Changes in forest landscape patterns resulting from recent afforestation in Europe (1990–2012): defragmentation of pre-existing forest versus new patch proliferation

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Abstract

• **Key message** Recent afforestation in Europe might involve deep changes on landscape composition and configuration. We show that afforestation promotes defragmentation of pre-existing forests and new patch proliferation, in forest-dominated and non-forest-dominated landscapes respectively, while it is not associated to decreasing landscape diversity. These processes are modulated by geographic factors and might affect functional connectivity and biodiversity conservation in newly forested landscapes.

• **Context** A recent forest increase in Europe might drive changes in the landscape pattern, with increasing forest defragmentation and connectivity but decreasing land cover diversity that, in turn, might affect biodiversity conservation. However, little is known about these patterns of change and their association with the environmental context.

• **Aims** To explore the association of forest cover increase with changes in the spatial pattern of European landscapes, while considering their original landscape composition, geographical position and elevation.

• **Methods** We obtained data from ESA and GFC land cover maps and other GIS layers and performed a set of GLM on randomly selected 752 landscapes with recent (1990–2012) forest increase.

• **Results** A decrease in landscape diversity in the last decades was not associated to forest increase but to high cropland and low scrub-grassland cover. A forest increase promoted the defragmentation of already-existing forests and new patch proliferation in forest-dominated and non-dominated landscapes, respectively. These processes also depend on elevation and geographical position, with forest defragmentation concentrated in Northern and Eastern Europe and new patch proliferation in southern and western regions, and in mid-elevation areas.

• **Conclusion** Changes in afforested landscapes are more complex than expected and cannot be solely attributable to forest increase, but also to landscape composition and location across elevation and geographical gradients across Europe.

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This article is part of the topical collection on *Establishment of second-growth forests in human landscapes: ecological mechanisms and genetic consequences*

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1 Introduction

Deforestation is a primary land-use change on a world scale (Pagnutti et al. 2013), yet the overall decline in forest cover has fallen in recent decades due to forest transition (Meyfroidt and Lambin 2011), which has determined a change from net deforestation to net reforestation at both national and regional scales particularly in the northern hemisphere (Rudel et al. 2009). Indeed, forest transition has been taking place in many European and North American regions since the beginning of the twentieth century (Rudel et al. 2005) and, more recently, in the northern Mediterranean Basin (Mazzoleni et al. 2004). Gerard et al. (2010) detected an overall increase in forest cover in Europe in the second half of the twentieth century using land cover maps for a specific set of landscape samples. Recent works have highlighted that forest transition continues nowadays in Europe, with a net gain of 1.4% of forest surface between 1992 and 2015 detected from the European Space Agency global land cover maps (M. Palmero-Iniesta, unpublished results).

It is largely known that forest cover increase is affecting biodiversity conservation in Europe, with a generalized recovery of forest organisms including threatened species targeted in conservation initiatives (Plieninger et al. 2013; EEA 2016a). However, it also promotes a rarefaction and local extinction of species living in open habitats, including butterflies, birds and plants (Plieninger et al. 2013; Melero et al. 2016; Regos et al. 2016). In contrast, the effects of forest expansion on changes in the spatial pattern of the European landscapes are mostly unknown. In a seminal review on habitat loss and fragmentation (i.e. the reverse process to that analysed here), Fahrig (2003) observed a primary effect of habitat loss on biodiversity conservation, while the effects of habitat fragmentation per se (i.e. changes in habitat configuration but not in habitat cover) were much weaker and both positive and negative (see also Fahrig 2017). This would disagree with other works showing the importance of forest spatial pattern in the conservation of biodiversity and ecosystem functions, especially in highly transformed landscapes (e.g. Guirado et al. 2007; Ramage et al. 2013) where local disturbance regimes favour the extinction of forest specialists and the colonization by non-forest ones (Vellend et al. 2007; Basnou et al. 2015). As most of these works have been performed at local and regional scales, specific socio-environmental context might largely determine the effects of landscape configuration on biodiversity. Once again, little is known about the influence of this context on the changes in the spatial pattern following forest recovery in Europe, which is the previous essential step for understanding the effects of these changes on biodiversity.

The present work is aimed at addressing the association between forest cover increase and spatial pattern change in the

European landscapes, while considering the landscape land cover composition and the altitudinal and geographical gradients. The study takes profit of a recent set of medium- to high-resolution land use and cover (LC) maps worldwide available: those of the Climate Change Initiative (CCI), which are derived from ENVISAT, POES and SPOT images by the European Spatial Agency (ESA 2017), and the forest cover change maps of the Global Land Cover Facility (GLCF) from the University of Maryland, which are derived from Landsat images (Hansen et al. 2013; Kim et al. 2014). Changes in landscape and in forest spatial pattern have been addressed through a set of classical landscape metrics regarding land cover diversity and habitat fragmentation and connectivity. We hypothesized that forest increase is determining (i) a decrease in the overall landscape diversity, (ii) a forest defragmentation and (iii) an increase in forest connectivity across Europe. Yet, these effects might depend on the initial forest cover if the association between forest cover increase and landscape change is not linear as observed by Fahrig (2003) in the reverse case of habitat fragmentation. Still, the geographical position determining climatic conditions responsible for differential forest recovery may modulate these landscape changes.

2 Materials and methods

2.1 Study area

The study was performed in Europe as the region bordered by the Arctic Ocean to the north, the Atlantic Ocean to the west, the Mediterranean Sea to the south and the Ural Mountains and the Caspian Sea to the east, and including the natural region of the Caucasus and the Anatolian Peninsula (Palmero et al. 2020). It comprises around 10^7 km² from 30 to 80° of latitude and – 30 to 70° of longitude in the north hemisphere. Latitudinal and longitudinal climatic gradients and orography determine strong climatic variety in Europe (EEA 2016b). The relief of Europe is dominantly flat (66% of the territory is below 200 m a.s.l.) although the influence of the mountains gives the territory a high ecological heterogeneity (IGN 2019). The current European landscape is the outcome of a long history of human land-use changes (Perlin and Journey 1989) in which forests and other wooded land now constitute the largest land cover type, extending over more than 43% of its area (EEA 2016b).

2.2 Data sets on forest change and landscape composition

Forest cover and its spatial pattern in 1990 and 2012 were derived from the GLCF datasets (Hansen et al. 2013; Kim et al.

2014) covering all Europe, but only including forests. We used the oldest dataset available (1990–2000; www.landcover.com) to obtain a 1990 forest cover map with three categories: (i) forest, which included those pixels with already-existing forest and forest lost between 1990 and 2000; (ii) non-forest, which included the non-forest and the forests gained between the same period; and (iii) noise, which included shadow, clouds and no data pixels in the GLCF 1990–2000 that were excluded in later steps. A similar forest cover map was obtained for 2012 (http://earthenginepartners.appspot.com/science-2013-global-forest/download_v1.4.html), the most recent one in the GLCF datasets by categorizing the pixels of already-existing forest and of forest gain between 2000 and 2012 as forest, and the rest as non-forest. We also assessed the overall landscape composition through the land cover maps annually produced within the Climate Change Initiative of the European Spatial Agency (ESA CCI-LC), which are the complete land cover maps with the highest spatial resolution (300 m of pixel size) covering the whole of Europe (Diogo and Koomen 2016). We selected 1992 and 2012 land cover maps for the present study. The original CCI-LC land cover categories were reclassified into those proposed by the Intergovernmental Panel on Climate Change (IPCC; Eggleston et al. 2006), using the correspondence tables of the CCI-LC Product (see Table 3 in Appendix 1; ESA 2017).

2.3 Sampling design and landscape metrics

To assess changes in forest spatial pattern and in landscape composition due to forest increase, we randomly selected 2000 circular landscapes of 5-km radius across the study area. As the original GFC 1990–2000 had some noise (e.g. clouds, shadows), we discarded those landscapes with any type of noise (a total of 667 points) to avoid misinterpreting changes. Then, we calculated forest cover area (ha) in 1990 and 2012 for the remaining landscapes and we selected those with a positive forest increase between these dates ($n = 752$).

Changes in forest spatial pattern between the study dates were assessed from the 30-m-pixel-sized binary (forest/non-forest) maps mentioned above, through a set of landscape metrics aimed at describing forest fragmentation and forest connectivity (McGarigal and Marks 1994; Kupfer 2012). Their selection was based on (1) comparability with previous landscape ecological studies (ex. Turner 2005; Weng 2007) and (2) appropriateness for indicating ecological conditions (Debinski and Holt 2005; Kupfer 2012) and (3) for describing contrasting dimensions of the selected landscape attributes (McGarigal and Marks 1994; Fahrig 2003). Patch number and both mean and largest patch sizes were chosen as metrics of forest fragmentation. Moreover, patch size is known to be related to species richness and abundance (Boulinier et al. 2001; Debinski and Holt 2005). The total forest edge was also selected as a proxy of relevant fragmentation effects related to habitat alteration (Saunders et al. 1999). We finally selected effective mesh size (ha) for its high

sensitivity to contrasting fragmentation processes (Jaeger 2000). Regarding forest connectivity, we selected the percentage of like adjacencies, which measures the degree of aggregation of patch types, and the Euclidean nearest neighbour distance, which measures the distance among patches of the same type and deals explicitly with the degree to which patches are spatially isolated from each other (McGarigal and Marks 1994).

On the other hand, to assess changes in land cover diversity, we calculated the Shannon diversity index for 1992 and 2012 for each study landscape using the CCI-LC map (300 m of pixel size). Landscape diversity is considered a key attribute of landscapes, indicative of its ability to house a variety of organisms and habitats (Turner 1989).

All these metrics were calculated for the selected study dates and study landscapes, using the datasets mentioned above and the R ‘landscapemetrics’ package (Hesselbarth et al. 2019).

2.4 Environmental covariates

In order to assess the modulating role of environmental context on the association between forest increase and landscape change, we included a set of variables regarding geographical position, topography and initial composition of the study landscapes in the study following the related literature (Heilman et al. 2002; Geri et al. 2010; Fernandes et al. 2011; Nagendra et al. 2013). The geographical position of landscapes is a proxy of their position along the observed climatic and socio-environmental gradients across Europe (Jongman 2002; Metzger et al. 2005), and it was described from the geographic coordinates of the landscape central point (latitude and longitude in UTM coordinates). Topography included mean elevation, obtained from the Global 30 Arc-Second Elevation (GTOPO30) dataset provided by the USGS (<http://edcwww.cr.usgs.gov/landdaac/gtopo30/gtopo30.html>). The initial composition of landscapes (i.e. percentage of each land cover category) was inferred from the CCI-LC map of 1992. We calculated the cover percentage of the dominant land cover categories, namely forest and cropland (mean cover and standard error $39.02 \pm 1.27\%$ and $37.34 \pm 1.31\%$, respectively; see Table 3, Appendix 1). We then summed the cover of grasslands, wetlands, shrublands and sparse vegetation into a shrub/grassland category, noticeably represented in the study landscapes ($10.94 \pm 0.65\%$). We did not include the agroforestry mosaics, as this category is an undefined mixture of forest, scrubland, grassland and croplands, although it has relevance in the study landscapes ($9.32 \pm 0.54\%$).

2.5 Statistical analyses

In order to test if these landscape metrics differed between 1990 and 2012 (1992 and 2012 for the Shannon diversity index), we performed eight non-parametric Wilcoxon signed rank tests for paired samples for each landscape metric, after confirming the non-normal distribution of these metrics through the

Kolmogorov-Smirnov test with Lilliefors modification. The significance of these tests was also adjusted with Bonferroni correction.

We performed eight general lineal models—one for each landscape metric—to test the association of changes in landscape metrics with forest increase, the environmental variables mentioned above and the interaction between both. To avoid multicollinearity, we firstly generated a correlation matrix with a Spearman rank and chose those less correlated variables ($r < |0.7|$) (Table 4, Appendix 1). So, explanatory variables finally used on the linear models were forest increase (ha), forest cover (%), cropland cover (%), shrub/grassland cover (%), elevation (m), latitude and longitude (degree) and the second-order interactions among the forest increase and the remaining variables. These interactions were included as we were particularly interested in exploring if the association between forest increase and landscape metrics varied according to environmental factors.

The simplest general lineal models were selected following a *dredge* procedure using MuMIn R package (Barton and Barton 2019), which removed non-significant variables from the general model, and assessed significant changes in model predictions using the Akaike information criterion (AIC). From the models with a difference in AIC relative to AICmin < 2 , we chose the most parsimonious model by selecting the model with fewest predictor variables following the procedure described in Crawley (2007) (see Table 5, Appendix 1). In addition, we carefully considered all plausible models in order to not leave out an important explanatory variable by exploring model averaging based on an information criterion (see Table 6, Appendix 1). Moreover, null models were also performed for each landscape metric to investigate whether an observed pattern could have arisen by chance producing a type I error (Gotelli and Graves 1996). All the analyses were carried out with software R 2.15.0 (R Core Team 2012).

3 Results

On average, a significant increase in the size of both the largest and the mean forest patch and in the forest effective mesh size was observed in the studied landscapes (Table 1). Forest total edge and the number of forest patches also significantly increased as the Euclidean nearest neighbour distance did (Table 1). In contrast, the Shannon diversity index significantly decreased in the same landscapes. Our analyses failed to detect any significant change on the percentage of forest like adjacencies during the study period.

The best adequate model for each of the eight landscape metric variables included the effects of the environmental factors specified in Table 2. There were 5 to 10 other plausible models for each metric (difference in AIC in relation to AICmin < 2) that varied in the presence of lower relative importance variables but always included the effects of all

the selected variables in the selected model (see model averaging results in Table 5 and Table 6, Appendix 1). As shown in Table 2, explanatory variables accounted for a substantial proportion of total variability for some landscape metrics, as the increase in forest largest patch size and forest effective mesh size, but not for others (increase in forest mean patch size or Euclidean nearest neighbour distance). Selected models suggest that forest increase during the study period was not significantly associated with the increase in all the studied metrics (Table 2). It was positively associated with the increase in forest largest patch size, effective mesh size, total edge and the number of forest patches while the test failed to detect any significant association with the increase in the Shannon diversity index and in the percentage of like adjacencies.

Several environmental context variables were also significantly associated with the increase in the studied landscape metrics, sometimes through significant interactions with forest increase (Table 2). Initial forest cover showed a significant interaction with forest increase in both forest largest patch and effective mesh size, as these metrics increase more rapidly with forest increase in forest-dominated landscapes than in the rest (Fig. 3a, b; Appendix 2). There was also a significant interaction between initial forest cover and forest increase in both forest total edge and the number of forest patches, but in this case, the increase in these metrics with forest increase was lower in forest-dominated landscapes than in the rest (Fig. 3c, d; Appendix 2). Figure 1 illustrates the different new forest distribution pattern in forest-dominated landscapes, where new forest grew coalescent to the pre-existing forest, and in non-forest-dominated landscapes, where forest grew in isolated patches.

Initial cropland cover showed a negative association with the number of forest patches and positive with the Shannon diversity index and the percentage of like adjacencies. It also showed a significant interaction with the increase in forest cover on that in some metrics. Thus, the increase in the percentage of like adjacencies following that in forest cover was higher in cropland-dominated landscapes than in the rest (Fig. 3e, Appendix 2). Shrub/grassland cover showed a negative association with the increase in both the number of forest patches and the Shannon diversity index and positive with that in the percentage of like adjacencies.

Besides, longitude and latitude showed a significant association with the increase in most of the metrics and some significant interactions with forest increase, and different patterns of forest growth were observed throughout Europe (Table 2, Fig. 2). Longitude showed a positive association with the increase in both the effective mesh size and the percentage of like adjacencies, and negative with the increase in forest total edge and in the number of forest patches. Latitude showed a positive association with the increase in both forest total edge and the Shannon diversity index, and negative with that in forest effective mesh size and in the percentage of like

Table 1 Changes in the studied metrics in our study landscapes between 1990 and 2012.

Wilcoxon test (paired samples) used to test significant differences. Significant codes: ‘.’ > 0.05, ‘*’ = 0.05, ‘**’ = 0.01, ‘***’ = 0.001

	Mean 1990 (SE)	Mean 2012 (SE)	V value	p value	Sign.
Forest largest patch size (ha)	1490 (76.75)	1860 (88.87)	29,816	< 0.0001	***
Forest mean patch size (ha)	36.6 (2.84)	46.4 (6.92)	205,050	< 0.0001	***
Forest total edge (m)	190,000 (6764.11)	257,000 (8611.18)	32,186	< 0.0001	***
Forest effective mesh size (ha)	819 (56.34)	1140 (71.19)	26,197	< 0.0001	***
Number of forest patches	56.4 (2.04)	129 (4.56)	18,583	< 0.0001	***
Euclidean nearest neighbour distance (m)	152 (9.47)	131 (4.41)	94,471	0.046	*
Percentage of forest like adjacencies (%)	67.8 (1.31)	72.3 (0.97)	125,796	0.276	.
Shannon diversity index	0.738 (0.02)	0.620 (0.02)	110,262	< 0.0001	***

Table 2 Summary of GLM results showing the association of forest increase and the landscape and geographic variables with changes in the studied landscape metrics. Each column shows the factor effect estimate (standard error) and the significant codes: 0, ‘***’; 0.001, ‘**’; 0.01, ‘*’; 0.05, ‘.’

	Forest largest patch size	Forest effective mesh size	Forest total edge	Number of forest patches	Shannon diversity index	Percentage of forest like adjacencies	Forest mean patch size	Euclidean nearest neighbour distance
Intercept	272.43 (14.42) ***	162.11 (14.06) ***	92,344 (4706) ***	95.35 (40.2) ***	− 0.12 (0.01) ***	3.13 (0.65) ***		
Forest increase (FI)	473.09 (22.73) ***	168.09 (23.57) ***	94,337 (8252) ***	57.55 (7.10) ***		− 1.67 (1.11)	− 15.57 (8.85)	18.39 (12.13)
Forest cover	146.06 (14.67) ***	299.90 (14.83) ***	− 21,084 (5182) ***	− 40.13 (7.12) ***			26.39 (5.73) ***	
Crops cover				− 38.37 (7.10) ***	0.05 (0.01) ***	3.04 (0.76) ***		
Shrub/grassland cover				− 21.90 (4.59) ***	− 0.02 (0.01) *	1.82 (0.57) **		
Elevation			13,730 (7132) .	1.16 (6.18)	− 0.04 (0.01) **			
Longitude		38.76 (13.85) **	− 23,907 (4447) ***	− 26.15 (3.68) ***		1.26 (0.59) *	13.22 (5.01) **	20.42 (9.16) *
Latitude		− 35.29 (16.03) *	29,849 (6111) ***	0.74 (5.41)	0.10 (0.01) ***	− 3.48 (0.64) ***		
FI: forest cover	221.9 (16.22) ***	469.65 (19.67) ***	− 88,460 (6561) ***	− 53.97 (5.59) ***			26.99 (6.32) ***	
FI: crops cover						− 4.10 (1.12) ***		
FI: elevation			43,153 (12026) ***	29.26 (10.19) **				
FI: longitude		44.45 (19.25) *	− 18,909 (6167) **					− 25.01 (11.52) *
FI: latitude		− 154.47 (23.45) ***	67,268 (8434) ***	14.61 (6.72) *				
Model fit ▼								
Residual standard error	341.4	324.5	10,350	0.75	0.31	14.35	132.8	207.7
R-squared	0.85	0.84	0.31	0.27	0.17	0.16	0.08	0.02
AIC model	10,913.19	10,826.24	19,512.46	8882.77	395.77	6141.62	9494.42	7936.39
AIC null model	12,280.84	12,212.15	19,771.98	9101.12	524.99	6256.30	9552.35	7943.53

Fig. 1 Examples of forest-dominated and non-dominated landscapes, where pre-existing patch coalescence and new patch proliferation were respectively observed

adjacencies. Further, the increase in effective mesh size following forest cover increase was higher the higher the longitude and latitude (Fig. 4 a and b, Appendix 2, respectively). Contrarily, the increase in the forest total edge in relation to forest cover increase was higher the lower the longitude and latitude (Fig. 4 c and d, Appendix 2, respectively). The increase in the number of forest patches following that in forest cover was higher the lower the latitude (Fig. 4e, Appendix 2).

Finally, elevation showed a positive association with the increase in the forest total edge, but negative with that in the Shannon diversity index. The increase in both forest total edge and in the number of forest patches following that in forest cover was highest between 500 and 1000 m above sea level (Fig. 5a, b; Appendix 2).

4 Discussion

Our results confirm our first hypothesis that European landscapes experiencing forest recovery in the last decades also exhibit a significant decrease in their land cover diversity, and an increase

in both forest defragmentation and connectivity. However, not all these changes are directly attributable to forest increase, as our models show that some of them were only concurrent with it. This is the case of land cover diversity, which decreases in landscapes where the forest increased, yet this decrease is not associated with forest increase or even to forest cover as suggested in previous regional-scale studies (e.g. Marull et al. 2015; Otero et al. 2015). Instead, we observe a significant effect of other land cover categories, namely cropland and scrub-grassland, on the land cover diversity of these landscapes. This striking result brings some additional dimensions to the complex debate about the conservation of agroforestry mosaics, considered as biodiversity hotspots in Europe and especially threatened by afforestation (Marull et al. 2015; Otero et al. 2015). Positive association with cropland cover suggests that forest recovery leads to higher landscape diversity in cropland-dominated landscapes that often result from agricultural intensification (Perfecto and Vandermeer 2010; Otero et al. 2015). In contrast, its negative association with scrub and grassland cover, frequently originated from crop and pasture abandonment, might indicate that forest increase is especially detrimental for landscape diversity where traditional

Fig. 2 Distribution of the study landscapes classified as patch coalescence (effective mesh size increase over the median of the sample while number of forest patches under the median of the sample), patch

proliferation (effective mesh size increase under the median of the sample while number of forest patches over the median of the sample) and both patch coalescence and proliferation (the remaining landscapes)

agroforestry mosaics have been abandoned (Otero et al. 2015). Concerning environmental drivers, changes in land cover diversity were also associated with elevation and latitude. Negative association with elevation might be related to the already known deep transformation of lowland landscapes, in which urban sprawl and road construction might substantially increase land cover diversity (Falcucci et al. 2007; Baśnou et al. 2013). Positive association with latitude might be due to the inverse

latitudinal gradient in land cover diversity (r -Spearman = -0.21 , $p < 0.001$): i.e. forest gain might increase land cover diversity more in the less diverse northern landscapes than in the southern ones.

Results regarding the effects of forest increase on changes in forest attributes suggest the coexistence of contrasting landscape processes on forest spatial pattern. On the one hand, forest gain determines a significant increase in both forest

largest patch and effective mesh size, which are mostly related to the growth and coalescence of pre-existing forest patches indicative of forest defragmentation. On the other hand, forest recovery also determines an increase in the number of forest patches and in total forest edge. These results might be viewed, paradoxically, indicative of forest fragmentation due to small patch proliferation, as edge per area unit increases more rapidly with new small isolated patches than with the growth of old big patches. Fahrig (2003) described a similar paradoxical situation regarding the opposite case of habitat loss, which might determine both habitat fragmentation and defragmentation depending on the spatial loss pattern (i.e. the loss and fragmentation of big versus small or nearby versus far habitat patches). The coexistence of these landscape patterns is probably the reason that there are non-significant changes in mean patch size associated with forest increase across Europe.

Our study also demonstrates that these landscape changes associated with forest increase depend on the original landscape composition (especially forest, but also cropland cover) and on a set of geographic and topographic variables. The first point illustrates the above-mentioned dichotomy of pre-existing patch growth and coalescence versus new patch proliferation associated with forest increase (Fig. 1). Thus, this last mostly determines patch growth and coalescence in forest-dominated (> 50% of forest cover) landscapes, but new patch proliferation in non-forest-dominated ones. Regarding the second point, our study shows the existence of significant geographic gradients in landscape change due to afforestation. While defragmentation (i.e. forest patch growth and coalescence) is especially concentrated northwards, new patch proliferation (indicated by increasing the patch number and, secondarily, by total edge) particularly affects the lowest latitudes (see Fig. 2). This pattern is probably due to a combination of climate and human land-use legacy, since new forests mostly are originated from old pastures and wet grasslands in northern landscapes with colder climates while they come mostly from croplands in the rest of the landscapes (M. Palmero-Iniesta, unpublished results). Moreover, pre-existing patch growth and coalescence concentrate eastwards where the landscape matrix is a forest-cropland mosaic, while the new patch proliferation is especially important in the western boundary where landscapes are especially affected by intense urbanization and fragmentation by infrastructures (Jongman 2002; Jaeger et al. 2016). Still, the study indicates that forest increase especially determines the new patch proliferation (as indicated by the increase in the total edge and in the number of patches; Fig. 5, Appendix 2) in medium elevations, probably because of a concentration of crop abandonment in uplands as suggested in previous works (Basnou et al. 2013; Cervera et al. 2019).

These results are, in turn, relevant for improving the strategies of forest biodiversity conservation, as they put in value the importance of considering the original composition of landscape and the socio-environmental context. Yet, the spatial arrangement of these new forests may influence forest resilience by increasing

the functional diversity of tree species and by modifying the connectivity, centrality and modularity of forest landscapes (Messier et al. 2019). Forest defragmentation in already highly forested landscapes will clearly promote the recovery of forest specialist species commonly occupying large and connected forest areas and often of large conservation concern (e.g. Saura and Pascual-Hortal 2007; Gil-Tena et al. 2013; Deinet et al. 2017), and this will help to reconnect both the existing populations and potential habitats, particularly in Northern and Eastern Europe and in main mountain ranges, thus reinforcing the ecological network of protected areas in Europe (EEA 2012). In contrast, the proliferation of new forest patches in lowland, highly anthropized landscapes in Southern and Western Europe might favour forest generalist species that commonly have less conservation concern, and even non-forest and alien species (Guirado et al. 2006; Basnou et al. 2015; Regos et al. 2016; Liebhold et al. 2017). Conversely, the new patch proliferation observed southwards and westwards suggests an increase in functional connectivity among forests (e.g. seed dispersal potential) and may facilitate migration and gene flow among tree populations in response to climate change (Breed et al. 2011) while, at the same time, preventing, especially in the south, the danger of the coalescence of large forest areas in light of the propagation of extreme wildfires (Bowen et al. 2007). Moreover, the new habitat availability may be especially relevant in Southern Europe, as habitat loss and fragmentation effects on species density and/or diversity is greatest in areas with high maximum temperatures and in areas where average rainfall has decreased more over time (see Mantyka-Pringle et al. 2012).

5 Conclusion

To sum up, our study shows that forest recovery in Europe is guessed by landscape changes in recently afforested landscapes. However, these changes are more complex than expected and they cannot be solely attributable to forest increase, but also to the original landscape composition and position across elevational and geographical gradients across the mainland.

Results may be especially relevant for the preservation of forest biodiversity and ecosystem services since they highlight the importance of the landscape context on the new forest spatial distribution pattern including forest fragmentation and connectivity and landscape diversity. Specific management policies might help to redirect these trends by designing both large forest recovery and priority connection areas in order to ensure large patch coalescence yet combined with prevention plans to avoid the deleterious effects of forest continuity in some of these regions (e.g. wildfires in Southern Europe; Duane et al. 2016).

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Data availability The datasets generated during and/or analysed during the current study are available in the Mendeley repository, <https://doi.org/10.17632/hwntrn78vc.1>

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix 1

Table 3 Summary of the composition of the 752 study landscapes randomly selected across Europe

Forest (%)	Agriculture (%)	Agroforestry mosaics (%)	Grassland (%)	Settlement (%)
Min., 0.00	Min., 0.00	Min., 0.00	Min., 0.00	Min., 0.00
1st Qu., 2.99	1st Qu., 1.64	1st Qu., 0.72	1st Qu., 0.00	1st Qu., 0.00
Median, 26.49	Median, 25.99	Median, 5.49	Median, 0.41	Median, 0.00
Mean, 37.03	Mean, 37.35	Mean, 9.32	Mean, 6.18	Mean, 0.85
3rd Qu., 68.75	3rd Qu., 70.97	3rd Qu., 14.99	3rd Qu., 5.28	3rd Qu., 0.21
Max., 100.00	Max., 100.00	Max., 86.30	Max., 93.63	Max., 60.78
Wetland (%)	Sparse vegetation (%)	Shrubland (%)	Bare area (%)	Water (%)
Min., 0.00	Min., 0.00	Min., 0.00	Min., 0.00	Min., 0.00
1st Qu., 0.00	1st Qu., 0.00	1st Qu., 0.00	1st Qu., 0.00	1st Qu., 0.00
Median, 0.00	Median, 0.00	Median, 0.00	Median, 0.00	Median, 0.00
Mean, 2.76	Mean, 1.17	Mean, 0.52	Mean, 0.31	Mean, 2.46
3rd Qu., 0.21	3rd Qu., 0.00	3rd Qu., 0.00	3rd Qu., 0.00	3rd Qu., 0.62
Max., 76.65	Max., 54.27	Max., 71.88	Max., 30.38	Max., 98.76

Table 4 Correlation matrix with a Spearman rank (r) for the landscape covariates used in the general lineal models

	Forest increase (ha)	Forest cover (%)	Crop cover (%)	Shrub/grassland cover (%)	Elevation (m)	Long. (°)	Lat. (°)
Forest increase (ha)	1.00						
Forest cover (%)	0.45	1.00					
Cropland cover (%)	−0.35	−0.64	1.00				
Shrub/grass. cover (%)	−0.11	−0.15	−0.31	1.00			
Elevation (m)	−0.15	0.04	−0.14	0.13	1.00		
Longitude (°)	0.23	0.17	−0.09	−0.08	−0.14	1.00	
Latitude (°)	0.37	0.46	−0.38	0.03	−0.52	0.43	1.00

Table 5 Components of the plausible models ($\Delta < 2$) after model selection for the general lineal models performed for each landscape metric. Factor code: crop cover (1), forest cover (2), forest increase = FI (3), latitude (4), longitude (5), elevation (6), grassland/shrubland cover (7), crop cover: FI (8), forest cover: FI (9), latitude: FI (10), longitude: FI (11), elevation: FI (12), grassland/shrubland cover: FI (13)

Component models:	df	logLik	AICc	Delta	Weight
Largest patch size					
2/3/9	5	-5451.56	10,913.19	0.00	0.07
2/3/5/9	6	-5451.10	10,914.32	1.13	0.04
1/2/3/8/9	7	-5450.27	10,914.69	1.50	0.03
2/3/4/9	6	-5451.39	10,914.90	1.71	0.03
2/3/6/9	6	-5451.51	10,915.13	1.93	0.03
Effective mesh size					
2/3/4/5/9/10/11	9	-5404.00	10,826.24	0.00	0.17
1/2/3/4/5/9/10/11	10	-5403.53	10,827.36	1.12	0.10
1/2/3/4/5/8/9/10/11	11	-5402.68	10,827.72	1.48	0.08
2/3/4/5/7/9/10/11	10	-5403.81	10,827.92	1.68	0.07
Mean patch area					
2/3/5/9	6	-4741.15	9494.42	0.00	0.07
2/3/5/9/11	7	-4740.55	9495.25	0.83	0.05
1/2/3/5/9	7	-4740.87	9495.90	1.48	0.03
1/2/3/5/8/9	8	-4739.91	9496.00	1.58	0.03
2/3/5/7/9	7	-4741.01	9496.16	1.74	0.03
2/3/4/5/9	7	-4741.04	9496.23	1.81	0.03
2/3/5/7/9/13	8	-4740.07	9496.34	1.92	0.03
Total edge					
2/3/4/5/6/9/10/11/12	11	-9742.98	19,512.46	0.00	0.27
2/3/4/5/6/7/9/10/11/12	12	-9745.46	19,513.27	0.81	0.18
1/2/3/4/5/6/9/10/11/12	12	-9744.88	19,514.19	1.73	0.11
1/2/3/4/5/6/7/8/9/10/11/12	14	-9742.88	19,514.34	1.88	0.11
Number of patches					
1/2/3/4/5/6/7/9/10/12	12	-4429.17	8882.77	0.00	0.14
1/2/3/5/6/7/9/12	10	-4431.64	8883.58	0.80	0.10
1/2/3/5/6/7/8/9/12	11	-4431.12	8884.60	1.83	0.06
1/2/3/4/5/6/7/8/9/10/12	13	-4429.10	8884.68	1.91	0.06
Euclidean nearest neighbour distance					
3/5/11	5	-3963.14	7936.39	0.00	0.04
1/3/5/11	6	-3962.37	7936.88	0.50	0.03
5	3	-3965.51	7937.06	0.67	0.03
1/3/4/5/11	7	-3961.59	7937.38	0.99	0.02
1/5	4	-3964.71	7937.50	1.11	0.02
3/4/5/11	6	-3962.80	7937.75	1.36	0.02
2/3/5/11	6	-3962.89	7937.92	1.54	0.02
1/4/5	5	-3964.01	7938.13	1.74	0.02
3/5/6/11	6	-3963.06	7938.26	1.87	0.01
Percentage of like-adjacencies					
1/3/4/5/7/8	8	-3062.71	6141.62	0.00	0.05
1/3/4/5/6/7/8/12	10	-3060.87	6142.04	0.42	0.04
1/3/4/5/7/8/10	9	-3062.22	6142.69	1.07	0.03
1/2/3/4/5/7/8	9	-3062.27	6142.78	1.16	0.03
1/3/4/5/7/8/13	9	-3062.34	6142.91	1.30	0.03
1/3/4/5/6/7/8/12/13	11	-3060.48	6143.32	1.70	0.02
1/2/3/4/5/6/7/8/12	11	-3060.53	6143.42	1.80	0.02
1/3/4/5/7/8/11	9	-3062.60	6143.45	1.83	0.02
1/3/4/5/6/7/8	9	-3062.65	6143.55	1.93	0.02
1/3/4/6/7/8/12	9	-3062.66	6143.56	1.94	0.02
Shannon diversity index					
1/4/6/7	6	-191.83	395.77	0.00	0.07
1/3/4/6/7	7	-191.51	397.17	1.40	0.03
1/2/4/6/7	7	-191.75	397.65	1.89	0.03
1/3/4/6/7/8	8	-190.75	397.70	1.93	0.03
1/4/5/6/7	7	-191.80	397.74	1.98	0.02

Table 6 Results of the relative variable importance from the *model.avg* function of the MuMin package (Barton and Barton 2019) for model selection for the general lineal models performed for each landscape metric. Variables are marked with asterisks in the selected model. Variables code: crop cover (1), forest cover (2), forest increase = FI (3), latitude (4), longitude (5), elevation (6), grassland/shrubland cover (7), crop cover: FI (8), forest cover: FI (9), latitude: FI (10), longitude: FI (11), elevation: FI (12), grassland/shrubland cover: FI (13)

Variable code:	1	2	3	4	5	6	7	8	9	10	11	12	13
Largest patch size model													
Importance:	0.49	1.00*	1.00*	0.39*	0.43*	0.38	0.38	0.30	1.00*	0.15	0.13	0.12	0.15
Containing models:	518	518*	729*	518*	518*	518	518	248	234*	243	243	243	243
Effective mesh size model													
Importance:	0.48	1.00	1.00	1.00	0.96	0.35	0.36	0.21	1.00*	1.00*	0.82*	0.11	0.11
Containing models:	518	518	729	518	518	518	518	243	243*	243*	243*	243	243
Mean patch area model													
Importance:	0.45	1.00*	1.00*	0.36	0.94*	0.40	0.41	0.19	1.00*	0.11	0.35	0.18	0.18
Containing models:	518	518*	729*	518	518*	518	518	243	243*	243	243	243	243
Total edge model													
Importance:	0.69*	1.00*	1.00*	1.00*	1.00*	0.99*	0.65*	0.20	1.00*	1.00*	0.98*	0.99*	0.17
Containing models:	518*	518*	729*	518*	518*	518*	518*	243	243*	243*	243*	243*	243
Number of patches model													
Importance:	1.00*	1.00*	1.00*	0.56*	1.00*	0.98*	1.00*	0.32	1.00*	0.39*	0.30	0.84*	0.30
Containing models:	518*	518*	729*	518*	518*	518*	518*	243	243*	243*	243	243*	243
Euclidean nearest neighbour distance model													
Importance:	0.56	0.37	0.76*	0.47	0.97*	0.35	0.34	0.14	0.09	0.11	0.57*	0.08	0.07
Containing models:	518	518	729*	518	518*	518	518	243	243	243	243*	243	243
Percentage of like adjacencies model													
Importance:	1.00*	0.53	1.00*	1.00*	0.78*	0.53	0.84*	0.94*	0.18	0.37	0.24	0.34	0.29
Containing models:	518*	518	729*	518*	518*	518	518*	243*	243	243	243	243	243
Shannon diversity index model													
Importance:	0.98*	0.42	0.82	1.00*	0.44	0.96*	0.83*	0.30	0.11	0.24	0.24	0.27	0.30
Containing models:	518*	518	729	518*	518	518*	518*	243	243	243	243	243	243

Appendix 2

Fig. 3 Association of forest increase between 1990 and 2012 with the increase in forest largest patch size (a), forest effective mesh size (b), forest total edge (c) and the number of forest patches (d) in the study landscapes, for two ranges of forest cover percentage (a, b, c, d) and cropland cover (e)

Fig. 4 Association of forest increase between 1990 and 2012 in the study landscapes with their increase in forest effective mesh size (a, b), in forest total edge (c, d) and number of forest patches (e) for diverse latitude and longitude ranges

Fig. 5 Association of forest increase between 1990 and 2012 in the study landscapes with their increase in forest total edge (a) and in the number of forest patches increase (b) for diverse elevation ranges

References

- Barton K, Barton MK (2019) Package “MuMIn.” Multi-model inference version 1
- Basnou C, Álvarez E, Bagaria G et al (2013) Spatial patterns of land use changes across a Mediterranean metropolitan landscape: implications for biodiversity management. *Environ Manag* 52:971–980. <https://doi.org/10.1007/s00267-013-0150-5>
- Basnou C, Iguzquiza J, Pino J (2015) Examining the role of landscape structure and dynamics in alien plant invasion from urban Mediterranean coastal habitats. *Landscape Urban Plan* 136:156–164. <https://doi.org/10.1016/j.landurbplan.2014.12.001>
- Boulmier T, Nichols JD, Hines JE et al (2001) Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology* 82: 1159–1169. [https://doi.org/10.1890/0012-9658\(2001\)082\[1159:FFABCD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[1159:FFABCD]2.0.CO;2)
- Bowen ME, McAlpine CA, House APN, Smith GC (2007) Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. *Biol Conserv* 140:273–296. <https://doi.org/10.1016/j.biocon.2007.08.012>
- Breed MF, Ottewell KM, Gardner MG, Lowe AJ (2011) Clarifying climate change adaptation responses for scattered trees in modified landscapes. *J Appl Ecol* 48:637–641. <https://doi.org/10.1111/j.1365-2664.2011.01969.x>
- Cervera T, Pino J, Marull J, Padró R, Tello E (2019) Understanding the long-term dynamics of forest transition: from deforestation to afforestation in a Mediterranean landscape (Catalonia, 1868–2005). *Land Use Policy* 80:318–331
- Crawley MJ (2007) The R book. In: The R book. John Wiley & Sons, Ltd, pp 1–942
- Debinski DM, Holt RD (2005) Review: A survey and overview of habitat fragmentation experiments. *Conserv Biol* 14:342–355
- Deinet S, Ieronymidou C, McRae L et al (2017) Wildlife comeback in Europe: the recovery of selected mammal and bird species. Final rep to Rewilding Eur by ZSL. BirdLife Int Eur Bird Census Counc London, UK ZSL
- Diogo V, Koomen E (2016) Land cover and land use indicators: review of available data. OECD Green Growth Pap No 2016/03, OECD Publ Paris. <https://doi.org/10.1787/5jlr2z86r5xw-en>
- Duane A, Aquilué N, Gil-Tena A, Brotons L (2016) Integrating fire spread patterns in fire modelling at landscape scale. *Environ Model Softw* 86:219–231. <https://doi.org/10.1016/j.envsoft.2016.10.001>
- EEA (2016a) Environmental indicator. EEA Report 30/2016. European Environment Agency, Copenhagen, Denmark, 60 pp.
- EEA (2016b) European forest ecosystems: state and trends. EEA Report 30/2016. European Environment Agency, Copenhagen, Denmark, 128 pp.
- EEA (2012) Protected areas in Europe - an overview. EEA Report No 5/2012. European Environment Agency, Copenhagen, Denmark, 130 pp.
- Eggleston HS, Buendia L, Miwa K, et al (2006) 2006 IPCC - guidelines for national greenhouse gas inventories. Japan
- ESA (2017) CCI land cover product user guide version 2.0. available at: http://maps.elie.ucl.ac.be/CCI/viewer/download/ESACCI-LC-Ph2-PUGv2_2.0.pdf, last access: 10 November 2019
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Annu Rev Ecol Evol Syst* 34:487–515. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132419>
- Fahrig L (2017) Ecological responses to habitat fragmentation per se. *Annu Rev Ecol Evol Syst* 48:1–23. <https://doi.org/10.1146/annurev-ecolsys-110316-022612>
- Faluccia A, Maiorano L, Boitani L (2007) Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landscape Ecol* 22:617–631. <https://doi.org/10.1007/s10980-006-9056-4>
- Fernandes MR, Aguiar FC, Ferreira MT (2011) Assessing riparian vegetation structure and the influence of land use using landscape metrics and geostatistical tools. *Landscape Urban Plan* 99:166–177. <https://doi.org/10.1016/j.landurbplan.2010.11.001>
- Gerard F, Petit S, Smith G et al (2010) Land cover change in Europe between 1950 and 2000 determined employing aerial photography. *Prog Phys Geogr* 34:183–205. <https://doi.org/10.1177/0309133309360141>
- Geri F, Rocchini D, Chiarucci A (2010) Landscape metrics and topographical determinants of large-scale forest dynamics in a Mediterranean landscape. *Landscape Urban Plan* 95:46–53. <https://doi.org/10.1016/j.landurbplan.2009.12.001>
- Gil-Tena A, Brotons L, Fortin MJ, Burel F, Saura S (2013) Assessing the role of landscape connectivity in recent woodpecker range expansion in Mediterranean Europe: Forest management implications. *Eur J For Res* 132:181–194. <https://doi.org/10.1007/s10342-012-0666-x>
- Gotelli NJ, Graves GR (1996) Null models in ecology, Smithsonian
- Guirado M, Pino J, Rodà F (2006) Understorey plant species richness and composition in metropolitan forest archipelagos: effects of forest size, adjacent land use and distance to the edge. *Glob Ecol Biogeogr* 15:50–62. <https://doi.org/10.1111/j.1466-822X.2006.00197.x>
- Guirado M, Pino J, Rodà F (2007) Comparing the role of site disturbance and landscape properties on understory species richness in fragmented periurban Mediterranean forests. *Landscape Ecol* 22:117–129. <https://doi.org/10.1007/s10980-006-9009-y>
- Hansen MC, Potapov PV, Moore R et al (2013) High-resolution global maps of 21st-century forest cover. *Change* 850:850–854. <https://doi.org/10.1126/science.1244693>
- Heilman GE, Strittholt JR, Slosser NC, DellaSala DA (2002) Forest fragmentation of the conterminous United States: assessing forest intactness through road density and spatial characteristics. *BioScience* 52: 411–422
- Hesselbarth MHK, Sciaini M, With KA, et al (2019) Landscapemetrics : an open-source R tool to calculate landscape metrics. *Ecography (Cop)* 1–10. doi: <https://doi.org/10.1111/ecog.04617>
- IGN (2019) Cartografía general del mundo y Europa del Instituto Geográfico Nacional. Atlas Nac. España <http://atlasnacional.ign.es>
- Jaeger JAG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecol* 15:115–130
- Jaeger JAG, Soukup T, Schwick C et al (2016) Landscape fragmentation in Europe. *Eur Landscape Dyn L Cover data*:157–198
- Jongman RHG (2002) Homogenisation and fragmentation of the European landscape: ecological consequences and solutions. *Landscape Urban Plan* 58:211–221. [https://doi.org/10.1016/S0169-2046\(01\)00222-5](https://doi.org/10.1016/S0169-2046(01)00222-5)
- Kim DH, Sexton JO, Noojipady P et al (2014) Global, Landsat-based forest-cover change from 1990 to 2000. *Remote Sens Environ* 155:178–193. <https://doi.org/10.1016/j.rse.2014.08.017>
- Kupfer JA (2012) Landscape ecology and biogeography: rethinking landscape metrics in a post-FRAGSTATS landscape. *Prog Phys Geogr* 36:400–420. <https://doi.org/10.1177/0309133312439594>
- Liebold AM, Brockerhoff EG, Kalisz S et al (2017) Biological invasions in forest ecosystems. *Biol Invasions* 19:3437–3458. <https://doi.org/10.1007/s10530-017-1458-5>
- Mantyka-Pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: a systematic review and meta-analysis. *Glob Chang Biol* 18:1239–1252. <https://doi.org/10.1111/j.1365-2486.2011.02593.x>
- Marull J, Otero I, Stefanescu C, Tello E, Miralles M, Coll F, Pons M, Diana GL (2015) Exploring the links between forest transition and landscape changes in the Mediterranean. Does forest recovery really

- lead to better landscape quality? *Agrofor Syst* 89:705–719. <https://doi.org/10.1007/s10457-015-9808-8>
- Mazzoleni S, di Pasquale G, Mulligan M et al (2004) Recent dynamics of the Mediterranean vegetation and landscape. John Wiley & Sons
- McGarigal K, Marks BJ (1994) FRAGSTATS: spatial pattern analysis program for quantifying landscapes structure. Gen tech rep PNW-GTR-351 US Dep Agric for Serv Pacific northwest Res Station Portland, OR 97331:134. [https://doi.org/10.1061/\(ASCE\)0733-9437\(2005\)131:1\(94\)CE](https://doi.org/10.1061/(ASCE)0733-9437(2005)131:1(94)CE)
- Melero Y, Stefanescu C, Pino J (2016) General declines in Mediterranean butterflies over the last two decades are modulated by species traits. *Biol Conserv* 201:336–342. <https://doi.org/10.1016/j.biocon.2016.07.029>
- Messier C, Bauhus J, Doyon F, Maure F, Sousa-Silva R, Nolet P, Mina M, Aquilué N, Fortin MJ, Puettmann K (2019) The functional complex network approach to foster forest resilience to global changes. *For Ecosyst* 6:1–16. <https://doi.org/10.1186/s40663-019-0166-2>
- Metzger MJ, Bunce RG, Jongman RHG et al (2005) A climatic stratification of the environment of Europe. *Glob Ecol Biogeogr* 14:549–563. <https://doi.org/10.1111/j.1466-822X.2005.00190.x>
- Meyfroidt P, Lambin EF (2011) Global forest transition: prospects for an end to deforestation. *Annu Rev Environ Resour* 36:343–371. <https://doi.org/10.1146/annurev-environ-090710-143732>
- Nagendra H, Reyers B, Lavorel S (2013) Impacts of land change on biodiversity: making the link to ecosystem services. *Curr Opin Environ Sustain* 5:503–508. <https://doi.org/10.1016/j.cosust.2013.05.010>
- Otero I, Marull J, Tello E et al (2015) Land abandonment, landscape, and biodiversity: questioning the restorative character of the forest transition in the Mediterranean. *Ecol Soc* 20. <https://doi.org/10.5751/ES-07378-200207>
- Pagnutti C, Bauch CT, Anand M (2013) Outlook on a worldwide forest transition. *PLoS One* 8. <https://doi.org/10.1371/journal.pone.0075890>
- Palmero M, Espelta JM, Gordillo J, Pino J (2020) Changes in forest landscape patterns resulting from recent afforestation in Europe (1990–2012): defragmentation of pre-existing forest versus new patch proliferation. *Mendeley Data*, V2, <https://doi.org/10.17632/hwntrn78vc.2>
- Perfecto I, Vandermeer J (2010) The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proc Natl Acad Sci U S A* 107:5786–5791. <https://doi.org/10.1073/pnas.0905455107>
- Perlin J, Journey AF (1989) The role of wood in the development of civilization
- Plieninger T, Gaertner M, Hui C, Huntsinger L (2013) Does land abandonment decrease species richness and abundance of plants and animals in Mediterranean pastures, arable lands and permanent croplands? *Environ Evid*:1–7
- R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>
- Ramage BS, Kitzes J, Marshalek EC, Potts MD (2013) Optimized floating refugia: a new strategy for species conservation in production forest landscapes. *Biodivers Conserv* 22:789–801. <https://doi.org/10.1007/s10531-013-0453-0>
- Regos A, Domínguez J, Gil-Tena A, Brotons L, Ninyerola M, Pons X (2016) Rural abandoned landscapes and bird assemblages: winners and losers in the rewinding of a marginal mountain area (NW Spain). *Reg Environ Chang* 16:199–211. <https://doi.org/10.1007/s10113-014-0740-7>
- Rudel TK, Coomes OT, Moran E et al (2005) Forest transitions: towards a global understanding of land use change. *Glob Environ Chang* 15: 23–31. <https://doi.org/10.1016/j.gloenvcha.2004.11.001>
- Rudel TK, Defries R, Asner GP, Laurance WF (2009) Changing drivers of deforestation and new opportunities for conservation. *Conserv Biol* 23:1396–1405. <https://doi.org/10.1111/j.1523-1739.2009.01332.x>
- Saunders DA, Hobbs RJ, Margules CR (1999) Biological consequences of ecosystem fragmentation: a review. *NCASI Tech Bull* 2:469–470
- Saura S, Pascual-Hortal L (2007) A new habitat availability index to integrate connectivity in landscape conservation planning: comparison with existing indices and application to a case study. *Landscape Urban Plan* 83:91–103. <https://doi.org/10.1016/j.landurbplan.2007.03.005>
- Turner MG (2005) Landscape ecology: what is the state of the science? *Annu Rev Ecol Evol Syst* 36:319–344. <https://doi.org/10.1146/annurev.ecolsys.36.102003.152614>
- Turner MG (1989) Landscape ecology: the effect of pattern on process. *Annu Rev Ecol Syst* Vol 20
- Vellend M, Verheyen K, Flinn KM et al (2007) Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. *J Ecol* 95:565–573. <https://doi.org/10.1111/j.1365-2745.2007.01233.x>
- Weng YC (2007) Spatiotemporal changes of landscape pattern in response to urbanization. *Landscape Urban Plan* 81:341–353. <https://doi.org/10.1016/j.landurbplan.2007.01.009>

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