leaves, twigs and understory vegetation and charred the bark of the trunks(Marañón-Jiménez & Castro, 2013)). Black pine (*Pinus nigra*) dominated the Low Plot, and Scot pine (*P. sylvestris*) the High Plot, according to each species' ecological requirements and elevational constraints. Both pine species are native to the south of the Iberian Peninsula, yet in our study site they constituted 40-60 year-old plantations (see Table 6.1 for a detailed description of dasometric parameters of the plots). The pines were situated on terraces established with bulldozers, previously a common reforestation practice on hill-sides in Spain. Climate in the area is Mediterranean, with mild, wet winters and hot, dry summers. In each plot, three replicates (subplots) of the following two burnt-wood management treatments were established (Figure 6.1):

1. Salvage Logging (SL), where all the burnt trees were manually cut and the trunks cleaned of branches with chainsaws. Trunks were manually piled (groups of 10-15 logs), the woody debris was masticated with a tractor, and the slash was spread on the ground. The Forest Service had planned to extract the trunks with a log-forwarder, but the foresters eventually cancelled this step due to difficulties in precisely operating machinery within the spatial arrangement of the plots. Masticated woody material (circa 2-5 cm in diameter) covered 32% of the surface right after treatment implementation (Castro *et al.*, 2011).The structure of the habitat was an open landscape with isolated groups of stacked logs covering less than 5% of the treatment area. The most characteristic microhabitat of this treatment was one devoid of dead wood (the logging slash had mostly decomposed by the time of sampling) and with herbs and grasses. Hence, in the SL treatment we sampled soils in this “bare-soil” microhabitat.

2. Partial Cut (PC), which consisted of felling ca. 90% of the burnt trees, lopping off the branches and cutting the logs in pieces of 2-3 m length. All the biomass was spread over the ground, without chopping. The remaining 10% of the burnt trees were left standing but they collapsed quickly until 100% had fallen after 5.5 years (Molinas-González *et al.*, 2017b). This treatment therefore represents a situation that would be reached by a passively managed burnt forest within a few years after the fire. The resulting habitat structure comprised logs and branches spread over the ground with an initial ground coverage of 45% (Castro *et al.*, 2011). In this treatment, besides the “bare-soil” microhabitat described above, there was a characteristic microhabitat where soil was covered by dead wood spread over the flat terrace bed. In the PC treatment, we sampled soils in the “bare soil” and the “under-logs” microhabitats.

Sampling design

We sampled soils to study macroarthropod soil communities within each of the twelve subplots in spring 2016 (10.5 years after the fire). GPS positions were recorded for each soil sample (Figure 6.1). In each of the

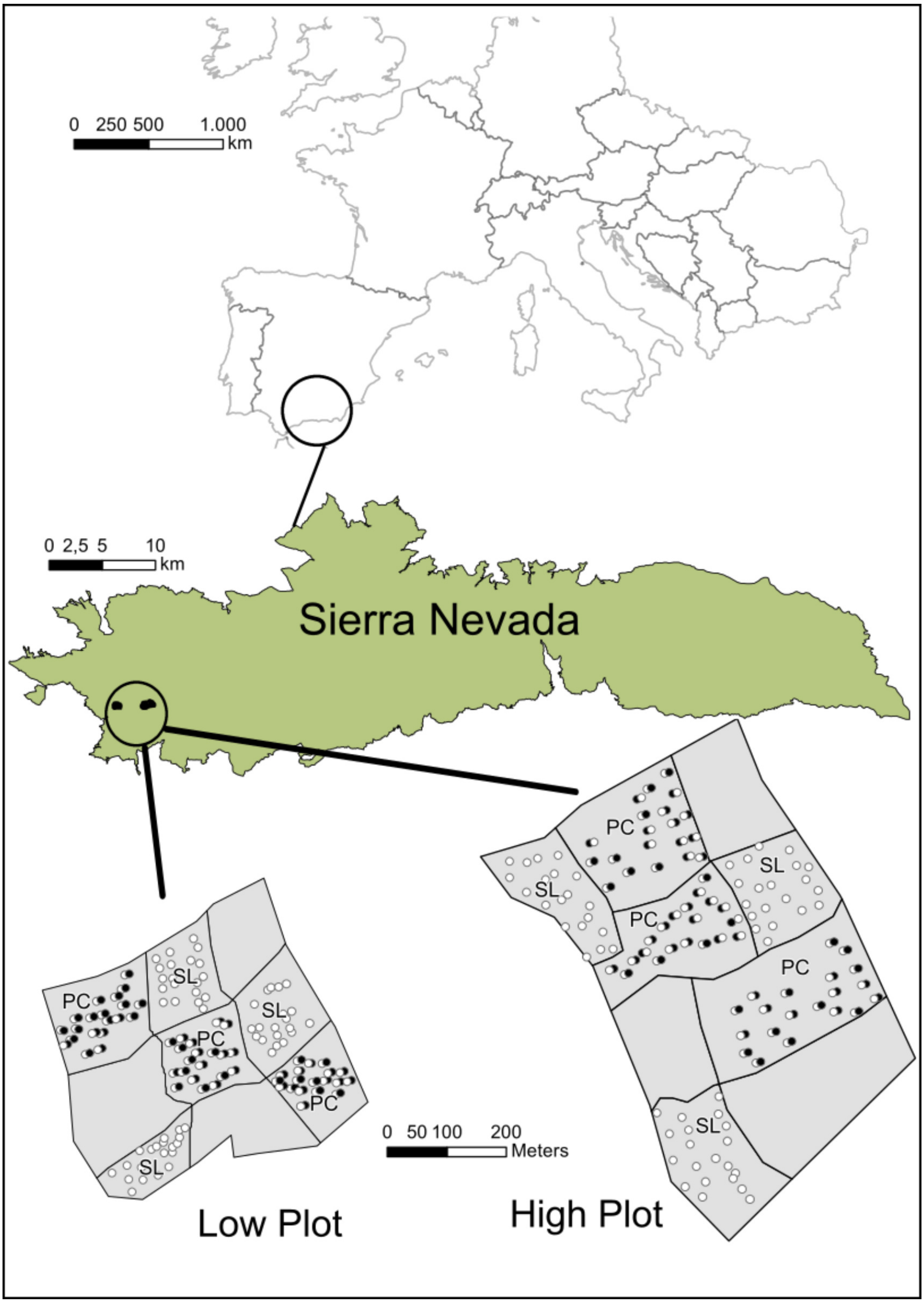


Figure 6.1: *Location of the two study plots* within Europe and the Sierra Nevada Natural Park. Each plot contained six subplots, which constituted three replicates of each of two post-fire treatments. SL = Salvage Logging; PC = Partial Cut. Black circles correspond to sampling points in the "under-logs" microhabitat, and white circles in the "bare-soil" microhabitat.

Table 6.1: Location and characteristics of the study plots.

	Plots	
	Low Plot	High Plot
Coordinates[1]	36°57´12” N 03°29´36” W	36°58´06” N 03°28´49” W
Area (ha)	17.7	31.7
Elevation (m above sea level)[1]	1477	2053
Slope (%)	25-30	35
Mean daily minimum temp. (°C)[2]	6.8 ± 0.2	3.4 ± 0.2
Mean daily maximum temp. (°C)[2]	17.1 ± 0.2	13.4 ± 0.2
Mean ann. precip. (mm)[2]	536 ± 41	630 ± 42
Dominant species	*Pinus pinaster/ P. nigra*	*P. sylvestris*
Tree density (individuals ha^{-1})[3]	1448 ± 66	1010 ± 49
Basal tree diameter (cm)[4]	17.7±0.15	15.7±0.13
Tree height (m)[5]	6.3±0.1	6.2±0.1
dbh (cm)[5]	13.3±0.2	10.8±0.2
Wood biomass (kg ha^{-1}) [6]	55,273	26,166
Representative plants[7]	*Ulex parviflorus, Festuca scariosa, Dactylis glomerata, Euphorbia flavicoma*	*Vaccaria hispanica, Sesamoides purpurascens subsp. prostrata, Senecio nebrodensis, Heliantemun appeninum*

[1] Measured at the centroid of each plot.

[2] Data obtained from interpolated maps of Sierra Nevada (1981–2010) generated at the Centro Andaluz de Medio Ambiente (CEAMA).

[3] Calculated just after the fire (autumn 2005) by counting the trees in four randomly placed 25x25 m quadrats for each subplot. Values were statistically higher in the Low Plot than in the High Plot, but there were no differences among treatments within plots (Wilconxon test; p>0.05 in both cases).

[4] Calculated from 30 randomly selected trees per each of the 25x25 m quadrats used to estimate tree density (360 trees per treatment and plot). Values were slightly different across treatments within each plot (p<0.05 in both plots), but without a consistent pattern, suggesting an spurious effect of the sampling protocol: 16.8±0.2 cm in SL and 19.1±0.2 in PC for the Low Plot, and 16.7±0.2 in SL and 14.8±0.2 in PC the High Plot.

[5] From (Marañón-Jiménez & Castro, 2013); calculated from 90 randomly selected trees in untreated areas within the experimental plots (which constituted a third treatment, non-intervention, not included in this study and that was representative of the initial conditions in the study area). dbh = diameter at breast height.

[6] From (Marañón-Jiménez & Castro, 2013); estimated from data on tree density, height and dbh by using the CubiFOR calculation tool (http://www.cesefor.com/contenido/cubifor-herramienta-descripcion), a model adjusted for the calculation of wood biomass in pine plantations in the Mediterranean basin ((Bravo *et al.*, 2011; Herrero *et al.*, 2019; Lizarralde *et al.*, 2017). (http://www.cesefor.com/contenido/cubifor-herramienta-descripcion)

[7] Sampled two years after the fire (Leverkus *et al.*, 2014)

subplots, we collected 20 cores from each available microhabitat. Thus, in each SL replicate, we collected 20 cores under “bare-soil”, and in each PC replicate we collected 40 cores: 20 cores under “bare-soil” and 20 cores “under-logs”. Sampling points in SL were located at least 10 m from each other. In the PC treatment, cores under “bare-soil” were obtained at least 50 cm away from cores “under-logs”, and these pairs were located at least 10 m from each other. This sampling procedure allowed us to address our three hypotheses. Our procedure resulted in 360 samples distributed across the two plots (Figure 6.1).

The timing of sampling was selected as to make it coincide with the arrival of flowering and the movement of soil invertebrates from lower soil layers, considering the difference in phenology across the two plots (Dowdy, 1944). We sampled the Low Plot in May-June and the High Plot in June-July. Soil cores were extracted with soil augers (10 cm diameter, 12-15 cm depth). Samples were put into plastic bags and carried to a laboratory on the same day. In the laboratory, soil cores were broken and sieved by hand. We chose this method because hand sorting has shown to be more efficient than several methods such as funnels and high-gradient funnels (André *et al.*, 2002). Furthermore, soil communities comprise a vast amount of life forms, including inactive, sessile, moving, and immature organisms, and sieving soil samples allows to capture all possible life forms (André *et al.*, 2002; Doblas-Miranda *et al.*, 2009; Sadaka & Ponge, 2003). The samples were fractionated meticulously, first at 1 cm mesh size to remove rocks, leaf litter and roots. They were then sieved at mesh sizes of 3 mm and 1 mm over a clean, white surface, where arthropods were visually sought. Each sample was screened for approximately 40 min. All specimens were conserved in 70% ethanol. Our final database consists of all the organisms identified at the level of orders and at the species level for ants.

Statistical Analyses

We analyzed the differences between dead-wood treatments and microhabitats on the diversity, abundance, and composition of soil macroarthropods. Each of the analyses described below was conducted independently for each of our hypotheses, namely:

a) Effect of dead-wood treatment (SL vs. PC) at the stand scale, pooling over the greater variety of microhabitats (“bare-soil” and “under-logs”) in the PC treatment. This allowed testing the overall differences between post-fire interventions (Hypothesis 1). Here, the tested factors were plot, dead-wood treatment, and plot by treatment interaction.

b) Effect of dead-wood treatment on the soil fauna found in the bare-soil microhabitat (i.e., PC "under-logs" excluded). With this we aimed to assess whether stand-scale management affected the communities that were found in an otherwise similar microhabitat (Hypothesis 2). The tested factors were plot, microhabitat, and plot by microhabitat interaction.

c) Difference between the two different microhabitats in the PC treatment. This allowed testing the effect of the presence of dead wood within the same stand-scale treatment on soil macroarthropod communities (Hypothesis 3). The tested factors were plot, microhabitat, and plot by microhabitat interaction.

To test the effect of dead-wood treatment and microhabitat on the abundance of soil macroarthropods (excluding ants), we used zero-inflated generalized linear mixed-effects models. To deal with the hierarchical sampling design and avoid pseudo-replication, we included an appropriate structure of random effects (soil samples within dead-wood replicates within plots). We generated final models through simplification while testing the significance of terms with likelihood ratio chi-squared tests, which compared the fit of models with and without each term Crawley (2013). We fitted these models with the "glmmTMB" function of the "glmmTMB" R package (Brooks *et al.*, 2017)..

We compared the diversity of orders of soil macroarthropods by fitting accumulation curves with confidence intervals with sample-based rarefaction and extrapolation with the iNEXT function of the iNEXT R package (Chao *et al.*, 2014). We used this function to assess the increase of order richness with a common sample size and to reveal differences in numbers of orders between dead-wood treatments. This was necessary for the case of Hypothesis 1, as the PC treatment had twice as many samples in this analysis as the SL treatment. Extrapolations were taken to twice the highest number of samples. Due to the high abundance of ants in some individual samples, and the species-level identification of this group, we analyzed ants separately.

We compared macroarthropod community assemblages among treatments and microhabitats using non-metric multidimensional scaling (NMDS).

The method does not use absolute abundance; rather, it maximizes rank order correlation between distance measures in an ordination space, assumes that dissimilarity is monotonically related to ecological distance and provides a robust and easily interpretable ordination method (Quinn & Keough, 2002). We used the “metaMDS” function to adequate dissimilarity measures, scaling several times until reaching a similar minimum stress. This value indicated how well the distribution of points on the plots matches the actual distances between dimensions; stress values were interpreted following the suggestions by Quinn & Keough (2002). We assessed dissimilarities variance to compare differences between community compositions across treatments and microhabitats using the “ANOSIM” function from the “vegan” package (Oksanen *et al.*, 2018). This procedure is based on the difference between average ranked values of distance on abundances among sample replicates. Interpretations were based on R values. R is scaled between -1 and +1, where negative values correspond to similarities across different treatments being greater than those within, with a value of zero as a null hypothesis of no difference among a set of samples (Chapman & Underwood, 1999). Significance was calculated over 1000 permutations.

We used the “vegdist” and “diana” functions from the “vegan” (Oksanen *et al.*, 2018) and “cluster” packages (Maechler *et al.*, 2018) for divisive hierarchical cluster analysis to assess macroarthropod groups not defined a priori. This method takes one large set of objects and then iteratively splits them into consistent groups in which similarity is greatest (Quinn & Keough, 2002). Analyses were based on “Bray–Curtis” similarity. Wilcoxon-Mann-Whitney U-tests were used to compare the abundance of the main arthropod taxa across plots, and across dead-wood treatments and microhabitats at each plot, using the “wilcox.test” function. Analyses were made in R version 3.3.1 (R Core Team, 2016).

6.3 Results

Variations in abundance, richness and diversity

The 360 soil samples yielded 524 macroarthropod individuals belonging to 13 orders. The most abundant orders were Hemiptera (54% of individuals), and Hymenoptera (24%, mostly ants). Among formicids, the most abundant species were *Bothriomyrmex meridionalis* (33% of the 124 ant individuals) and *Proformica ferrari* (22%) (Table Supplementary information 6.6).

The zero-inflated mixed-effects models –which excluded ants– showed that macroarthropod abundance was affected by an interaction between Plot and Treatment (Table 6.2). Abundance was higher in the Low Plot (2.05 ± 0.34 individuals sample^{-1}) than in the High Plot (0.16 ± 0.03), and it was also greater in the PC treatment than in SL (Table 6.3). However, the effect of treatment varied across plots, as between-treatment differences were greatest in the Low Plot (Table 6.3). The same trend was found when considering only the bare-soil microhabitat across both deadwood treatments (i.e., Hypothesis 2; Tables 6.2 & 6.3). The comparison of microhabitats in the PC treatment (Hypothesis 3) showed only the negative effect of the High Plot on macroarthropod abundance (Tables 6.2 & 6.3).

A different trend was observed for richness, where a significant treatment by plot interaction (Table 6.2) showed that order richness was similar (~ 0.6 orders samples $^{-1}$) across treatments in the Low Plot whereas in the High Plot the PC treatment had higher values (Table 6.3). Again, microhabitats in the PC treatment produced no significant effect on richness (Table 6.2).

Richness curves

Sample-based rarefaction and extrapolation revealed significantly higher richness of macroarthropod orders and of ant species in PC than in the SL treatment at the Low Plot (Figure 6.2a; Hypothesis 1). This trend was also found in the High Plot (Figure 6.5a), although the results for this plot are less robust because the macroarthropod abundance was very low overall (Table 6.3). When the two burnt-wood treatments are compared considering only the under-soil microhabitat (Hypothesis 2), there were

Table 6.2: Model selection for the effects of dead-wood treatment, microhabitat, and plot on the abundance and richness of macroarthropod individuals (excluding ants), estimated with zero-inflated GLMM

	Macroarthropod abundance			**Macroarthropod richness**		
Hypothesis		**X2**	**P-value**		**X2**	**P-value**
1						
	Treatment x Plot	7.34	<0.01	Treatment x Plot	5.5	**<0.05**
2						
	Treatment x Plot	6.30	<0.05	Treatment x Plot	9.69	**<0.01**
3						
	* Microhabitat x Plot	0.064	0.8	* Microhabitat x Plot	2.06	0.15
	* Microhabitat	0.01	0.891	* Microhabitat	0.11	0.738
	Plot	7.16	**<0.001**	Plot	4.69	**<0.05**

The tested hypotheses were the differences between:
1) Dead-wood treatments (SL, PC)
2) Treatments but only under similar microhabitat (both treatments under bare soil)
3) Microhabitats in the PC treatment.
Significant differences are denoted by boldface at $\alpha = 0.05$.* Terms excluded from the final model.

no significant differences in the number of macroarthropod orders or ant species across treatments at the Low Plot (Figure 6.2b), although at the High Plot differences appeared due to the virtual absence of macroarthropods from samples in salvage-logged subplots (Figure 6.5b). Microhabitats within the PC treatment did not significantly differ in the number of orders (Hypothesis 3), but under-log samples hosted a greater richness of ant species at both the Low Plot (Figure 6.2c) and the High Plot (Figure 6.5c).

Table 6.3: Mean abundance (number of individuals/samples ± 1 SE of the mean) of macroarthropods and richness of orders across burnt-wood treatments and microhabitats.

	Low Plot			High Plot		
Response	Salvage logging	Partial cut		Salvage logging	Partial cut	
		Bare soil	Under logs		Bare soil	Under logs
Abundance1	1.65±0.41	2.26±0.74	2.25±0.61	0.00±0.00	0.28±0.09	0.21±0.06
Richness1	0.61±0.01	0.51±0.09	0.7±0.11	0.00±0.00	0.23±0.06	0.2±0.05

[1] Number of samples per plot: 60 for Salvage logging (all under bare soil) and 120 for partial cut (where 60 samples were taken under bare soil and 60 under logs).

Community assemblages and Cluster analysis

Non-metric multidimensional scaling ordination of assemblages showed an overall pattern of stratification across treatments at the Low Plot (Figure 6.3), but the effect of treatments was not significant (ANOSIM R = 0.02; $P > 0.05$). Also, microhabitats did not create significant differences (ANOSIM R = -0.03; $P > 0.05$). Divisive hierarchical clustering showed that macroarthropod assemblages differed markedly (60% of dissimilarity) between plots and, secondarily, similar microhabitats were more similar in composition (Figure 6.4).

Differences between treatments in the abundance of individual orders were not significant except for Lepidoptera ($P<0.05$), which was significantly associated to the SL treatment (Table 6.4 and 6.4). When differences between microhabitats were assessed (Hypothesis 3), the two microhabitats did not show characteristic communities (Table 6.6).

Table 6.4: Mean abundance (number of individuals/samples ± 1 S.E. of the mean) of the main macroarthropod taxa across treatments and microhabitats.

Low plot								
Treatment					Dead-wood microhabitat			
Taxa	Salvage logging	Partial cut	Z	P1,2	Partial cut		Z3	P1,2,3
					Bare soil	Under logs		
Hymenoptera	0.133 ±0.05	0.566±0.209	-1.11	0.266	0.283±0.142	0.85±0.332	-1.689	0.091
Lepidoptera	0.216± 0.064	0.008±0.006	2.25	0.023	0	0.016±0.011	NA	NA
Hemiptera	1.100±0.217	1.775±0.378	-0.65	0.513	2.000±0.524	1.550±0.396	0.192	0.847
Aranea	0.016±0.009	0.008±0.006	0.5	0.616	0.016±0.011	0	NA	NA
Geophilomorpha	0.050±0.016	0.041±0.017	0.53	0.59	0.033±0.016	0.050±0.026	-0.01	0.98
Isopoda	0.016±0.009	0.125±0.095	-0.006	0.994	0	0.250±0.165	NA	NA
Diptera	0.100±0.029	0.150±0.043	-0.701	0.483	0.166±0.063	0.133±0.04	0.005	0.996
Coleoptera	0.116±0.027	0.083±0.022	0.579	0.562	0.033±0.016	0.133±0.035	-1.73	0.082

[1] p-values are the results of Wilcoxon-Mann-Whitney U-tests.
[2] Significant differences are denoted by boldface at $\alpha = 0.05$.
[3] NA= not applicable

Table 6.5: Mean abundance (number of individuals/samples ± 1 S.E. of the mean) of the main macroarthropod taxa across treatments and microhabitats (cont).

High plot								
Taxa	Treatment				Dead-wood microhabitat			
	Salvage logging	Partial cut	Z3	P1,2,3	Partial cut		Z3	P1,2,3
					Bare soil	Under logs		
Hymenoptera	0.167	0.225±0.126	-0.244	0.806	0.433±0.21	0.016±0.01	1.387	0.165
Lepidoptera	0	0	NA	NA	0	0	NA	NA
Hemiptera	0	0.050±0.018	NA	NA	0.066±0.02	0.033±0.01	0.47	0.638
Aranea	0	0.008±0.006	NA	NA	0	0.016±0.011	NA	NA
Geophilimorpha	0	0.008±0.006	NA	NA	0.016±0.0111	0	NA	NA
Isopoda	0	0.008±0.006	NA	NA	0	0.016±0.01	NA	NA
Diptera	0	0.016±0.009	NA	NA	0.033±0.016	0	NA	NA
Coleoptera	0	0.141±0.032	NA	NA	0.150±0.043	0.133±0.035	0.004	0.996

[1] p-values are the results of Wilcoxon-Mann-Whitney U-tests.
[2] Significant differences are denoted by boldface at α= 0.05.
[3] NA= not applicable

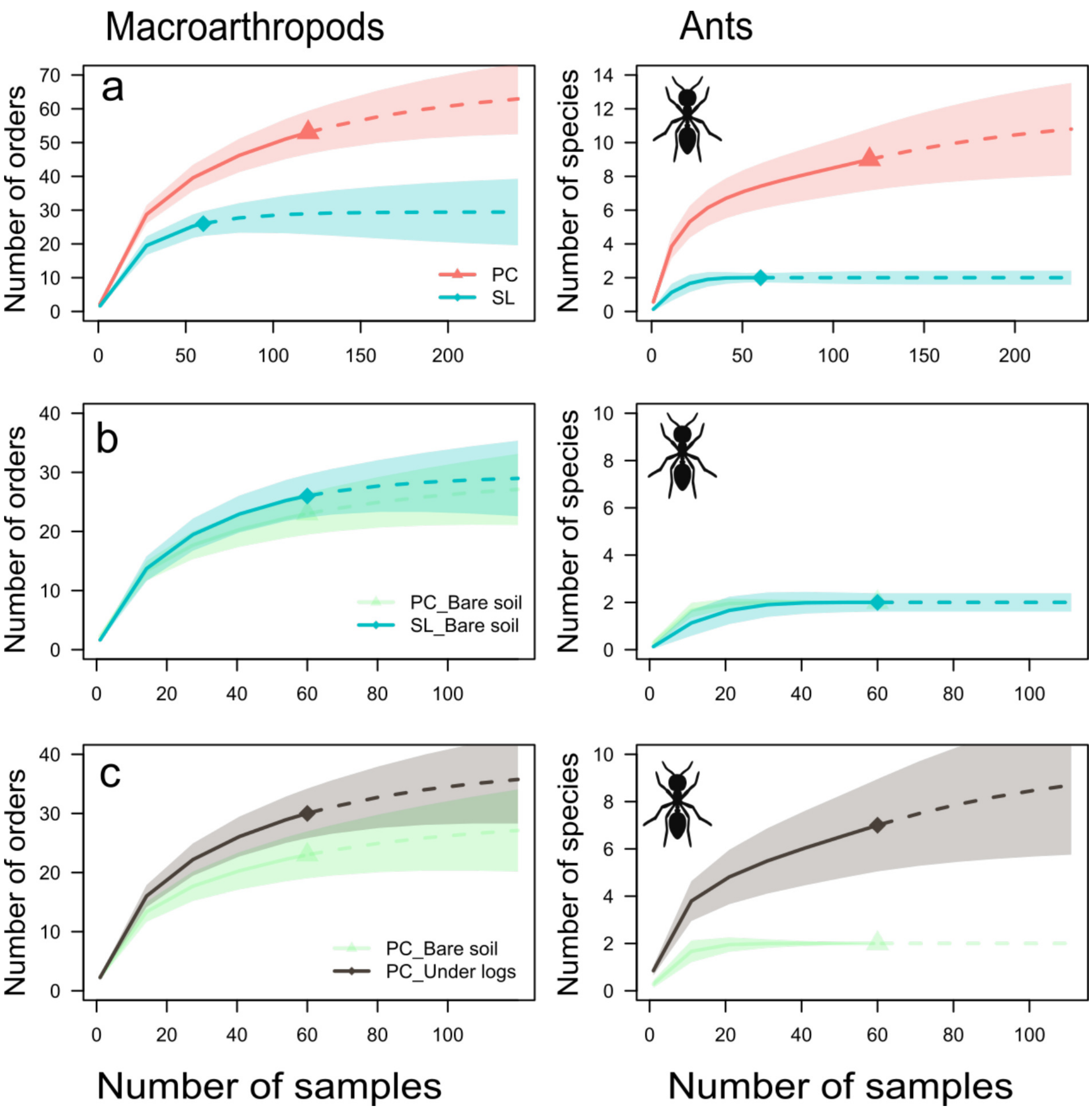


Figure 6.2: Sample-based rarefaction (solid lines) and extrapolation (dotted lines) until reaching twice the maximum sample size for macroarthropod orders and ant species at the Low Plot. Shaded areas represent 95% confidence intervals. The lettering of the panels indicates the three hypotheses of this study: differences between (a) dead-wood treatments, (b) treatments under the bare-soil microhabitat only, and (c) microhabitats in the PC treatment. Curves for the High Plot are shown in the Supplementary information Figure 6.5. Dead-wood treatments are SL = Salvage logging and PC= Partial Cut.

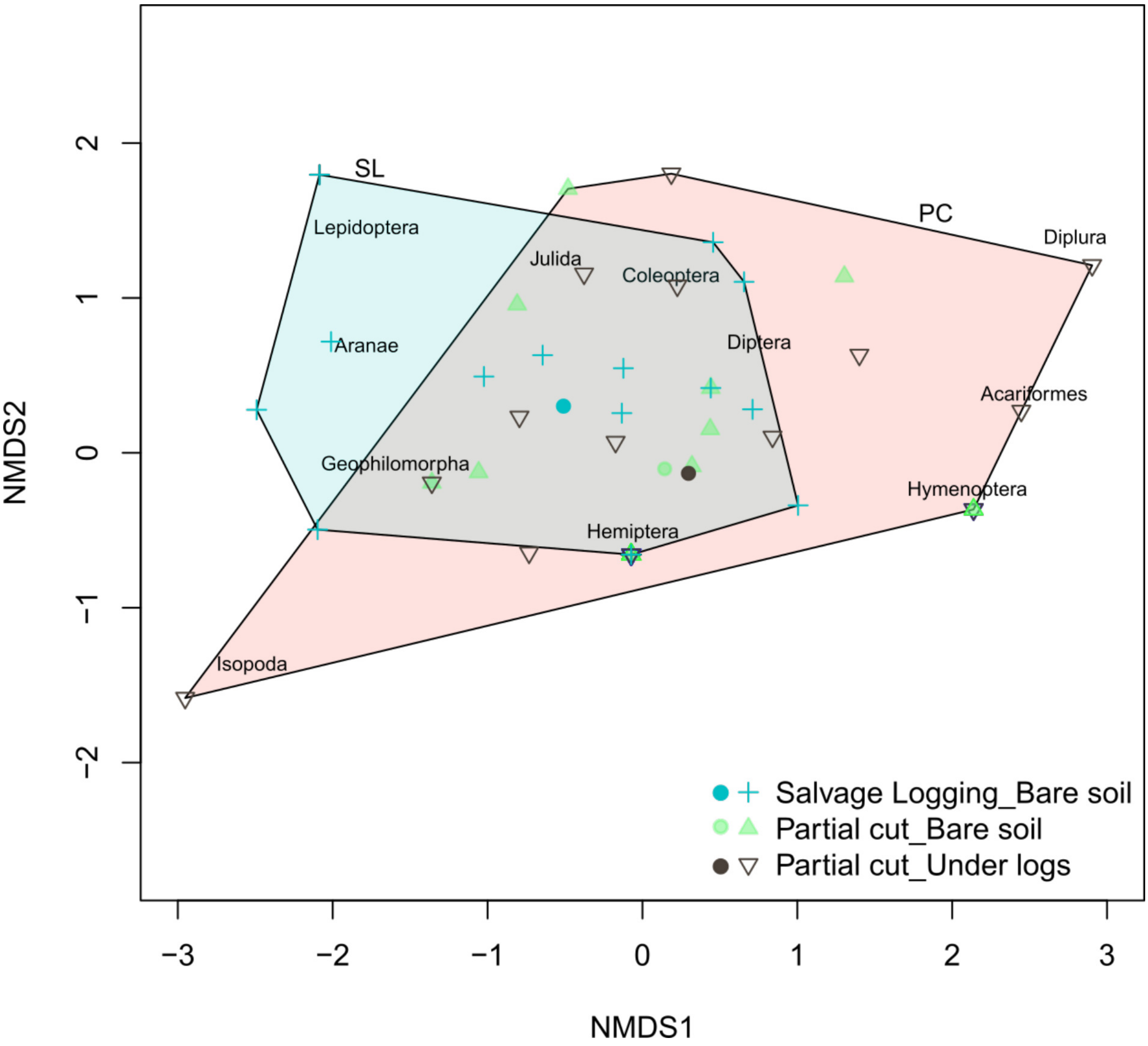


Figure 6.3: Non-metric multidimentional scaling ordination using Bray-Curtis distance of belowground macroathropod communities under two different treatments and microhabitats (stress coefficient = 0.088). The solid circles indicate the centroid for each dead-wood treatment by microhabitat combination, and the other symbols indicate each treatment replicate. Polygons are the groups for the salvage logging (blue) and the Partial cut (red) treatment.

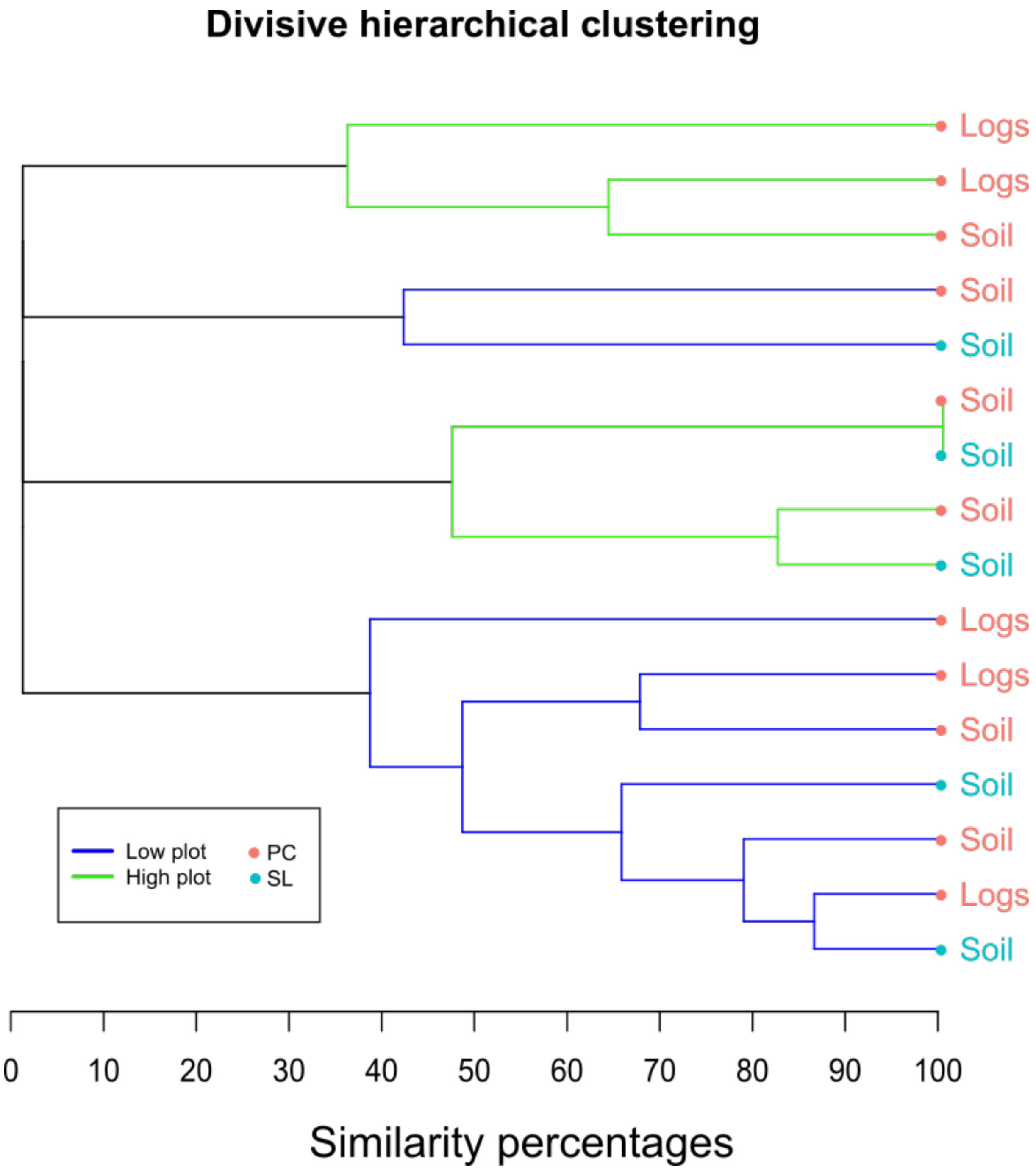


Figure 6.4: Divisive hierarchical clustering of macroarthropod communities using Bray-Curtis similarity. Branches correspond to plots at different elevation and microhabitat replicated three times.

6.4 Discussion

Our study shows that different landscape-scale management of dead wood after a wildfire produced differences in the abundance and richness of soil macroarthropod communities. In general, the treatment that included microhabitats with dead wood contained greater abundance and diversity of soil arthropods. However, differences were overridden by the effect of the elevation at which dead-wood treatments were applied, and we did not detect significant effects of treatments or microhabitats on composition. This study contributes to understanding the responses of an understudied group of organisms to common management actions after wildfires.

Overall abundance and differences across elevations

In our study, we found an overall low abundance and diversity of soil macroarthropods compared to other Mediterranean-type ecosystems (Broza & Izhaki, 1997; Doblas-Miranda *et al.*, 2007; Mateos *et al.*, 2011) as well as other temperate and boreal ecosystems (Bengtsson *et al.*, 1997; Jabin *et al.*, 2004; Marra & Edmonds, 1998; Pressler *et al.*, 2019). Low abundances throughout our study could be attributed to the effects of fire, which can have both direct effects in reducing arthropod abundance through mortality (Doamba *et al.*, 2014), and indirect effects through habitat damage from high soil temperatures (Malmström, 2008). Such changes in habitat quality are a frequent cause of resource depletion and may be an important factor affecting the recovery of soil organisms (Korobushkin *et al.*, 2017). Further, the history of the site, characterized by a dense and homogeneous pine afforestation established on terraces made with bulldozers (Gómez-Aparicio *et al.*, 2009; Molinas-González *et al.*, 2017b), could have reduced the initial species pool as well as the spatial heterogeneity in burn conditions at the forest floor, which, in turn, could explain a small proportion of soil animals surviving wildfire (Gongalsky *et al.*, 2012). To survive under the environmental conditions prevailing early after fire, particular traits are generally required (Wardle, 2002). For example, wildfire does not only remove pre-existing habitat –it produces new habitat and resources, primarily in the form of dead wood (Bowd *et al.*, 2018; Franklin & MacMahon, 2000). Therefore, saproxylic organisms –those directly associated with dead wood– are generally abundant after fire and other natural disturbances compared to non-saproxylic taxa (Stokland *et al.*, 2012).

However, the link between post-fire dead wood and the fauna that dwells belowground had so far remained less established, and it is likely that more time is required for the full recolonization by soil animals than those living aboveground. Finally, the low abundance of organisms in our study could also be related to the sampling method we used, as hand sorting could have limited the detection of all organisms in our samples.

Belowground faunal abundance and richness were greatest in the Low Plot. This was not surprising, as decreases with greater elevation are a general trend observed across many taxa (McCain & Grytnes, 2010; Rahbek, 1995). Interpretations mostly rely on factors such as rough environmental conditions (chiefly temperature), low productivity, shorter vegetative periods, and smaller habitat areas at higher elevation (Decaëns, 2010; Körner, 2007; Rahbek, 1995). In our study, plot elevation also generated clear differences in species composition, shown by the hierarchical clustering producing its main branches separated by plots. However, a factor that could have influenced our between-plot comparisons was the timing of sampling. We carefully selected the timing to sample according to the phenology at each elevation, yet this could have introduced error. Thus, the primary implications of the effect of plot that we interpret from our study were in its potential to modify the effect of dead-wood treatment and microhabitat.

Differences between dead-wood treatments

We found support for our first hypothesis, namely that different dead-wood treatments produce differences in macroarthropod abundance and richness. Overall, the abundance of individuals and the number of orders were lowest in the salvage logging treatment, and communities differed between treatments. Similar results have been obtained in previous studies (Grodsky *et al.*, 2017; Ober & DeGroote, 2011; Siira-Pietikäinen & Haimi, 2009; Wermelinger *et al.*, 2017), showing a reduction in the abundance of several invertebrate groups following the large-scale implementation of wood and litter removal treatments (though note that our study did not include an unmanaged control treatment). In fact, the common practice of salvage logging can affect many different groups of organisms, particularly those dependent on dead wood, in a consistent way, as shown by a recent global meta-analysis (Thorn *et al.*, 2018).In that global study, the dependence on dead wood of the most negatively affected taxa suggested that major effects likely arise from the removal of the dead-wood resource, rather than other effects such as microclimatic differences among treatments (Fontaine *et al.*, 2010), changes in vegetation (Leverkus *et al.*, 2014), or direct soil disturbance produced by the harvesting machinery (Wagenbrenner *et al.*, 2015). We should note that, although in our Salvage logging treatment the felled trees could not be removed by the log-forwarder, logs were piled and the branches were masticated, leaving most of the ground without coarse woody debris. In contrast, the Partial cut treatment may have enhanced soil fauna, as felling the trees provided a high burnt-wood cover and sped up its contact with the ground, which may have fastened the recovery of soil conditions. In this sense, our results are conservative, as any potential effect of the piled logs on soil fauna (despite being unlikely given that samples were collected at a secure distance from the piles) imply that the differences respect to the less aggressive treatment would magnify in a situation of complete salvage logging (which includes log removal). In addition, not only the abundance of downed wood over the ground surface differed across the two treatments but also the diversity of microsites, so the results related to our first hypothesis could arise from the existence of the two different microhabitat types sampled in the PC treatment (Thorn *et al.*, 2016).

Our second hypothesis –that stand-scale dead-wood treatment would affect soil communities even when sampling under similar microhabitats– was also supported by our data, although less so. The bare-ground microhabitat differed between the two dead-wood treatments, as in the PC treatment it had an enhanced macroarthropod abundance and richness (although richness only differed in the High Plot). At the Low Plot, the difference between the SL and the PC treatments after hypothesis 1 was thus greatly driven by the availability of the under-logs microhabitat in the latter treatment. On the other hand, our results also suggest that the availability of different microhabitats likely yielded a greater species pool in the PC treatment, with more taxa –and more individuals– able to colonize even beyond the reach of the trunks. This would suggest that the dead wood spread over the ground in the PC treatment favored a greater species pool than the masticated wood and the scattered log piles of the SL treatment. However, there were no differences between microhabitats (under logs vs. bare soil) in abundance and richness when comparing within the PC treatment, so we did not find support for our hypothesis 3. Although this may be related to the great abundance of zeros in our dataset, the lack of differences across microhabitats could also indicate that the effect of managing dead wood occurred mainly at the spatial scale of management intervention.

The enhancement of soil macroarthropod communities in the PC treatment can be related to several non-mutually exclusive mechanisms, several of which are related to how dead wood can enhance soil biota. First, as the logs decompose, they lose integrity, causing the wood to crumble and increasing the amount and heterogeneity of resources available for taxa involved in wood decay, such as wood-boring beetles (Coleoptera) (Lee *et al.*, 2014) and termites (Termitoidae) (Ulyshen, 2016). Logs had lost an overall 23% of their mass at the time of the present study, and they showed a high degree of fragmentation and many tunnels bored by insects (Molinas-González *et al.*, 2017a). Besides providing shelter, food, and soil nutrients (Doblas-Miranda *et al.*, 2009; Ulyshen & Anula, 2009), dead wood can also ameliorate microclimatic conditions, especially during the long, dry Mediterranean summer (Amaranthus *et al.*, 1989; Castro *et al.*, 2011). Grounded dead wood also provides suitable overwintering habitats for many species, including many that have at least one life stage belowground (Danks, 1991). It should be mentioned that we lacked data on the total cover of dead wood across treatments (but see (Castro *et al.*, 2011) for data on ground cover at the beginning of treatment establishment). Differences other than dead-wood abundance may have influenced our results too; for instance, the dead-wood treatments produced markedly different plant communities, which tended to be richer in the PC treatment (Leverkus *et al.*, 2014). Plants change the biophysical environment through facilitative, inhibitory and competitive interactions, and they thereby enhance soil habitat heterogeneity and ultimately influence soil biota (Wardle, 2002). As a result, the interplay between the aboveground structural complexity produced by burnt wood (Leverkus *et al.*, 2015a), its effects on the physical and chemical environment, and its contribution to the composition of the plant community may have greatly determined the composition of soil invertebrate communities in our study (Auclerc *et al.*, 2019; Doblas-Miranda *et al.*, 2009), and these factors may have driven the effects of dead-wood treatments.

We did not detect significant differences in community composition across the two treatments. However, such lack of an effect could have resulted from a low overall abundance of organisms, as dead-wood management can determine the habitat selection of particular groups of organisms. For instance, Lepidoptera were highly associated with the salvage logging treatment in our study. This treatment generated open habitat with high solar irradiance, which is the kind of habitat sought by some moth species such as the processionary caterpillar to burrow and pupate (Torres-Muros *et al.*, 2017). In contrast, the Hemiptera that we found included several species that suck on the roots of a wide variety of plants (Foldi, 2005), and these would likely be more associated with the more diverse plant communities of the PC treatment (Leverkus *et al.*, 2014). Moreover, the high amount of Isopoda, found mostly under logs, likely results from their diet, which consists mostly of decaying wood, and from their preference for moist soils (Paoletti & Hassall, 1999). Finally, the greater richness of ant species found in the PC treatment could result from their preference for dead wood both as nesting habitat (Boucher *et al.*, 2015) –wood provides warmer nesting sites than soils (Higgins & Lindgren, 2004), especially important for thermophilic species such as *Cataglyphis velox* and *C. Iberica* (Cerdá & Retana, 1997)– and as feeding habitat for species like *Aphaenogaster* spp. that prey on termites (Buczkowski & Bennett, 2007).

6.5 Conclusion

Soil biota is generally overlooked in the setting of management goals and in the evaluation of restoration actions. Our study points out that belowground macroarthropod communities are sensitive to the manipulation of dead-wood legacies after wildfire. The cumulative effects of repeated perturbations (fire, post-fire management) in already extremely modified ecosystems such as Mediterranean pine afforestations may markedly affect the natural development of disturbed areas and ultimately impact important soil processes such as nutrient cycling. In particular, removing burnt wood diminishes the heterogeneity of habitats and the amount of resources available for macroarthropods.

6.6 Supplementary information

Table 6.6: Total number of macroarthropod individuals under two treatments (SL= Salvage logging, PC= Partial cut) and microhabitats (bare soil vs. under logs) collected at the study site ten years after post-fire dead-wood management.

					Low plot			High plot		
					SL	PC		SL	PC	
Class	Superorder	Order	Family	Species	Bare soil	Bare soil	Under logs	Bare soil	Bare soil	Under logs
Malacostraca		Isopoda			1	0	15	0	0	1
Diplopoda		Julida			1	1	2	0	0	0
Chilopoda		Geophilomorpha			3	2	3	0	1	0
		Scolopendridae			0	0	0	0	1	0
Arachnida		Aranae			1	1	0	0	0	1
	Acariformes				0	0	2	0	0	0
Hexapoda		Diplura			0	0	2	0	0	0
		Embioptera			1	0	0	0	0	0
		Hemiptera			66	120	93	0	4	2
		Diptera			6	10	8	0	2	0
		Lepidoptera			13	0	1	0	0	0
		Coleoptera			7	2	8	0	9	8
		Hymenoptera			0	0	0	0	0	1
		Hymenoptera	Formicidae	*Bothriomyrmex meridionalis*	0	0	42	0	0	0
				Cataglyphis velox	2	0	0	0	4	0
				Tapinoma nigerrimum	0	10	0	0	0	0
				Proformica ferrari	0	0	0	7	21	0
				Cataglyphis iberica	0	0	0	0	1	0
				Aphaenogaster dulcinea	0	0	8	0	0	0
				Aphaenogaster gibbosa	0	7	0	0	0	0
				Tetramorium forte	0	0	0	16	0	0
				Tetramorium semilaeve	4	0	0	0	0	0
				Pheidole pallidula	2	0	0	0	0	0

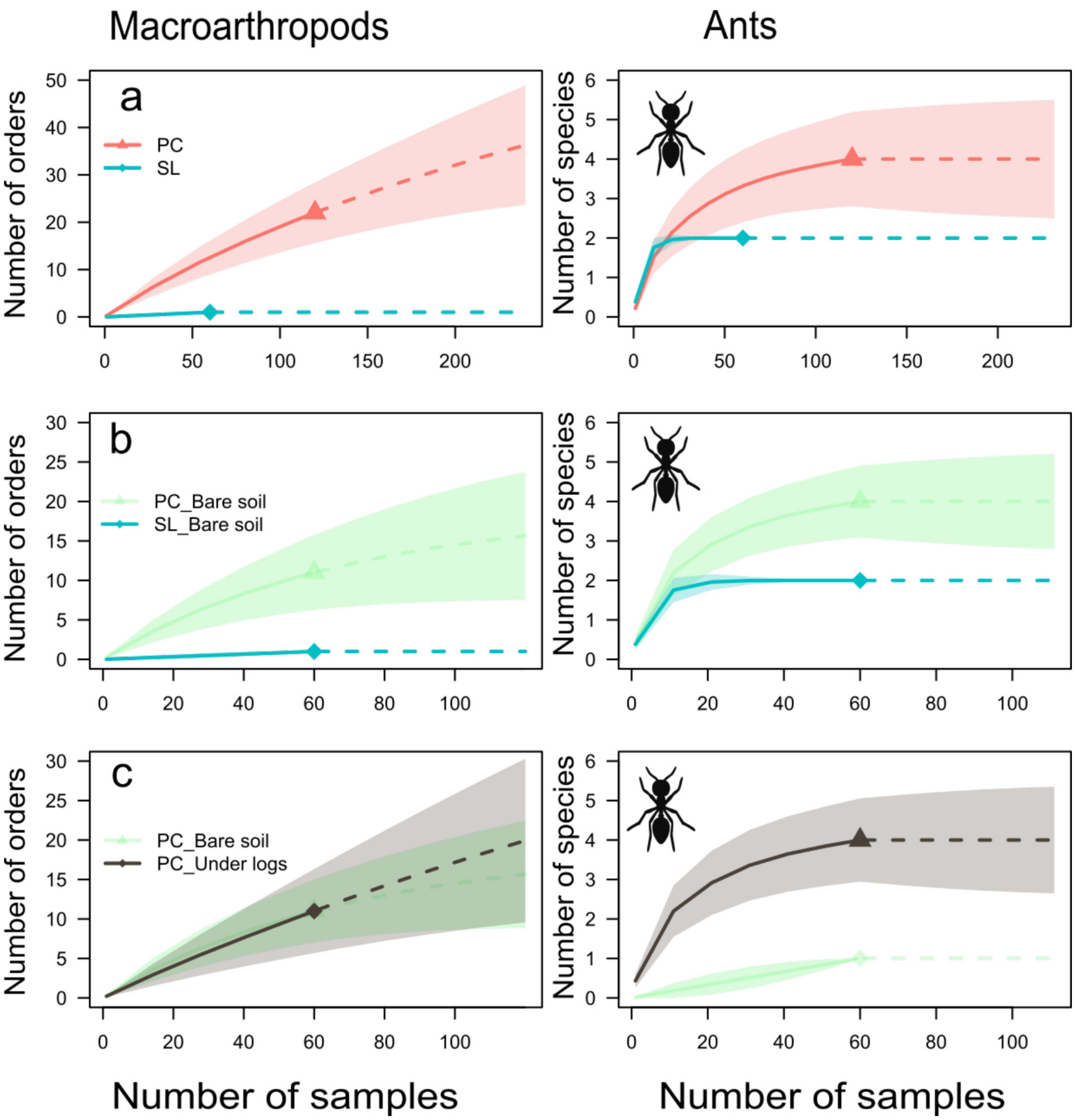


Figure 6.5: Sample-based rarefaction (solid lines) and extrapolation (dotted lines until reaching twice the maximum sample size) of macroarthropod orders and ant species at the High plot. Shaded areas represent 95% confidence intervals. Panels show the three questions of this study: differences between (a) dead-wood treatments, (b) treatments under the bare-soil microhabitat only, and (c) microhabitats in the PC treatment. Dead-wood treatments are SL = Salvage logging and PC= Partial Cut.

Part III

Discusión general | General discussion

7. Discusión general

En la presente tesis, he analizado la dinámica post-incendio de la madera muerta a medio plazo (10 años tras los tratamientos de la madera y 11 desde el incendio). La transición entre un árbol erguido a un tronco en el suelo fue el resultado de un período inicial con una tasa de caída lenta, con un tiempo de retraso de dos años en donde se registró escasa caída de arbolado, seguido de un período con una alta tasa de caída alcanzando el 100 % de los árboles entre el quinto y el sexto año tras el incendio. Los troncos quemados representaron uno de los legados biológicos más relevantes debido a que su descomposición resultó ser lo suficientemente rápida como para ser considerado un proceso que puede apoyar la recuperación del suelo a través de su efecto sobre el ciclo de nutrientes. En especial, la presencia de este recurso tuvo un efecto positivo, aunque moderado, sobre la abundancia y diversidad de macroartrópodos edáficos.

7.1 ¿Cómo afecta el manejo post-incendio a la dinámica de la madera muerta?

Tras el incendio, el manejo silvícola (la tala del arbolado quemado, con una selección no aleatoria del tamaño de los árboles) y la densidad del arbolado (influida mediante aclareo en el tratamiento de intervención intermedia) determinaron el tiempo de residencia de los árboles que se mantuvieron en pie, independientemente de la altitud a la cual se encontraban (***Capítulo 1***). La velocidad de caída resultó significativamente mayor en el tratamiento de Intervención intermedia a partir del tercer año tras el incendio, sin considerar el efecto del tamaño de los árboles (Fig. 4.3, Capítulo 1), alcanzando el 100 % de los árboles a los 5.5 años tras el incendio. En comparación, otros estudios han observado un mayor tiempo de permanencia a los obtenidos en el ***Capítulo 1***. Por ejemplo, Chamber & Mast (2005) encontraron que tras 7 años los árboles que permanecieron erguidos en las parcelas quemadas eran árboles rectos de gran diámetro en grupos densos. Al igual que en Ritchie *et al.* (2013) el tiempo de residencia fue de alrededor de 8 años. Harrington (1996) concluye que del 75 al 80 % de los árboles que mueren tras un incendio caerán en aproximadamente 10 años. Esto abre una ventana muy reducida de tiempo para su uso como perchas por parte de la fauna asociada a árboles muertos que se mantienen en pie (Castro *et al.*, 2010; Cavallero *et al.*, 2013; Rost *et al.*, 2009). Muchos trabajo reportan un retraso en la tasa de caída de 2 años (***Capítulo 1 y*** Mitchell & Preisler, 1998) y hasta 5 años (Garber *et al.*, 2005; Harrington, 1996; Lee, 1998; Russell *et al.*, 2006) después, los árboles comenzarán a caer al menos con una mayor rapidez.

La alta tasa de caída de árboles registrada el tercer año tras el incendio puede ser el resultado de diferentes factores atribuibles a las características del rodal, como por ejemplo la alta densidad de arbolado previa al incendio (Ritchie *et al.*, 2013) o el tipo de incendio (Ganey & Vojta, 2005). Las heridas producidas en los árboles durante un incendio son el principal punto de entrada para hongos (Littke & Gara, 1986; Penttilä & Kotiranta, 1996), lo que supone la perdida de estabilidad estructural debido a la rápida descomposición de la raíces (Huggard, 1999).

El tratamiento post-incendio resultó más determinante para el tiempo de permanencia de los árboles tras el incendio que el gradiente altitudinal en el que se encontraban las parcelas. Primero, modificando la densidad de arbolado que se mantuvo en pie tras el incendio lo que genero un mayor tiempo de retención en rodales con mayor densidad de arbolado. En este sentido, Russell & Weiskittel (2012) y Chamber & Mast (2005) encontraron que grupos de árboles más densos permanecían erguidos por más tiempo, al bloquear el efecto producido por el viento. No obstante, en algunos casos la densidad puede determinar una mayor tasa de caída debido a que la caída de un árbol determina la caída de otro cercano (Acker *et al.*, 2013), aunque este efecto no sería dominante en la zona de estudio de esta tesis.

Segundo, el diámetro resulto positivo para el tiempo de retención de los árboles debido a que tienen una mayor cantidad de volumen de madera para descomponerse, incluida una mayor cantidad de duramen resistente a la descomposición (Chamber & Mast, 2005; Parish *et al.*, 2010; Perry &

Thill, 2013; Vanderwel *et al.*, 2006). El tratamiento modifico el efecto del diámetro sobre la permanencia de los árboles. Como resultado el efecto del diámetro resultó más débil en el tratamiento de Intervención intermedia, haciendo que la resistencia conferida por un mayor diámetro disminuya en este tratamiento (Fig. 4.4, Capítulo 1).

Tras el colapso de los árboles afectados por el incendio, una importante cantidad de biomasa en la forma de madera muerta pasó a formar parte del suelo. Una de las diferencias fundamentales entre la madera muerta en pie y caída se encuentra en el tipo de hábitat que representa (***Capítulo 2 y Capítulo 3***) y en una mayor velocidad de descomposición una vez que los troncos tocan el suelo (Shorohova & Kapitsa, 2014; Song *et al.*, 2017; Yatskov *et al.*, 2003; Garrett *et al.*, 2010).

Tras el incendio de Lanjarón, los troncos quemados perdieron alrededor de un cuarto de su densidad tras 10 años de descomposición (***Capítulo 2***). La descomposición de la madera muerta provee de soporte a procesos físicos y químicos del suelo como el ciclo de nutrientes (Angers *et al.*, 2010; Lasota *et al.*, 2018), lo que permite que una importante cantidad de nutrientes sean liberados al suelo. Por ejemplo, en Marañón-Jiménez & Castro (2013), la madera quemada liberó alrededor del 40 y el 65 % de su contenido inicial de fósforo tras 4 años de descomposición. Los factores relacionados con la altitud tales como la temperatura y humedad, suelen determinar la tasa de descomposición (Liu *et al.*, 2013; Shorohova & Kapitsa, 2014), en nuestro caso la descomposición de la madera quemada resultó más lenta en la parcela de mayor altitud y para troncos de menor diámetro (Fig. 5.3, Capítulo 2).

El diámetro de los troncos es uno de los aspectos que determinaron la velocidad de descomposición (Tabla 5.2, Capítulo 2). Esto ha sido reportado en otros trabajos en ecosistemas boreales (Erickson *et al.*, 1985; Jonsell *et al.*, 2007; Mackensen *et al.*, 2003). Sin embargo, el efecto hallado fue contrario al esperado, ya que se esperaba que los troncos más pequeños se descompusieran más rápidamente debido a poseen una menor relación de superficie volumen (Mackensen *et al.*, 2003; Weedon *et al.*, 2009). En contraste, en este estudio los troncos de mayor tamaño tuvieron una mayor tasa de descomposición. Ello coincidió con la presencia de larvas de insectos xilófagos en los troncos más gruesos (Fig. 5.1, capítulo 2), que se alimentan directamente de la madera (Ulyshen, 2016). Las galerías que horadan debilitan la estructura de los troncos (Lee *et al.*, 2014; Saint-Germain *et al.*, 2007), permitiendo que otros organismos detritívoros colonicen la madera muerta (Grove, 2002; Ulyshen, 2016) y acelerando el proceso de descomposición (Stokland *et al.*, 2012).

La mayor velocidad de descomposición en troncos de mayor tamaño provee al suelo de heterogeneidad en la distribución de los nutrientes contenidos en la madera quemada (***Capítulo 2***), además de retener una mayor proporción de humedad (Means *et al.*, 1992; Pichler *et al.*, 2012), lo que favorece la actividad biológica en ecosistemas mediterráneos (Castro *et al.*, 2011; Marzano *et al.*, 2013). La diferencia fundamental entre los tratamientos post-incendio con efectos directos sobre la dinámica de la madera quemada se centra en la ausencia a gran escala de madera muerta y los procesos derivados de su descomposición tales como la recuperación de la fertilidad del suelo y la disponibilidad de nutrientes a largo plazo (Kishchuk *et al.*, 2015; Marañón-Jiménez & Castro, 2013).

7.2 Implicaciones del manejo de la madera quemada sobre las comunidades de insectos

La abundancia y riqueza de macroartrópodos edáficos tras el incendio resultó baja en comparación con otros ecosistemas (Broza & Izhaki, 1997; Doblas-Miranda *et al.*, 2007), quizás como consecuencia de los efectos directos o indirectos del incendio (Doamba *et al.*, 2014; New, 2014). Los diferentes tratamientos post-incendio de la madera muerta produjeron diferencias en la abundancia y riqueza de macroartrópodos edáficos. En general, la abundancia de individuos y el número de órdenes fueron más bajos en el tratamiento de Extracción de la madera (***Capítulo 3***). Esta reducción de organismos edáficos asociados a la implementación a gran escala de la Extracción de la madera ha sido consistente con resultados obtenidos en otras partes del mundo (Thorn *et al.*, 2018), particularmente para aquellos organismos que dependen de la madera muerta (Siira-Pietikäinen *et al.*, 2003; Siitonen, 2001; Verkerk *et al.*, 2011) o que tienen fuertes vínculos con atributos de hábitat de sucesión temprana post-incendio (Azeria *et al.*, 2012; Swanson *et al.*, 2011). También, se ha observado que el efecto de la Extracción de la madera tras un incendio resulta del impacto acumulado entre perturbaciones sucesivas como un incendio y las operaciones de manejo de la madera quemada (Kishchuk *et al.*, 2015; Leverkus *et al.*, 2018a; Slesak *et al.*, 2015) en especial la extracción de la madera altera los vínculos naturales entre insectos que se alimentan de la madera y la dinámica de nutrientes (Cobb *et al.*, 2010).

Por otra parte, el tipo de hábitat resultante del manejo de la madera quemada afectó a las comunidades edáficas, en especial entre hábitats similares (sin presencia de troncos). El microhábitat sin presencia de troncos difería entre los dos tratamientos de la madera muerta, ya que el tratamiento de Intervención intermedia tenía una mayor abundancia y riqueza de macroartrópodos (aunque la riqueza solo difería en la parcela de mayor altitud). Esto sugiere que la disponibilidad de diferentes microhábitats probablemente produjo un mayor grupo de especies en el tratamiento de Intervención intermedia, con más taxones y más individuos capaces de colonizar incluso más allá del alcance de los troncos (***Capítulo 3***). Sin embargo, no hubo diferencias entre la abundancia y riqueza de microhábitats (bajo de troncos versus sin presencia de troncos) en el tratamiento de Intervención intermedia, demostrando que las diferencias se dieron a escala de tratamiento.

Los troncos quemados que permanecen en el suelo son uno de componentes estructurales más importantes tras un incendio debido a que representan un reservorio de nutrientes (Marañón-Jiménez *et al.*, 2013b), su tasa de descomposición resulta ser lo suficientemente rápida (***Capítulo 2***) como para ser considerado un proceso que permite incrementar el retorno de los nutrientes contenidos en la madera quemada. Además, la recuperación de la diversidad estructural del suelo asociado a la presencia de troncos en diferentes estados de descomposición pudo haber aportado a la recuperación de la biota del suelo (Déchêne & Buddle, 2010; Yurkov *et al.*, 2012). La presencia de insectos xilófagos observados durante el proceso de descomposición y la mayor tasa de degradación en troncos de mayor diámetro, del ***capítulo 2***, aumentaron la heterogeneidad de los recursos disponibles para diferentes taxones asociados a la madera muerta (Stokland *et al.*, 2012; Ulyshen, 2016). La madera muerta puede almacenar una gran cantidad de humedad (Pichler *et al.*, 2012) y mejorar las condiciones microclimáticas, especialmente efectivas durante el largo y seco verano mediterráneo (Castro *et al.*, 2011; Marzano *et al.*, 2013).

La composición de las comunidades del suelo no se vio significativamente afectada por los tratamientos de la madera muerta, a pesar de que el cambio en el ensamblaje de las especies ha sido generalmente registrado como un efecto compuesto de la extracción de la madera tras un incendio en gasterópodos (Bros *et al.*, 2011), insectos saproxílicos (Cobb *et al.*, 2011; Koivula & Spence, 2006) y otros grupos taxonómicos (Thorn *et al.*, 2018). Sin embargo, en el ***capítulo 3*** se presentan indicios de que el manejo de la madera muerta puede determinar la selección del hábitat por parte de algunos organismos. Por ejemplo, el grupo de lepidópteros se encontró altamente asociado con el tratamiento de Extracción de la madera. Este tratamiento se caracteriza por ser un hábitat abierto con alta irradiación solar, microhábitat preferido por algunos organismos para excavar y pupar, tales como las orugas de la procesionaria (Torres-Muros *et al.*, 2017) y que determina en gran medida tanto la tasa de emergencia de mariposas como su fenología (Hódar *et al.*, 2012) e incluso su predación (Hódar *et al.*, 2013).

En contraste, los Hemípteros encontrados incluían varias especies que se alimentan de raíces de una amplia variedad de plantas (Foldi, 2005), y que estarían más asociadas con comunidades de plantas más diversas en tratamientos con presencia de madera quemada en descomposición (Leverkus *et al.*, 2014). Además, la gran cantidad de Isópodos, que se encontraron principalmente bajo troncos, probablemente sea el resultado de su dieta, que consiste principalmente en madera en descomposición, y de su preferencia por los suelos húmedos (Paoletti & Hassall, 1999).

Finalmente, la mayor riqueza de especies de hormigas encontradas en el tratamiento de Intervención intermedia (***Capítulo 3***) podría resultar de su preferencia por la madera muerta tanto como hábitat de anidación como de alimento (Boucher *et al.*, 2015; Buczkowski & Bennett, 2007; Cerdá & Retana, 1997).

La biota del suelo generalmente no ha sido tenida en cuenta en los planes de gestión y restauración ecológica tras los incendios forestales (Kardol & Wardle, 2010; Wardle *et al.*, 2004). Los resultados de esta tesis destacan que la biodiversidad local por debajo del suelo se relaciona con la distribución de materia orgánica muerta por encima del suelo, pero aún más con su descomposición, que determina la abundancia y heterogeneidad en la composición de los recursos y la diversidad de los microhábitats del suelo, características altamente influenciados por el manejo post-incendio.

Parte IV

Conclusiones | conclusions

8. Conclusiones generales

1. El manejo post-incendio, al influir en la densidad y el grosor del arbolado que permanecía en pie, influyó en el tiempo de residencia de los árboles muertos que se mantuvieron en pie tras el incendio, independientemente de la altitud a la cual se encontraban. El colapso de los árboles fue un proceso rápido y culminó tras 5,5 años, lo que provocó que una gran cantidad de materia orgánica entrase en contacto con el suelo.
2. El diámetro de los árboles en pie determinó su tiempo de permanencia en rodales donde la densidad de árboles era mayor. En cambio, a menor densidad, los árboles cayeron independientemente de su diámetro. En el tratamiento Intervención intermedia la densidad de árboles en pie fue menor que en No Intervención, con lo que se encontraban más aislados y expuestos a condiciones ambientales. Sin embargo, los árboles que permanecieron en pie fueron los de mayor diámetro debido a la selección de árboles por los operarios, lo que le confirió una mayor resistencia a los que permanecieron. La combinación de menor densidad pero mayor diámetro en el tratamiento Ii hizo que la velocidad de caída entre ambos tratamientos fuese similar.
3. La madera quemada perdió alrededor de una cuarta parte de su densidad tras 10 años de descomposición. La descomposición de la madera fue un proceso temporalmente heterogéneo. La madera localizada en la parcela de mayor altitud se descompuso más lentamente, probablemente debido a la menor temperatura. Sin embargo, la velocidad de descomposición de las otras dos parcelas no mostró un gradiente consistente con la altitud. Las diferencias en velocidad de descomposición entre las parcelas también pueden atribuirse a otros factores bióticos y abióticos.
4. Los troncos de mayor diámetro se descompusieron más rápidamente. Ello probablemente se debió a la colonización de insectos saproxílicos

en los troncos más grandes.

5. El tipo de manejo de la madera muerta afectó la abundancia y riqueza, mas no la composición, de las comunidades de macroartrópodos edáficos 10 años después del manejo. El tratamiento Extracción puede reducir la recuperación de los macroartrópodos edáficos en comparación con tratamientos con un manejo menos intenso.
6. No se hallaron diferencias en la abundancia y riqueza de macroartrópodos edáficos entre los dos tipos de microhábitats dentro del tratamiento de intervención intermedia (bajo tronco y bajo suelo desnudo). Esto hace suponer que el efecto del manejo de la madera quemada sobre esta comunidad biótica es efectiva a nivel del rodal más que a de microhábitats.
7. La transformación de la estructura física y química de la madera muerta durante la dinámica post-incendio demostró ser un proceso heterogéneo que varió de acuerdo a las condiciones ambientales de las distintas parcelas estudiadas y del manejo post-incendio. El manejo de la madera influyó en estas dinámicas post-incendio, principalmente modulando la tasa de caída del arbolado. Con ello, afectó el tiempo durante el que la madera muerta se encontraba a nivel del suelo para favorecer a la recuperación de los macroartrópodos edáficos.

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