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Depopulation impacts on ecosystem services in Mediterranean rural areas

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ABSTRACT

Despite the exponential increase in human population at global scale, some rural areas have experienced a progressive abandonment over the last decades. Under particular socioecological and policy contexts, changes in demography may promote land-use changes and, consequently, alter ecosystem services (ES) supply. However, most studies on this topic have targeted urban population increase, whereas depopulation has been rarely addressed. Here, we examined how shifts in demographic variables (human population, population density, and number of villages) affect provisioning (water supply, food and biomass production) and regulating (soil retention, water and nutrient regulation) ES in Mediterranean rural areas with contrasting environmental, socioeconomic and land-use contexts. When depopulation results in underuse of socio-ecological systems, we expected a decrease of provisioning and an increase of regulating ES, whereas we expected the opposite pattern when it results in land-use intensification. To test this hypothesis, we compared demographic data and ES estimated with Soil and Water Assessment Tool (SWAT) linked to land-use changes between the 1950s and 2000s in three rural areas of Aragón (NE Spain). Generalized Additive Mixed Models and Linear Mixed-Effect Models were used to analyze demographic trends, ES changes and the relationship between them.

We found severe depopulation (−42% inhabitants) and associated land-use changes in the three areas, which was particularly evident in isolated mountainous zones (−63% inhabitants). Depopulation trends significantly affected land use and, consequently, all of the ES evaluated. In mountainous depopulated areas, land abandonment and rewilding resulted in the increase in water regulation (>1000%) and soil retention (>400%). In contrast, agriculture was intensified in more fertile and easy-to-access lowland areas, boosting the food production service (>600%). Accordingly, the interactions among depopulation, crop production and regulating ES should be considered in the management schemes and policies targeting rural areas for a balanced and sustainable supply of ES in the long term.

1. Introduction

Ecosystem services (ES) supply becomes unsettled as human population increases, maximizing provisioning services at the expense of other ES (Cumming et al., 2014). These changes are encouraged by technological advances, through the increase in food production and security, economic growth and life expectancy. Land conversion to feed the growing global population is one of the main drivers of ES

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degradation (Tscharntke et al., 2012). It has been estimated that 75% of the land surface is significantly altered (IPBES, 2019) and 60% of ES have been globally degraded over the 20th century as a consequence of population increase and economic growth (Otero et al., 2020). Furthermore, human-induced land degradation will be further exacerbated considering the projected growth in global human population from 7.7 to 9.7 billion by 2050 (Stehfest et al., 2019; United Nations, 2019). However, this process is not spatially homogeneous across the globe, countries and even regions; while human population inhabiting urban zones has steadily increased over the last decades, some rural areas have experienced a progressive abandonment (MEA, 2005; Jacob et al., 2008).

The divergence in demographic trends between urban and rural areas is especially evident in Mediterranean countries (García-Ruiz et al., 1996; De Aranzabal et al., 2008), where the exponential growth of medium and big cities, especially on the coast, contrasts with a persistent rural depopulation inland. In particular, despite the overall depopulation trend of Western Mediterranean rural areas (Pinilla et al., 2008), different management and political schemes are leading to contradictory land-use trends. Some zones are experiencing unsustainable land-use intensification (e.g. flat and fertile lowlands with high water availability), which causes varied environmental impacts that modifies ES supply, such as soil degradation, biodiversity loss, water pollution and abstraction (Tscharntke et al., 2012; Smith et al., 2016). In contrast, other zones with lower productive value (e.g. mountainous areas) are being progressively depopulated and traditional uses abandoned (García-Ruiz et al., 1996; Santos-Martín et al., 2019). Previous studies have shown that land-use changes are closely related to rural depopulation in Mediterranean areas (Kosmas et al., 2002), especially in mountains (Lasanta et al., 2017) where it is regarded as one of the main reasons for agricultural abandonment (MacDonald et al., 2000). In this context, three main drivers of land abandonment have been identified: ecological (e.g. topography, soil, erosion and climate), socioeconomic (market, depopulation, technological level, land ownership, accessibility, etc.), and land management (Rey-Benayas et al., 2007). In particular, socioeconomic factors seem to control land-use changes, while environmental factors determine the type of change (Sluiter and De Jong, 2007).

In Spain, depopulation was exacerbated by an intense rural exodus during the 1960s (García Coll and Stillwell, 1999), especially in the northeast (Guillén-Gracia and Zúñiga-Antón, 2020). This exodus was rooted in the scarce economic profitability of farming production mainly based on self-sufficiency, amplified in some cases by reservoir construction, large afforestation works, abandonment of seasonal sheep transhumance and lifestyle expectancy, among others (Collantes and Pinilla, 2004). Frequently, depopulation and rural abandonment promotes vegetation recovery, especially at steeper slopes and closer to natural areas (Silva et al., 2016; Malandra et al., 2019). This spontaneous and passive afforestation could enhance diverse key ES such as timber production (provisioning), pollination, climate regulation, clean water, flood prevention, erosion control, carbon sequestration (regulating), habitat provision (supporting), cultural and recreational activities (Miura et al., 2015; Riis et al., 2020). On the other hand, land intensification tends to maximize provisioning ES such as food and energy production at the expense of some regulating ones (Emmerson et al., 2016; Smith et al., 2016; Tscharntke et al., 2012).

Rural areas are crucial for sustainable development because they provide essential ES (e.g. water regulation and supply, food production, aesthetic value, recreational services, etc.) to the whole territory (Gutman, 2007). Despite demographic changes can influence land-use regime (i.e. land intensification or abandonment), the effects of human depopulation and rural abandonment on ES are hardly the focus of research (Beilin et al., 2014; Silva et al., 2016; Mauerhofer et al., 2018; Hashimoto et al., 2019). Furthermore, most ES studies have explored the spatial patterns and variations related to different management schemes, land-use intensity and anthropogenic influence (e.g. Rey-Benayas et al., 2007; Vidal-Legaz et al., 2013; Malandra et al., 2019), without quantitatively evaluating the effect of depopulation on ES supply. However, temporal trends in both depopulation and land-use should be considered to anticipate and mitigate further undesired and/or unexpected ES changes in a context of global change. Given the potential relevance of depopulation as one of the drivers of land-use change and consequently ES supply in Mediterranean areas, this study focused on: i) exploring depopulation trends (from 1900 to 2018) of three scarcely populated rural areas in Aragón (NE Spain); ii) detecting significant temporal and spatial changes in provisioning (water supply, food and biomass production) and regulating ES behind land-use changes (soil retention, water and nutrient regulation); and iii) identifying relationships between demographic variables and the changes observed on land-use and ES supply between the mid-20th and the early 21st century. We hypothesized increases in regulating ES (soil retention, water and nutrient regulation) and decreases in provisioning ES (especially, food production and water supply) when strong depopulation trends result in land abandonment and the opposite pattern when they result in land intensification (Fig. A.1 in Appendix A). We provide spatially-explicit information about trends in population, land use and ES supply which is fundamental for a well-informed decision-making in a region considered as extremely depopulated. Our findings can serve as a basis to anticipate changes in ES supply, help decision-making processes and improve land-use policies in similar Mediterranean rural areas undergoing depopulation.

2. Methods

2.1. Study area

We selected three different sparsely populated zones of Aragón, NE Spain, (Hecho, Estercuel and Monegros), corresponding to three different sub-watersheds (Aragón-Subordán, Estercuel and Filadas streams, respectively), as representative of environmental, socioeconomic and land-use gradients and temporal evolution of Mediterranean rural areas (Fig. 1).

Hecho valley is a high-altitude (750–2700 m.a.s.l.), mountainous and humid (transitional climate between Mediterranean and Oceanic; Cuadrat et al., 2007), sub-watershed (Subordán river, 216 km^2) in the Pyrenees mountain range. The area of influence (794 km^2) around this sub-watershed is inhabited by a population of 2275 (INE, 2018). Landscape is dominated by coniferous and broadleaf forests (49%), grasslands and pastures (32%; Fig. 2a; see Appendix A for detailed information). During the last decades, mountain traditional agrosystems (mainly extensive livestock) decayed progressively, leading to depopulation and the subsequent abandonment of pastures and grasslands, which favored shrub encroachment and forest regeneration (Lasanta and Marín-Yaseli, 2007; Lasanta and Vicente-Serrano, 2007). Nowadays, the local economy is shifting from traditional extensive farming to ecotourism and tertiary sector (Lasanta and Marín-Yaseli, 2007).

Estercuel is located at middle-altitude (700–1100 m.a.s.l.), submediterranean-continental sub-watershed (Estercuel river, 308 km^2)

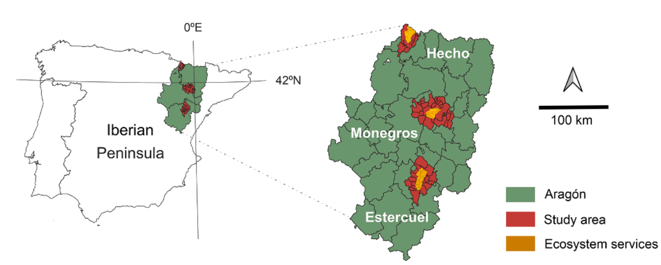

Fig. 1. Location of the three watersheds and municipalities in the influence area of three rural zones of Aragón (Hecho, Estercuel and Monegros), NE Spain, where ecosystem services and population trends were assessed.

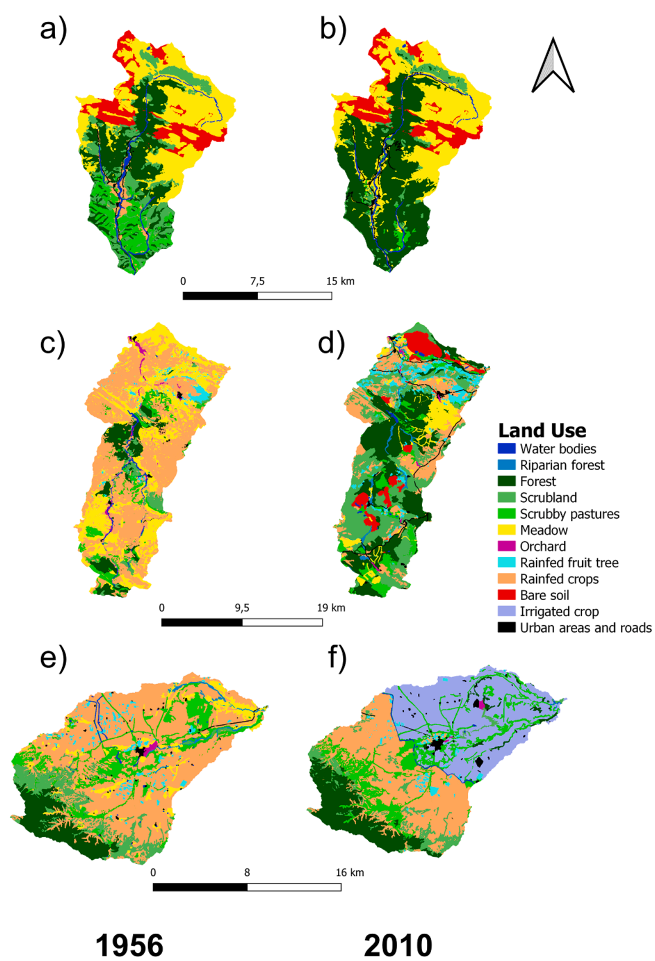

Fig. 2. Land use in the three watersheds of the study years: a) Hecho, b) Estercuel and c) Monegros. Red areas (bare soil) correspond to coal mines in Estercuel and bedrock in Hecho. Source: Prepared by the authors on the basis of the orthophotos from the American Flight 1956–57 USAF Aerial Photography of Spain and 2000–2010 land use map by the Ministry of Agriculture, Fisheries and Food. See Appendix B for further details.

in the Iberian mountain range (Cuadrat et al., 2007). The area of influence (1682 km^2) around this sub-watershed is inhabited by a population of 18,310 (INE, 2018). Landscape consists of a mosaic of semi-natural habitats (scrublands = 37% and sclerophyllous forests = 27%), rainfed agriculture (cereal and olive trees = 16%) and mining areas (surface coal mines and clay quarries = 6%; Fig. 2b; Appendix A). This landscape is a consequence of the transition from agricultural to mining economy (1970–1990), and then towards a recently started post-mining period (due to the low coal profitability and tightening of environmental laws), leading to a strong socio-economic uncertainty.

Monegros corresponds to low-altitude (250–700 m.a.s.l.), semi-arid, agricultural sub-catchment within the Flumen river watershed (Filadas stream, 204 km^2). The selected area of influence (2072 km^2) around this sub-catchment is inhabited by a total population of 13,344 (INE, 2018). Agriculture is the main land use with a vast irrigated area dominated by corn, alfalfa and rice (41%), as well as rainfed cereal crops (26%). Pine afforestations and holm oak forests are also present in the hilly parts of the area (Pedrocchi-Renault, 1998). The construction of Monegros water transfer system from the Pyrenees (construction between 1915 and 1982) has promoted agricultural intensification and the expansion of irrigated crops to the detriment of extensive rainfed ones (Gómez-Benito, 2005; Fig. 2c). Consequently, new villages and diverse hydraulic infrastructures were built following this socio-economic transition, which also involved immigrant workforce from other areas of Spain.

2.2. Ecosystem services

Water supply, food and biomass production were selected as representative of meaningful provisioning ES, whereas soil retention, water and nutrient regulation were selected as representative of regulating ES at catchment scale. Water supply and regulation are especially relevant in a context of climate change and water scarcity in Southern Europe, which depends primarily on precipitation and transmission losses, and water storage and retention ability, respectively (de Groot et al., 2002). The inverse value of sediment yield was used as an indicator of soil retention, a key ES for land productivity and soil fertility, and determined by vegetation cover (Egoh et al., 2008). Nutrient regulation is associated with the maintenance of 'healthy' and productive soils (De Groot et al., 2002). Nitrogen turnover (and particularly NO_3) is frequently used as a surrogate of nutrient regulation (Burkhard et al., 2012; De Groot et al., 2010). This parameter is regulated by the ability of vegetation and soil to avoid exports and to consume it (Conte et al., 2011). Within provisioning ES, food, fiber and fuel provision are among the most evaluated (Lautenbach et al., 2013). Food production was represented by the cereal yield (barley, wheat and corn), the most relevant type of crops in the study area. Regarding fuel provision, it was measured by the dry weight of annual plant biomass (aboveground and roots, MEA, 2005; De Groot et al., 2010).

Soil and Water Assessment Tool (SWAT, Arnold et al., 1998) was run to calculate ecohydrological variables that were subsequently used directly (food and biomass production) or indirectly (inverse value or combination of SWAT outputs) as ES indicators (Table 1). The SWAT

Table 1
Detailed list of ecosystem services with the corresponding indicators calculated by SWAT and supporting references. WYLD = Water Yield (mm), SW = Soil water content (mm), TLOSS = Transmission losses (mm), P = Precipitation concentration period, SURQ = Surface runoff (mm), LATQ = Lateral flow contribution to streamflow (mm), GWQ = Groundwater contribution to streamflow (mm), ORGN = Organic nitrogen yield (kg N/ha), NSURQ = Nitrates in surface runoff (kg N/ha), NLATQ = Nitrates in lateral flow (kg N/ha), NO3L = Nitrates leached from the soil profile (kg N/ha), NO3GW = Nitrates transported into the main channel in the groundwater loading (kg N/ha), P = Provisioning ES, R = Regulating ES.

Ecosystem service	Indicator	SWAT output variables (HRU scale)	References
Water supply (P)	Water production (mm)	WYLD = SURQ + LATQ + GWQ – TLOSS –POND	Fan and Shibata, 2014
Food production (P)	Cereal yield (ton/ha)	Cereal yield (barley, wheat and corn; YLD)	Self calculation
Biomass production (P)	Total biomass (ton/ha)	Total biomass (aboveground and roots; BIOM)	MEA, 2005; De Groot et al., 2010.
Water regulation (R)	Combination of soil water content, surface runoff, lateral flow and groundwater contribution per precipitation rate (% of precipitation in mm)	Average of: SW/P + SURQ/P + LATQ/P + GWQ/P	Schmalz et al., 2016
Soil retention (R)	Inverse value of sediment yield (ton/ha)	Inverse value of sediment yield (SYLD)	Arias et al., 2011; Gathenya et al., 2011; Kauffman et al., 2014; Lant et al., 2005; Schmalz et al., 2016
Nutrient regulation (R)	Inverse value of nitrogen export (organic and mineral; ton/ha)	Inverse value of $\sum$ ORGN + NSURQ + NLATQ + NO3L + NO3GW	Clark et al., 2002; Alamgir et al., 2016; Lee et al., 2018

model is one of the most used tools for the spatial modelling of ES (Ochoa and Urbina-Cardona, 2017) based on hydrological models combining vegetation, soil, water, management, weather and components of landscapes. We focused on modelling soil hydrology, plant growth and nutrient transport. Prior to running the model, the selected basin was divided into multiple sub-basins, which were subdivided into Hydrologic Response Units (HRUs), i.e. polygons with similar slope, soil characteristics, land use and management. Daily rainfall and snow, as well as water stored on soil and aquifers were used to estimate the total volume of water in each HRU. Flow, sediments and nutrient loads were calculated for each sub-basin through the river system according to the concept of the hydrological cycle, and the water volume within each HRU could be stored as snow, soil profile (0–2 m), surface aquifer (usually 2–20 m) or deep aquifer (>20 m).

Water flows (all components: runoff, lateral, surface and deep aquifer), nutrient (NO_3 and organic N) and sediment balances, climatic and soil processes (infiltration, water content, physico-chemical and hydrological properties of soils associated to land use, management and vegetation cover), plant biomass production and agricultural harvests were modelled for 10-year periods: 1954 to 1964 and 2006 to 2016 (mean annual values within these decades were used in further calculations). For this, a combination of topography (25 m grid digital elevation model; IGN, 2015), climate (daily precipitation, maximum and minimum temperature, relative humidity, solar radiation and wind speed from 14 meteorological stations, provided by the National Meteorological Agency – AEMET 1945–2018), land-use (manual object-based classification to aerial orthophotos for 1956 from the American flight 1956–57 USAF Aerial Photography of Spain; scale 1:32000 and pixel size 0.5–1 m, and crop and land-use maps for the period 2000–2010 from the Spanish Ministry of Agriculture, Fisheries and Food; scale 1:50000 and pixel size 0.25–0.5; MAPA, 2009) and soil data (texture, bulk density, organic carbon content, saturated hydraulic conductivity, pH, $CaCO_3$) from sampling campaigns of AMUSE project (CGL2014-53017 C2-1-R, Spanish Ministry of Economy and Competitiveness) and existing databases for the area (Trueba et al., 1998; García-Pausas et al., 2007; Vidal et al., 1997; Nicolau, 2002; Nadal-Romero et al., 2016; Regüés et al., 2017; Lizaga et al., 2019) were used in the calculations to infer water flows, sediment load, agricultural and biomass productions, both in the 1950s and the 2000s. All formulas and the methodology (including model algorithms and simulation processes) applied to the estimation of hydrological and nutrient variables are available in SWAT model documentation (Neitsch et al., 2011). See Appendix B for full methodological information about data, SWAT and ES calculation.

2.3. Population data

Number of inhabitants, population density and number of villages per municipality (n = 50) in the three geographical zones were calculated from a decadal census compiled by the Aragonese Stats Institute (1900–2018), to describe depopulation trends. The values of each ES were aggregated at municipality scale based on the corresponding values of HRUs polygons within each municipality (summation) to be able to relate ES to population dynamics in subsequent analysis. For this, we selected a subset of municipalities (n = 21) corresponding to the main sub-watershed in each study area where ES were quantified, both in the 1950s and 2000s. To verify the demographic representativeness of the three sub-watersheds within the zones, we checked that the population dynamics of the subset was not significantly different from the other municipalities through Linear Mixed-Effects models (LMEs, Kuznetsova et al., 2017; considering date, subset and interaction as fixed factors, and municipalities as random factor). Spearman's correlations were performed among population variables (inhabitants, population density and number of villages) to discard potential highly correlated variables.

2.4. Data analysis

To check depopulation trends, the change during the last century (from 1900 to 2018) in the number of inhabitants, population density and number of villages per municipality and decade were analyzed through Generalized Additive Mixed Models (GAMM; Wood, 2006). GAMM was chosen instead of other regression procedures because of its ability to deal with nonlinear relationships between the response and the predictor and time series data (Guisan et al., 2002). In this case, we fitted GAMM with four degrees of freedom to allow for linear, quadratic and cubic responses. Spearman's correlations were also performed between the change in population variables (inhabitants, population density and number of villages) and percentage of land-use type per municipality to confirm the underlying relationship between depopulation and land use. LME was applied to compare ES supply between the 1950s and the 2000s (fixed factors: date, area and the interaction between them; random factor: municipalities), and another one to investigate the role of depopulation in these changes (fixed effects: inhabitants, population density and number of villages). Goodness of fit was evaluated with Marginal R^2 and conditional R^2. Likelihood ratio tests were implemented to compare these models (fixed and random effects) with null ones (only random effects) and detect model significance. Additionally, an extended LME was performed to check if these relationships between population variables and ES differed among zones and dates (adding them as fixed factors).

Homoscedasticity and normality of residuals were visually checked for GAMM and LMEs (Appendix C). Logarithmic transformations were applied to population variables and ES prior to LMEs to improve linearity against response variables. All statistical analyses were performed using R statistical software (libraries: "effects", "ggplot", "lme4", "lmerTest", "MuMIn", "mgcv", "nlme" and "stargazer"; R Core Team, 2019).

3. Results

3.1. Population dynamics from 1900 to 2018

The number of inhabitants (adjusted R^2 = 0.9) and population density (R^2 = 0.83) experienced a general decrease from 1900 to 2018 in the three geographical zones (Fig. 3; Appendix D), being particularly noticeable between the 1950s and the 2000s (−41.7% in population and −44.7% in population density). However, the depopulation rate differed among zones (interaction "Date:Area", p-value < 0.001), being the lowest in Monegros (from 20,101 to 13,344 residents and 9.7 to 6.4 inhabitants/km^2) and the highest in Hecho (from 9015 to 2275 residents and 11.4 to 3.4 inhabitants/km^2; Table D.1). Hecho's municipalities included a greater number of villages than Monegros' and Estercuel's during the whole studied period. This variable experienced a significant increase in Monegros but a decrease in Estercuel which started during the 1940s. Finally, we also detected significant correlations between demographic variables and land uses. The increases in irrigated crops, orchards and meadows were positively correlated with population, density and/or number of villages per municipality, whereas the opposite pattern was found for forests (especially riparian ones) and scrublands (Table 2).

3.2. Change in ecosystem service supply between the 1950s and 2000s

In general, water supply, water regulation, food and biomass production increased in the study area between the mid-20th and the early 21st century whereas nutrient regulation decreased (Table 3, Fig. 4, Fig. E.1–E.6 in Appendix E). The overall improvement in water supply was mainly driven by changes observed in Monegros, with Estercuel and Hecho showing non-significant increases. Similarly, the growth in food and biomass production was particularly pronounced in Monegros. On the contrary, nutrient regulation and soil retention acutely decreased in

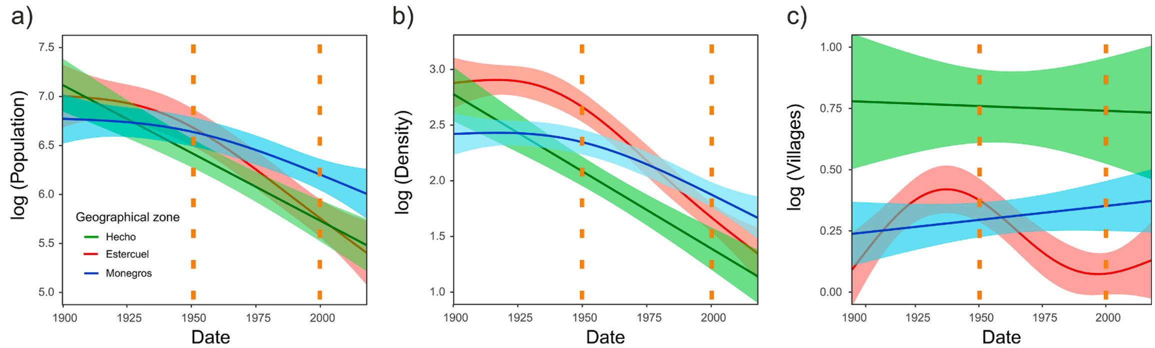

Fig. 3. Generalized Additive Mixed Model (GAMM) results about temporal (1900–2018) and spatial changes (geographical zones) of a) mean population, b) mean population density and c) mean number of villages per municipality in the study area. The 95% confidence intervals (shaded colours) and the dates used to compare demographic variables with ecosystem services (orange discontinuous lines) are shown.

Table 2
Spearman's correlation between demographic variables and land uses. Asterisks display the correlation significance (***p < 0.001; **p < 0.01; *p < 0.05). Significant results have been highlighted in bold.

Land Use/Demographic variables	Population	Population density	Number of villages
Bare soil	−0,21	**−0.47***	−0,24
Urban areas and roads	−0,3	−0,22	−0,12
Irrigated crops	0,25	**0.53***	**0.71*****
Riparian forests	**−0.44***	**−0.87*****	**−0.45***
Forests	−0,32	−0,35	**−0.43***
Rainfed fruit trees	0,15	0,21	−0,11
Orchards	**0.44***	**0.7*****	0,03
Meadows	0,13	**0.64****	0,13
Scrublands	−0,13	**−0.68*****	−0,23
Scrubby pastures	−0,04	−0,29	−0,16
Water bodies	0,08	0,21	0,37
Rainfed crops	−0,01	0,34	−0,22

Monegros but significantly increased or remained stable in Hecho and Estercuel.

Among the three zones, Monegros displayed the greatest values of nutrient regulation, food and biomass production followed by Estercuel and Hecho in both dates (Fig. 4). Contrarily, the inverse spatial pattern was found for water supply. Finally, soil retention was significantly lower in Hecho, whereas no significant spatial pattern was detected for water regulation (similar values within all the zones).

3.3. Population dynamics vs ecosystem services

Water regulation was negatively related to population density (Fig. 5a). Similarly, soil retention was weaker in more inhabited and densely populated municipalities (Fig. 5b and c). The number of villages was negatively associated with soil retention (Fig. 5d) but positively with food (Fig. 5e) and biomass production (Fig. 5f). Regarding best-fitting models, only soil retention incorporated two population variables (i.e. population and number of villages) that improved the performance of individual models (see Table 4). Water supply was significantly ($p < 0.001$) related to population (R^2m = 0.57), population density (R^2m = 0.35) and number of villages (R^2m = 0.45, Fig. E.7 in Appendix E), whereas population density had an influence on nutrient regulation (R^2m = 0.88, $p < 0.001$), in models including date and/or zone as fixed factors (Tables E.1–E.3). Thus, greater water supply was detected in scarcely populated municipalities of Hecho whereas Monegros followed the inverse spatial pattern, particularly in the 2000s. In fact, diminished water supply was found in more densely populated areas of Monegros only in the 1950s (Fig. E.7c). Regarding nutrient regulation, it was related to population density but this pattern was only significant (positive relationship) within the zone of Monegros in the 1950s (Fig. E.8; Table E.4). Exploratory correlations pointed to stronger relationships between demographic variables and ES in the 1950s (minimum r > 0.2) than the 2000s (r > 0.08).

4. Discussion

4.1. Depopulation trends

Throughout the 1900–2018 period (Fig. 3), depopulation was especially intense during the second half of 20th century (total population decreased from 58,247 inhabitants in the 1950s to 37,507 in the 2000s), coinciding with the time of changes in ES supply. This decrease was not spatially homogeneous due to divergent socioeconomic and land-use trends: depopulation was particularly evident and occurred earlier (from the 1900s) in the more natural and mountainous high-altitude zone of Hecho. Here, depopulation was boosted by reduced accessibility, scarce economic alternatives and regional socioeconomic shifts, leading to a reduction in extensive livestock farming (mainly ovine and caprine), which favored the recovery and expansion of scrublands and

Table 3
Results of linear mixed-effect models (LMEs) on ES indicators. Marginal R^2 (R^2m) and conditional R^2 (R^2c) and *P*-values for the whole model and the different terms (date, geographical zone and the interaction between them) are shown. The sign and trend of the relationship for each term is also displayed i.e. temporal (date), spatial (geographical zone) and spatiotemporal trends (Date:Zone). Significant results (if *p*-value < 0.05) have been highlighted in bold. Ester = Estercuel; Mone = Monegros; P = Provisioning ES; R = Regulating ES.

Response Variable	Model			Date		Geographical zone		Date: Zone	
	P-value	R^2m	R^2c	*P*	Temporal trend	*P*	Spatial trend	*P*	Trend
Water supply (P)	**<0.001**	**0.36**	**0.95**	**<0.001**	+	**0.03**	Hecho > Estercuel > Monegros	**<0.001**	Monegros (+)
Water regulation (R)	**<0.001**	**0.93**	**0.93**	**<0.001**	+	**0.049**	=	0.08	=
Soil retention (R)	**<0.001**	**0.91**	**0.96**	0.34	=	**<0.001**	Monegros = Estercuel > Hecho	**<0.001**	Mone (-), Ester (+), Hecho (+)
Nutrient regulation (R)	**<0.001**	**0.86**	**0.86**	**<0.001**	-	**<0.001**	Monegros > Estercuel > Hecho	**<0.001**	Monegros (-), Hecho (+)
Food production (P)	**<0.001**	**0.83**	**0.89**	**<0.001**	+	**<0.001**	Monegros > Estercuel > Hecho	**<0.001**	Monegros (+)
Biomass production (P)	**<0.001**	**0.72**	**0.91**	**<0.001**	+	**0.002**	Monegros > Estercuel > Hecho	**<0.001**	Mone (+), Ester (+), Hecho (+)

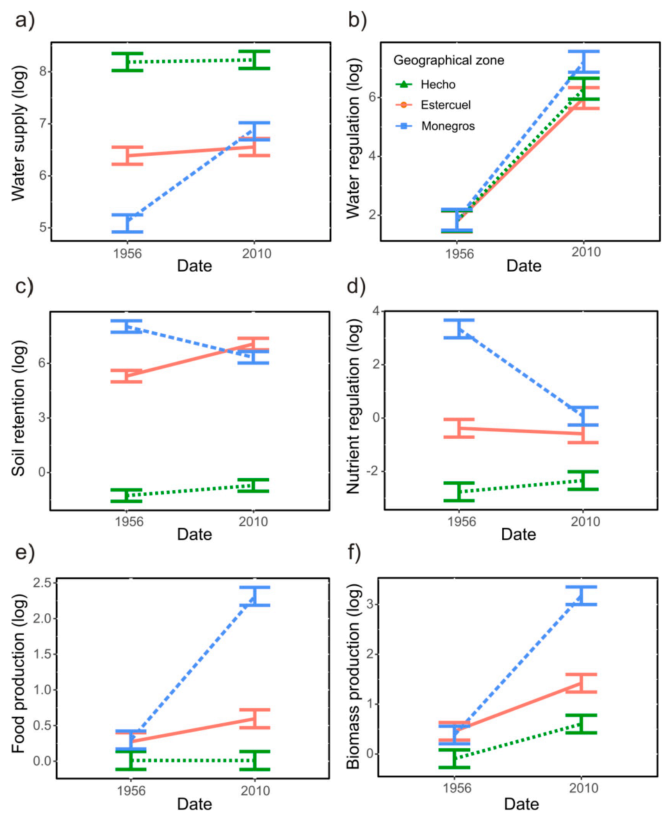

Fig. 4. Observed (mean) significant differences in ES indicators between the 1950s and the 2000s according to linear mixed-effect models (LMEs): a) Water supply, b) Water regulation, c) Soil retention, d) Nutrient regulation, e) Food production and f) Biomass production in Hecho (green), Estercuel (red) and Monegros (blue).

forests (Lasanta and Marín-Yaseli, 2007; Vidal-Macua et al., 2018). Depopulation was also noticeable but lagged in time (1950s) in the mountainous mid-altitude zone of Estercuel where opposite trends were found between municipalities that opened mines (stable or positive) and those whose economy was based on agriculture or where crops were abandoned (negative). These differences in land-use policies promoted population movements within the area, particularly during the first half of the 20th century (Fabro, 2007). The lowest depopulation rates were found in the agricultural lowlands of Monegros, where workforce immigration from the Pyrenees and other parts of Spain, strong agricultural intensification and irrigated land expansion have taken place since the 1960s, pointing to demographic trade-offs between Hecho and Monegros (source and sink of migratory fluxes, respectively), which could have softened yet not avoided rural depopulation.

The structure and distribution of population, represented here by the number of villages within each municipality, did not display a common pattern. Within Monegros, new villages were created between 1950 and 1970 as a consequence of colonization linked to land-use policies such as the conversion of rainfed crops into irrigated ones. In contrast, some human settlements disappeared within Hecho and Estercuel as a result of the decay of traditional farming and the end of the first golden age of coal (1930s–1940s), respectively, leading to intense human migration to industrial urban areas. The combination of the observed outcomes pointed to a generalized loss of population but without the complete abandonment of human settlements.

Rural depopulation has been shown to have a major role on land-use schemes and ES supply in Mediterranean areas (Kosmas et al., 2002; Lasanta et al., 2017), and particularly on our spatial and case-specific context (Table 2; See Appendix F for detailed explanation). For example, in Italy, land-use changes seem to be associated with population density, which appear to be inversely related to the increase in forest cover and decrease in pastures and traditional agricultural uses (Falcucci et al., 2007). In the case of Spain, low population density in rural areas has been demonstrated to promote land abandonment since infrastructures and services are scarce, dispersed and inefficient, which

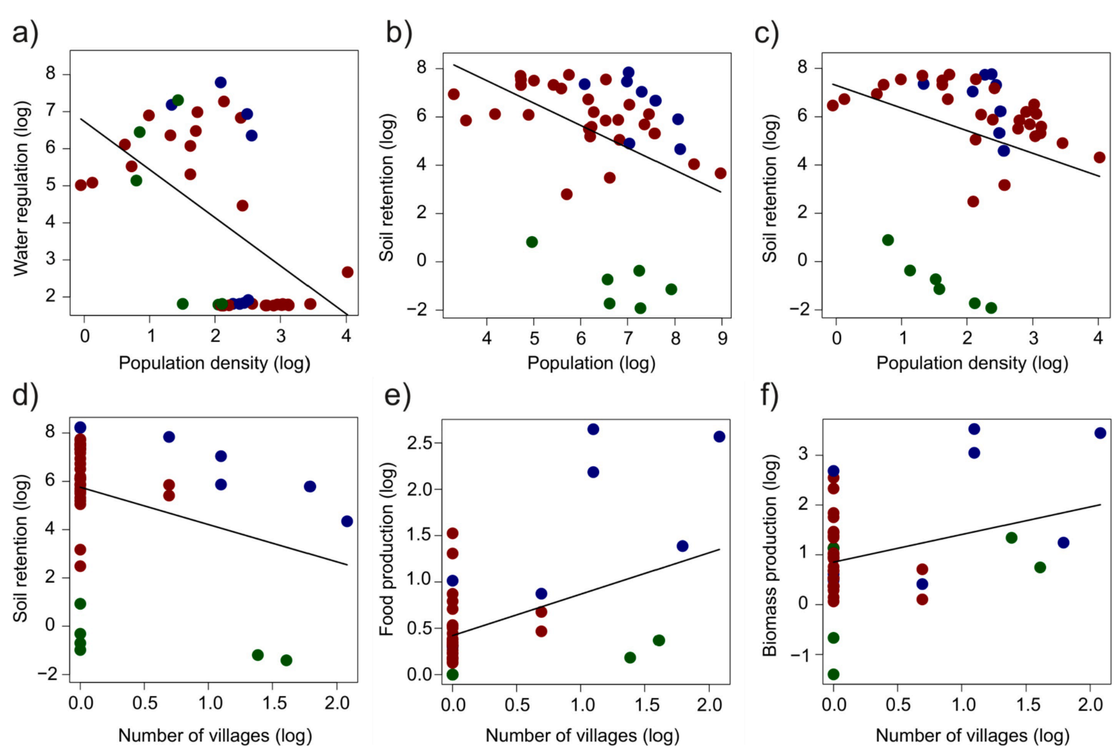

Fig. 5. Scatterplot showing only significant relationships ($p < 0.05$) between population variables and ES indicators: a) water regulation, b-d) soil retention, e) food production, and f) biomass production according to LMEs. Solid line represents fitted LME models. Hecho (green dots), Estercuel (red) and Monegros (blue) samples are shown.

Table 4
Results of linear mixed-effect models (LMEs) relating population variables and ES indicators. Marginal R^2 (R^2m), *P*-values and Estimates (indicating the sign of the relationship) are shown for each model and the best one for each ecosystem service. Asterisks display the significance of the best models (***p < 0.001; *p < 0.05). Significant results have been highlighted in bold. P = Provisioning ES; R = Regulating ES.

Variables	Human population			Population density			Number of villages			Best model	
	P-value	R^2m	Est.	*P*-val.	R^2m	Est.	*P*-val.	R^2m	Est.	R^2m	Equation
Water supply (P)	0.48	0.01	−0.08	0.53	0.01	−0.09	0.15	0.05	0.54	-	–
Water regulation (R)	0.053	0.07	−0.54	**0.001**	**0.24**	**−1.3**	0.5	0	0.45	**0.24*** **	Y = −1.3 log(Density) + 6.7
Soil retention (R)	**<0.001**	**0.13**	**−0.93**	**<0.001**	**0.07**	**−0.94**	**0.049**	**0.08**	**−1.54**	**0.22*** **	Y = −0.9 log(Population) −1.6 log(Villages) + 11.5
Nutrient regulation (R)	0.35	0.02	0.18	0.31	0.02	0.24	0.99	0	0.001	–	–
Food production (P)	0.77	0	0.02	0.63	0	−0.05	**0.015**	**0.14**	**0.45**	**0.14***	Y = 0.45 log(Villages) + 0.42
Biomass production (P)	0.39	0.02	−0.11	0.26	0.03	−0.19	**0.049**	**0.09**	**0.55**	**0.09***	Y = 0.55 log(Villages) + 0.85

impacts negatively in competitiveness (Perpiña-Castillo et al., 2020). This is particularly true for marginal, inland areas with a stagnant job market, elderly population and poor soils (Stellmes et al., 2013; Serra et al., 2014), like our study area where such a link seems to be particularly strong (García-Ruiz and Lasanta-Martinez, 1990; Collantes and Pinilla, 2004; Vicente-Serrano et al., 2004). In fact, the expansion of forests also reflects the decreasing use of fuelwood and timber because of population decline and the replacement of forest resources by other energy sources and materials (Poyatos et al., 2003).

Land-use intensification could partially and temporally buffer population declines, but it does not seem an effective strategy to stop rural exodus and population aging in the long-term (Vidal-Legaz et al., 2013), which continues nowadays at a high rate in the study area (Pinilla et al., 2008).

4.2. Ecosystem services supply

When population shifts entail land-use conversion and associated environmental impacts (biodiversity loss, landscape homogenization and alteration of ecosystem functioning, among others), it usually results in meaningful changes in ES (Vidal-Legaz et al., 2013; Elmhagen et al., 2015). As expected, the more intense depopulation and land-use transformation, the greater changes in ES supply (Tables 3 and 4; Figs. 5 and 6). Interestingly, crop production and regulating ES (namely nutrient regulation and soil retention) showed a contrasting response to demographic and land-use changes. Such a phenomenon is especially evident (Fig. 4) in the Mediterranean basin, where land use has been the outcome of a long and close historical interaction between natural and social systems (Blondel, 2006).

In recent decades, agricultural intensification and the creation and expansion of farming villages and towns (which smoothed depopulation trends) translated into increased food production but decreased nutrient regulation and soil retention, particularly in Monegros. This process also implied the agricultural invasion of marginal lands, new roads and power lines, drainage pipes and trenches, irrigation ponds and machinery traffic, which reduced native vegetation and simplified agricultural fields (Castañeda and Herrero, 2008) with a negative impact in regulating ES. Thus, the landscape which was previously dominated by an irregular agricultural mosaic adapted to the round-shaped depressions and sinkholes, have now become homogeneous and square-shaped (see an example in Fig. E.9). The high-water supply values detected in the most populated municipalities result from an artificial increase because of the Monegros water transfer from the Pyrenees (averaged flow of 2.1 $m^3\ s^{-1}$), which enabled the massive transformation from rainfed to irrigated agriculture (increasing from 0% to 41% of the surface). Recent external inputs (mainly water and synthetic fertilizers) and mechanization seem to be softening the relationship between demography and ES supply in intensive agricultural areas during the last decades: despite depopulation, provisioning ES experienced an increase while key regulating ES decreased.

Spatial aggregation of both land intensification and abandonment patches can provide buffer areas which prevent from ecological homogenization and therefore attenuate biodiversity and ES decline (Jacob et al., 2008; Katayama et al., 2015). This seems to be the case of mid-altitude and mixed landscape in Estercuel, where land-use intensification associated with mining activities on some plots (Fig. E.10) contrasts with the expansion of scrublands (expanding from 3.5% to 37% of area) and forests (from 10% to 27%) in the remaining territory. Thus, depopulation and ecological succession after pasture abandonment in this area could have partially buffered a greater modification on

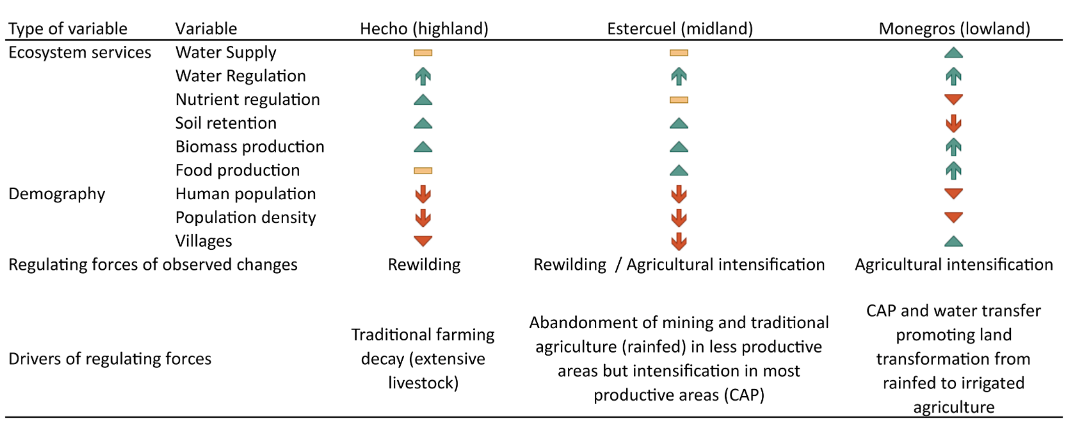

Fig. 6. Temporal trend (1950s–2000s) of population and ES indicators, regulating forces and drivers. High increase/decrease is denoted by green/red arrows, respectively, while moderate increase/decrease is denoted by green/red triangles. Yellow horizontal line indicates the variable remains stable. P = Provisioning ES; R = Regulating ES; CAP = Common Agricultural Policy.

the ES scheme at wider scale.

Although highlands are usually more intensively affected by rural depopulation (Weissteiner et al., 2011), the dominant natural land use (49% of the area is forest), the abrupt topography and the isolation from centuries have driven minor land-use changes in Hecho (see example in Fig. E.11). Mountainous rural areas that maintain extensive land management supply important provisioning (e.g. water supply) and regulating (e.g. water regulation) ES, not only for rural but also for urban areas downstream (Vidal-Legaz et al., 2013). Despite the overall loss of agricultural surface in mid- and high-altitude areas (Estercuel and Hecho), food production at municipality scale was maintained or even increased by the technification of agriculture and the selection of highly productive areas for farming even without significant external water inputs. In addition, the rewilding process observed in vast extensions within mountainous areas due to depopulation and land abandonment, explain the general increase in regulating ES (soil retention, water and nutrient regulation) and the potential decrease in water supply due to reduced runoff as water consumption, evapotranspiration and interception by plants continue increasing (García-Ruiz et al., 2011). It must be noted that land abandonment and the subsequent passive afforestation and biomass production could also involve relevant disservices in Mediterranean areas such as increased fire susceptibility (Moreira et al., 2011) or invasive species (Munroe et al., 2013), which could reverse the observed increase in regulating ES. Although not studied here, land abandonment may also imply biocultural diversity loss resulting in ES decline (Mauerhofer et al., 2018). On the other hand, rewilding is associated with an increase in cultural ES such as recreation and ecotourism (Cerqueira et al., 2015).

4.3. Main methodological limitations

Although the municipality scale (the smaller scale presenting reliable long-term population data) used in this study seems suitable for a meaningful assessment of ES supply, complementary analysis at finer scale may facilitate a more accurate analysis of the relationships between depopulation and ES (Felipe-Lucia et al., 2014). Spatial resolution of land-use data was accurate enough to evaluate ES supply in both periods but it was greater for the 2010 than 1956. Despite our data represented three different Mediterranean rural areas along a gradient of altitude and land use, we acknowledge the need for spatial replication in further studies in order to confirm the observed patterns. One of the main limitations when analyzing a greater number of areas arises from the scarcity of reliable environmental data for ES in the 1950s and previous decades, which has also prevented the correct calibration and validation of the SWAT model. However, calibration can have a relatively minor effect on the selection of sediment and nutrient critical source areas, which is why SWAT has also been applied in watersheds lacking calibration data (Niraula et al., 2011; Appendix B for detailed justification).

Despite there were isolated and slight violations of model assumptions (Appendix C), mixed-effect models have been identified as remarkable robust tools for these cases (Schielzeth et al., 2020). Although the changes observed in ES between 1956 and 2010 were assumed to be mainly determined by demographic and land-use shifts between these years, previous changes (1900–1956) could have also influenced the ES supply through lagged effects (e.g., meaningful increases in regulating ES could require decades of depopulation and land abandonment). In order to have a complete picture of ES supply as well as the potential trade-offs with provisioning and regulating ES, further studies should consider cultural ES. In addition, studies exploring depopulation and ES relationships would benefit from including not only ES supply indicators but also demand ones to obtain the realized flow of nature's contribution to people.

4.4. Implications for land management policy

To face the increasing demand for food, fodder and fiber, agricultural modernization has been essential to maximize the supply of provisioning ES but to the detriment of regulating ES (MEA, 2005; Raudsepp-Hearne et al., 2010). At European level, land consolidation supported by governmental funds and the Common Agricultural Policy subsidies, has fueled agricultural intensification in Mediterranean rural areas. This has promoted the multiplication of average field size, irrigated surface, chemical fertilizers and pesticides, mechanization, simplification and specialization of agroecosystems through landscape homogenization and the abandonment of less fertile and isolated areas for food production (Barceló et al., 1995; Van Zanten et al., 2014).

Although it is assumed that large-scale agricultural intensification would raise benefits for landowners (at least in the short run), it is also associated with high environmental cost and collateral social impacts, because of losses in stored carbon and negative impacts on soil and water quality and quantity, aquatic and terrestrial habitats, consequently decreasing species diversity and abundance across a hierarchy of trophic levels and spatial scales (Polasky et al., 2011; Stehle and Schulz, 2015; Emmerson et al., 2016). Moreover, it has been recently pointed out that regulating ES can contribute even more than provisioning ES to human well-being (Zhang et al., 2021).

The high investments in rural areas to increase agricultural productivity have not favored rural population fixation (Lasanta and Marín-Yaseli, 2007). As observed in Monegros, rural depopulation can also occur in areas where agricultural intensification takes place given that land consolidation, monoculture, modernization, technification and mechanization reducing the required agricultural workforce (Enyedi and Volgyes, 1982). Land intensification can also jeopardize the long-term sustainability of rural populations since habitats in a favorable conservation status sustain higher biodiversity and have a greater potential to supply ES, particularly regulating and cultural ones, than habitats in an unfavorable conservation status (Maes et al., 2012). Furthermore, this intensification can ultimately impair even food production in the long term due to reduced key ES, such as biological control of agricultural pests (Thies and Tscharntke, 1999) and pollination (Kennedy et al., 2013). Moreover, soil nutrient loss (namely phosphorous) from agricultural systems aggravated by soil erosion will jeopardize food and feed production, not only locally but also globally in the long term (Alewell et al., 2020).

Recent agronomic advances can help to improve and recover some traditional techniques such as crop rotation, use of green manure and crop residues, which combined with economic diversification strategies and consumption of local products (slow food and km 0 products), extensive management and restoration, could balance the supply of provisioning and regulating ES at the same time that it contributes to human well-being and fixing population in rural areas (Garibaldi et al., 2016; Garibaldi et al., 2019; García-Ruiz et al., 2020). This strategy would minimize the use of costly synthetic inputs (fertilizers, pesticides, imported pollinators and water), improve water quality and promote biodiversity while maintaining crop yields (Isbell et al., 2017; Qaswar et al., 2019). In addition, a mosaic landscape showing a balanced distribution between forests, scrublands, pastures and crops that limits overall biomass production can optimize ES supply and boost key ES in Mediterranean areas such as wildfire mitigation (Moreira et al., 2011), balanced water supply-flood prevention (Nelson et al., 2009) and ecotourism (Campbell and Ortiz, 2011), which could succeed in limiting population decrease and maintaining an effective environmental protection (Valaoras et al., 2002).

In a context of global change, the negative effects of climate change on ES are predicted to be exacerbated in water-limited catchments (Schröter et al., 2005; here Monegros and Estercuel), where water shortages will be more recurrent and intense, so food production based on irrigated intensive agriculture could be at risk (Iglesias et al., 2011), particularly those based on inter-catchment water transfers (Bates et al., 2008; Pittock et al., 2009). Climate projections for the end of the 21st century predict reduced runoff because of increasing temperature and evapotranspiration in natural vegetation (expanding as a consequence of land abandonment) and lower precipitation and snowpacks, so maintaining water supply under increasing demand constitutes a challenge for policy-makers and managers that cannot be solved by just increasing water storage capacity through reservoirs (López-Moreno et al., 2011). The explosive combination of global warming, depopulation and rewilding in vast Mediterranean rural areas can boost megafires with catastrophic effects on supporting, provisioning, regulating and cultural ES at regional scale, which would require of preventive management (e.g. land stewardship) and policy measures (e.g. economic and social incentives to fix population). To construct an alternative promising and viable strategy for rural areas that reflect both environmental and social returns, it seems necessary to consider the importance of a balanced ES supply in land-use management and decision making to fix population in a sustainable way and reach multifunctional landscapes (García-Llorente et al., 2012; Mauerhofer et al., 2018).

5. Conclusions

Severe population declines were detected during the 20th and the beginning of the 21st centuries. Human population and population density halved from 1900 to 2018, being depopulation particularly acute between the 1950s and the 2000s, when ES were evaluated. We detected significant differences in ES supply modulated by population dynamics between semi-natural highlands and agricultural lowlands, which accounted for the most intense land-use transformations and the greatest changes in ES supply. Thus, contrasting patterns were found between more fertile, inhabited and easy-to-access areas where agriculture was intensified, and less productive, isolated, and depopulated mountainous ones where natural recovery of vegetation was observed, boosting food production and regulating services, respectively.

Rural depopulation has been shown to have a relevant role on ES supply in our spatial and case-specific context. Demographic trends resulted relevant for land-use changes and, consequently, for all the ES evaluated, especially for water regulation, soil retention and food production. Thus, greater values in demographic variables were related to land intensification and reduced regulating ES supply, such as soil retention and water regulation, but higher delivery of provisioning services, such as food and biomass production. The relationships of water supply and nutrient regulation with demographic variables were modulated by external inputs (i.e. water and fertilizers), resulting in differences between zones and dates. However, it must be noted that ES changes may vary depending on the spatial scale considered (i.e. contrasting results between municipal and regional scales).

From a management perspective, local socioeconomic factors, degree of use of natural capital and land-use policies have been shown to crucially drive ES supply under similar depopulation scenarios (Hashimoto et al., 2019). Rural depopulation can also occur in areas experiencing land-use intensification, so given its high environmental costs in terms of biodiversity and ES supply, such a strategy does not seem cost-effective for fixing rural population in the long term. In this context, a mosaic of land uses (from forests to crops and other intensive land uses) providing multiple ES will offer different benefits and economic alternatives for their inhabitants, which could help to implement successful policies aiming at stopping and reversing depopulation in Mediterranean rural areas.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2021.101369.

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