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Combining climate, land use change and dispersal to predict the distribution of endangered species with limited vagility

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Abstract

Aim: Many rare species are dispersal-limited; their colonization capacity can be impacted by land use and climate changes. Most ecological niche models predict the distribution of species under future climate and land use change scenarios without incorporating species-specific dispersal abilities. Here we investigate the effect of climate and land use change on low vagile species accounting for their dispersal capacity and define accessible areas in the future.

Location: Europe.

Taxon: Saproxylic beetles.

Methods: We used the current (2007–2012) occurrences of six endangered saproxylics to develop ecological niche models using current climate and land use conditions. We projected species distributions under four future climate and land use change scenarios to estimate their potential occurrences. Finally, accounting for species-specific dispersal, we limited their distributions to accessible areas in 2040–2050.

Results: Without accounting for dispersal abilities we found a strong and positive impact of climate change on the distribution of *Cerambyx cerdo*, *Cucujus cinnaberinus*, *Morimus funereus* and *Rosalia alpina* and a positive effect of land use change on the distribution of *Lucanus cervus* and *Osmoderma eremita*. When species-specific dispersal was included, we found a strong and positive impact of land use change on the distribution of all the species. In this case climate change had a lower but positive effect on the distribution of *C. cerdo*, *C. cinnaberinus*, *L. cervus* and *R. alpina*, and a negative effect on the distribution of *O. eremita*.

Main conclusion: We found that climate change would promote the expansion of saproxylic beetles only in the unrealistic case of unlimited dispersal. Accounting for dispersal abilities, the expansion of our species would be mainly conditioned by the effect of land use change. Thus, we encourage researchers to combine climate and land use change with dispersal when projecting species distribution under future scenarios to accurately identify areas with fundamental species-specific resources.

KEYWORDS

ecological niche models, future scenarios, global change, macroecology, *n*-dimensional hypervolume, saproxylic beetles, species traits

1 | INTRODUCTION

Many rare species are dispersal limited, exhibiting a low probability of colonizing new sites and establishing viable populations (Baur, 2014). The current and future distributions of these species are highly influenced by human-related environmental change, such as climate and land use change, creating insurmountable barriers to their dispersal across space and time (Jaeschke, Bittner, Reineking, & Beierkuhnlein, 2013). Although both climate and land use change are considered dominant drivers of biodiversity at a global scale (Barbet-Massin, Thuiller, & Jiguet, 2012; Pimm et al., 2014), only the former has been widely used as a predictor for modelling future species distributions (e.g. Markovic et al., 2014; Titeux et al., 2016). Indeed, during the last 25 years, more than 85% of published research in this field explored the impact of future climate change alone on biodiversity (Titeux et al., 2016). Moreover, in the few studies that considered the impact of land use change on species distribution (Milanesi, Breiner, Puopolo, & Holderegger, 2017; Radinger et al., 2016), the combined effect with climate change was rarely investigated (Mantyka-Pringle, Martin, Moffatt, Linke, & Rhodes, 2014; Radinger et al., 2016). As species range shift varies depending on site-specific climate–land use combinations, neglecting the effect of land use change could lead to biased predictions of species distributions under future conditions. Especially, this holds true for species with limited dispersal capacities, for which even minimal land use changes can dramatically impact their colonization capacity (McCauley, Davis, Werner, & Robeson, 2014; Velo-Antón, Parra, Parra-Olea, & Zamudio, 2013).

Actually, the Biotic-Abiotic-Mobility framework ('BAM'; Soberón & Peterson, 2005) highlighted also the importance of species-specific dispersal characteristics in determining species distribution (De Marco, Montemurro, & Cannas, 2011; Nobis & Normand, 2014; Vasudev, Fletcher, Goswami, & Krishnadas, 2015). Incorporating dispersal in ecological niche models (ENMs) improves predictions for current and future species occurrence compared with standard ENMs (Engler & Guisan, 2009; Smolik et al., 2010; Vasudev et al., 2015). However, most studies developing ENMs to predict the distribution of species under future scenarios have not incorporated species-specific dispersal abilities, relying on overly simplistic conceptualizations of dispersal (Franklin, 2010; Peterson et al., 2011).

Taking into account these limitations, in this study we (a) investigated the effect(s) of climate and land use change on species with short-distance dispersal abilities and (b) defined areas that should be accessible to them in the future. We used the current (2007–2012) occurrences of six endangered saproxylic beetles, widely considered to be umbrella species for biodiversity conservation (Bełcik, Goczał, & Ciach, 2019; Buse, Schröder, & Assmann, 2007; Campanaro, Toni, Hadersen, & Grasso, 2011; Ranius, 2002; Russo, Cistrone, & Garonna, 2011; Solano et al., 2013), to develop ENMs using current climate and land use conditions. We then projected the distributions of our target species under future scenarios to estimate species

potential occurrences in the years 2040–2050 (based on four different climate and land use change scenarios). Finally, taking into account the species-specific dispersal abilities of our target species, we limited their distributions in 2040–2050 to areas accessible to them across Europe.

2 | MATERIALS AND METHODS

2.1 | Study area and species data

Our study area consisted of all continental European countries (excluding Belarus, Moldova, Russia and Ukraine because of the lack of data in national biodiversity repository servers and in other official archives; Figure 1). The study area ranges from 0 to 4,810 m a.s.l., and is characterized by forests (33.3% of the total area), croplands (32.4%), shrub lands (11.5%) and, to a lesser extent, grasslands (7.8%) and human settlements (4%).

We selected six threatened species of saproxylic beetles (of the 21 saproxylic beetles species listed in the EU habitat directive), namely, *Cerambyx cerdo*, *Cucujus cinnaberinus*, *Lucanus cervus*, *Morimus funereus*, *Osmoderma eremita* and *Rosalia alpina*, for which information on observed dispersal distances was available in literature (Table S1).

We obtained species occurrence data for the period 2007–2012 from (a) the European Environment Information and Observation NETwork (EIONET, 2013) Central Data Repository server (<http://cdr.eionet.europa.eu/>), (b) the Swiss Biological Records Center (<http://lepus.unine.ch/carto/>) and (c) the Norwegian Taxonomy Initiative (<http://www.biodiversity.no/>). All species occurrences were resampled at the same spatial resolution of EIONET data (10 × 10 km grid cell size; Figure 1), resulting in a total of 4,310 cells for *C. cerdo*, 3,561 for *C. cinnaberinus*, 11,535 for *L. cervus*, 2,211 for *M. funereus*, 5,248 for *O. eremita* and 2,628 for *R. alpina*. We tested for overestimation of saproxylic species occurrences calculating a modified version of the Multivariate Environmental Similarity Surface (Milanesi, Herrando, Pla, Villero, & Keller, 2017). We find consistent results (Figures S1–S6) and, thus, we included all data collected in the further analysis.

2.2 | Species ecological requirement

The species considered in this study (Table S1) are highly susceptible to both climate and land use changes (Gough et al., 2015). In fact, being highly specialized wood-living beetles, their survival is, above all, linked to the availability of suitable forest habitat. As such, their ability to respond to climate change is mainly influenced by habitat degradation (Ball-Damerow, M'Gonigle, & Resh, 2014; Filz, Wiemers, Herrig, Weitzel, & Schmitt, 2013). Moreover, the study species are characterized by low dispersal distances (Schiegg, 2000), and inhabit most of the European deciduous old-growth forests currently threatened by large-scale human

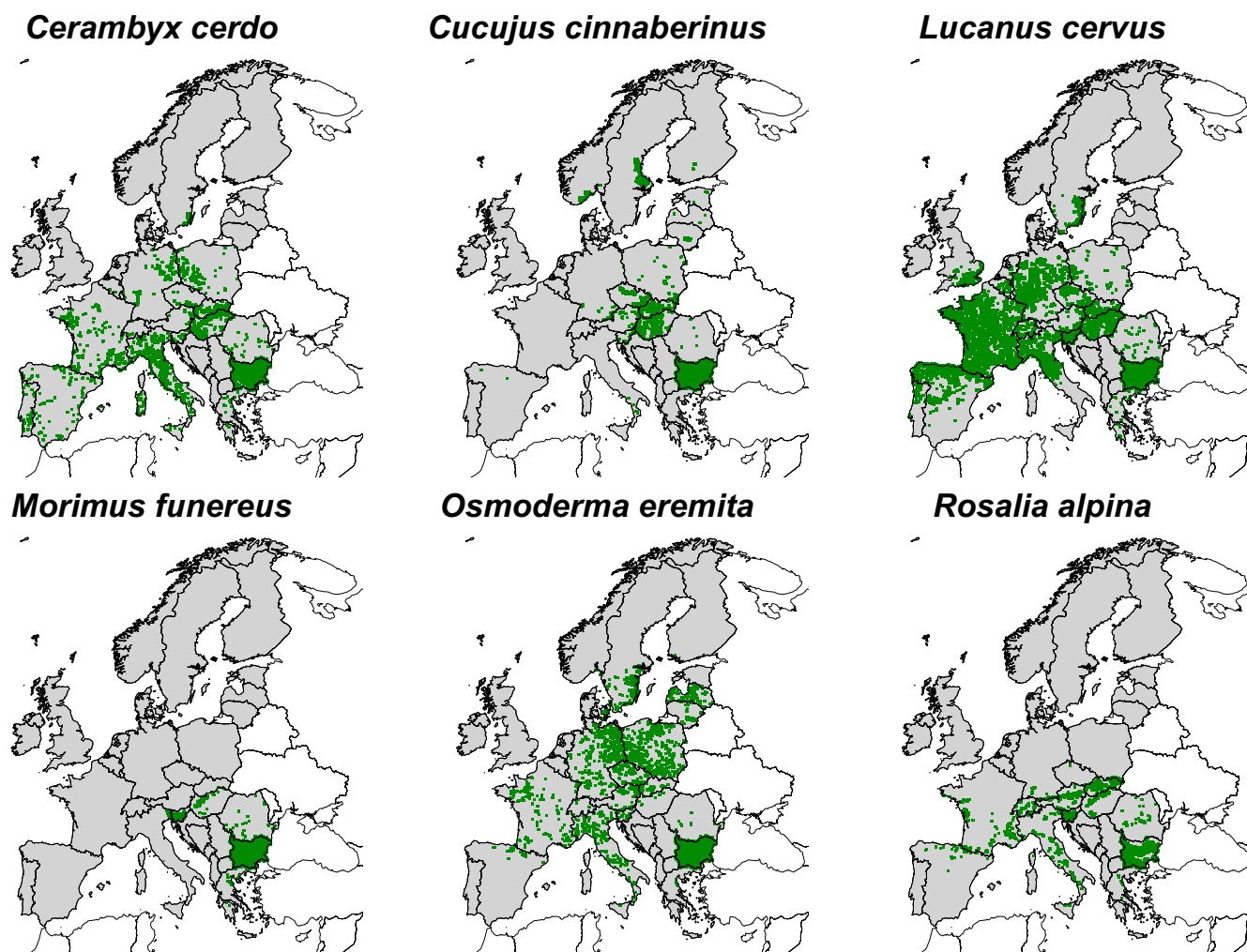


FIGURE 1 Study area (in grey) and current species ranges, according to European Environment Information and Observation Network (EIONET) Central Data Repository server, Swiss Biological Records Center and Norwegian Taxonomy Initiative, of the six saproxylic species considered (in green) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jbi.13804)]

disturbance (Stokland, Siitonen, & Jonsson, 2012; Wirth, Messier, Bergeron, Frank, & Fankhänel, 2009).

Cerambyx cerdo is widespread in most parts of Europe, but more common in the Mediterranean regions, generally associated with oak forests consisting of mature or partially dead, and sun-exposed trees (Sama, 1988). This species occurs in semi-open forest patches of lowland and hilly forests (Redolfi de Zan et al., 2017).

Cucujus cinnaberinus is a poorly known species (Horák, 2011) limited to Europe, scattered, distributed throughout the continent, probably because of past population decline and local extinctions (Horák & Chobot, 2009; Horák, Vávrová, & Chobot, 2010). This species live under the bark of dead tree trunks (Horák, Chobot, Kohutka, & Gebauer, 2008) in lowland poplars and willows forests or partially mixed mountain forests (e.g. Horák et al., 2010).

Lucanus cervus is widely spread across Europe and is associated with mature deciduous forests. It can be found especially in lowland and medium-altitude oak woodlands, where the saproxylic larvae feed on rotten deadwood at ground level (Campanaro et al., 2011). This species may also be common in urban habitats (e.g. city parks,

private gardens; Harvey, Gange, Hawes, & Rink, 2011; Hawes, 2008).

Morimus funereus inhabits mature beech, poplar and oak forests (Sama, 2009) within a relatively narrow geographical zone in south-eastern Europe (Carpaneto et al., 2015; Jurc, Ogris, Pavlin, & Borkovic, 2008). Even though their preferred habitats are mature forests, populations of this species often occur in coppiced stands, characterised by old stumps and decaying wood on the ground (Hardersen et al., 2017).

Osmoderma eremita is a genus that includes many species. Based on genetic studies (Audisio et al., 2007, 2009), there is now consensus that *O. eremita* is just one of four species occurring in Europe. However, in our analysis, we considered all these species as belonging to *O. eremita*. It is generally associated with hollow veteran trees (Ranius & Hedin, 2001; Svensson, Sahlén, Brage, & Larsson, 2011) of the ecotonal areas and clearings of mature forests, agricultural and urban landscapes (Maurizi et al., 2017).

Rosalia alpina lives mainly in the mountainous regions of central and southern Europe and is associated with beech forests, but also maples

and elms (Bosso, Rebelo, Garonna, & Russo, 2013; Lachat, Ecker, Duelli, & Wermelinger, 2013). It prefers open and semi-open woodlands (Russo et al., 2011), reproducing mainly in mature, dead (or declining) and sun-exposed trees (Campanaro, Redolfi De Zan, et al., 2017).

2.3 | Predictor variables

For the period 2007–2012, we considered a total of 28 predictors of species occurrence, accounting for the assumed habitat characteristics of the target species, and for which continuous spatial data were available for the entire study area (Table S2). We considered two topographic variables (ASTER GDEM; gdem.ersdac.jspacesystems.or.jp), seven land use variables (CORINE Land Cover 2012; <https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012>) and the Euclidean distances to human settlements (Table S2). Moreover, we considered 19 bioclimatic variables (<http://www.worldclim.org>; Table S2). All predictors were resampled at a 10 × 10 km grid cell size.

For the period 2040–2050, we considered four different scenarios of climate and land use change. Specifically, thanks to recent advances in the development of socioeconomic storylines and their potential effect on future land use patterns, we used four land use change scenarios addressing both changes in land cover and land use intensity, reflecting socioeconomic, cultural, political, and technological changes in the EU (Stürck et al., 2015; <http://labs.kh.hercules-landscapes.eu/labs/themeLD.html>). These scenarios, namely Libertarian Europe (A1), Eurosceptic Europe (A2), Social Democracy Europe (B1) and European Localism (B2), represent strong, high, moderate and low economic interventions and growth, respectively (see Table S3 and Stürck et al., 2015 for details on the scenarios).

Similar to Ihlow et al. (2016), we considered four climate change scenarios (Representative Concentration Pathways, RCPs) for the year 2050 averaging 11 general circulation models (GCMs: BCC-CSM1-1, CCSM4, GISS-E2-R, HadGEM2-AO, hadGEM2-ES, IPSL-CM5A-LR, MIROC-ESM-CHEM, MIROC-ESM, MIROC5, MRI-CGCM3 and Nor-ESM1-M). These scenarios were obtained from the fifth assessment of the Intergovernmental Panel for Climate Change (IPCC AR5WG1 2014; <http://www.ipcc.ch>). The selected RCPs represent four possible greenhouse gas emission trajectories, including low (RCP 2.6), moderate (RCP 4.5), high (RCP 6) and strong (RCP 8.5) increases in global radiative forcing (Ihlow et al., 2016). Based on these scenarios, we used the same predictors for the period from 2007 to 2012, available at a 10 × 10 km grid cell size (the same resolution as current climatic conditions) from the Worldclim website (<http://www.worldclim.org>).

2.4 | Data analysis

To avoid multicollinearity among predictors, we estimated the variance inflation factor (VIF) for each predictor. Thus, in the further analysis we retained 13 (ecologically relevant; Bosso et al., 2013; Campanaro, Hardersen, et al., 2017; Thomaes, Kervyn, & Maes,

2008) of 28 predictors due to VIF values lower than 3 (i.e. poorly correlated with other predictors; Zuur, Ieno, & Elphick, 2010; Table S2).

Thus, we applied a recently developed ENMs, namely, "n-dimensional hypervolume" (R package `HYPERVOLUME` 2.0.11; Blonder, Lamanna, Violle, & Enquist, 2014; Blonder, Morrow, et al., 2017), considering current species occurrences, climate and land use conditions but projecting on different future (2040–2050) climate and land use change scenarios (see Table S4 for details on model parameters). *N*-dimensional hypervolume has several benefits compared with other extant ENMs as it (a) considers all the dimensions (predictors) to measure the volume of a high-dimensional shape (including holes or other complex geometrical features; Blonder et al., 2014; Blonder, Morrow, et al., 2017), (b) allows delineation of the entire hypervolume without generating unbounded volumes (Blonder et al., 2014; Peterson et al., 2011) and (c) while relying on presence-only data, correctly classified false absences through robust bandwidth estimation methods (e.g. Silverman estimator; Blonder, Lamanna, Violle, & Enquist, 2017).

Similar to Jaeschke et al. (2013), we identified suitable areas accessible to our target species in the future multiplying the yearly dispersal distance of each species (Table S1) for the total number of years ($n = 33$, from 2013 to 2045, average of 2040–2050). The resulting distances were divided by the number of years larvae would take to develop in the adult stage (Table S1) plus one and then used to define accessible areas around current occurrences.

3 | RESULTS

Without taking into account species-specific dispersal abilities, we found that suitable areas for the saproxylic beetles for the period 2040–2050 would vary between 3,345,200 km² and 4,661,300 km², corresponding to the scenario A2–RCP 2.6 for *M. funereus*; and scenario B2–RCP 6 for *L. cervus* respectively (Table 1). Specifically, suitable conditions for *C. cerdo* would occur all over Europe, mainly in the central-eastern part of the continent, while those for *C. cinnaberinus* would occur in many areas of central-eastern Europe (excluding Switzerland). For *L. cervus* suitable areas would be mainly located from eastern to western Europe (excluding the southern part of the European continent), while those of *O. eremita* would be in central-eastern Europe, including Sweden and Finland. Finally, suitable areas for *M. funereus* would be widely located across central-eastern Europe, whereas *R. alpina* would be distributed throughout Europe, although most concentrated in France, Lithuania and Latvia.

When examining the suitable areas available for the six modelled species (generated without accounting for dispersal abilities), we found a higher impact of climate change relative to land use change on the distribution of *C. cerdo*, *C. cinnaberinus*, *M. funereus* and *R. alpina*. For these species we found a direct relationship between climate change increase and the availability of suitable areas (Figure 2). Conversely, the suitable area of *L. cervus* and *O. eremita* is more susceptible to land use change than climate change, reaching



TABLE 1 Suitable areas (km²) for saproxylic beetles in Europe without considering species-specific dispersal distances under future (2040–2050) scenarios

| Species | RCP | A1 | A2 | B1 | B2 |
|-----------------------------|-----|-----------|-----------|-----------|-----------|
| <i>Cerambyx cerdo</i> | 2.6 | 4,350,600 | 4,364,800 | 4,340,000 | 4,347,600 |
| | 4.5 | 4,393,000 | 4,408,100 | 4,385,600 | 4,383,300 |
| | 6 | 4,414,500 | 4,428,000 | 4,411,600 | 4,412,100 |
| | 8.5 | 4,423,000 | 4,421,700 | 4,415,600 | 4,406,800 |
| <i>Cucujus cinnaberinus</i> | 2.6 | 4,357,500 | 4,359,000 | 4,352,500 | 4,351,600 |
| | 4.5 | 4,370,100 | 4,383,700 | 4,378,900 | 4,377,700 |
| | 6 | 4,355,800 | 4,370,100 | 4,363,500 | 4,360,300 |
| | 8.5 | 4,437,500 | 4,445,500 | 4,441,900 | 4,440,900 |
| <i>Lucanus cervus</i> | 2.6 | 4,545,800 | 4,616,000 | 4,585,600 | 4,646,100 |
| | 4.5 | 4,532,300 | 4,608,900 | 4,558,300 | 4,624,800 |
| | 6 | 4,567,800 | 4,636,200 | 4,604,100 | 4,661,300 |
| | 8.5 | 4,508,300 | 4,577,100 | 4,539,600 | 4,601,900 |
| <i>Morimus funereus</i> | 2.6 | 3,392,800 | 3,345,200 | 3,409,900 | 3,366,800 |
| | 4.5 | 3,499,200 | 3,451,400 | 3,507,600 | 3,479,300 |
| | 6 | 3,476,700 | 3,429,100 | 3,487,700 | 3,446,400 |
| | 8.5 | 3,531,600 | 3,486,700 | 3,543,500 | 3,507,700 |
| <i>Osmoderma eremita</i> | 2.6 | 3,906,500 | 3,839,500 | 3,897,500 | 3,853,400 |
| | 4.5 | 3,879,700 | 3,817,500 | 3,864,200 | 3,814,800 |
| | 6 | 3,852,700 | 3,786,500 | 3,832,600 | 3,784,900 |
| | 8.5 | 3,880,500 | 3,817,500 | 3,862,700 | 3,822,000 |
| <i>Rosalia alpina</i> | 2.6 | 3,858,000 | 3,903,100 | 3,891,900 | 3,923,500 |
| | 4.5 | 3,867,900 | 3,921,000 | 3,906,400 | 3,945,200 |
| | 6 | 3,916,400 | 3,974,200 | 3,974,500 | 3,996,100 |
| | 8.5 | 3,923,200 | 3,975,100 | 3,966,900 | 3,996,900 |

Note: Four land use change scenarios: Libertarian Europe (A1), Eurosceptic Europe (A2), Social Democracy Europe (B1) and European Localism (B2), representing strong (A1), high (A2), moderate (B1) and low (B2) economic interventions and growth (Stürck et al., 2015), and four Representative Concentration Pathways (RCP) derived by 11 general circulation models (GCMs) were combined to project species distribution in 2040–2050. RCPs represent four possible greenhouse gas emission trajectories: low (RCP 2.6), moderate (RCP 4.5), high (RCP 6) and strong (RCP 8.5) increases in global radiative forcing (Inlow et al., 2013).

Source: RCPs: Intergovernmental Panel on Climate Change 5th assessment—Coupled Model Intercomparison Project Phase 5.

the maximum extent in land use change scenarios B2 and A1 respectively (Figure 2).

When we combined climate and land use change with species-specific dispersal abilities, we found that from 2040 to 2050 accessible suitable areas for the six saproxylic beetles would range between only 5.05% and 38.98% of the total available suitable areas calculated previously (Table 2; Table S5). When considering dispersal abilities, *C. cerdo* would reach 24% of its suitable area available from 2040 to 2050 (Figure S7), whereas *C. cinnaberinus* would reach only 13% (Figure S8), mainly located in Eastern Europe, Fennoscandian and Baltic countries. *Lucanus cervus* would reach the largest percentage of its suitable area available from 2040 to 2050 in relation to the other species considered, corresponding to 36%–38% (Figure S9), whereas *M. funereus* would reach only 5% of its suitable area for this timeframe (Figure S10), mainly located in Slovenia, Hungary, Bulgaria, Southern Romania and Northern Greece. Finally, *O. eremita*

would reach 26% of its suitable areas available in 2040–2050 (Figure S11), mainly located in central Europe, whereas *R. alpina* would reach 14% of its suitable area available during this timeframe (Figure S12), mainly located in the mountainous and hilly areas of Southern Europe (excluding Bosnia, Montenegro, Albania and Kosovo).

When including species-specific dispersal abilities we generally found a higher impact of land use change on the distribution of all six saproxylic beetles compared with when dispersal abilities were excluded (Figure 3). Specifically, the highest percentage of accessible suitable areas for *C. cerdo* and *M. funereus* would be reached in the context of land use change scenario B1, whereas for *C. cinnaberinus* and *R. alpina*, it would be land use change scenario B2 (Figure 3). Finally, for *L. cervus* and *O. eremita*, the highest percentage of available suitable area reached corresponds to the A1 land use change scenario (Figure 3). In general, an increase in greenhouse gas emissions corresponds to an increase in the available suitable areas for *C.*

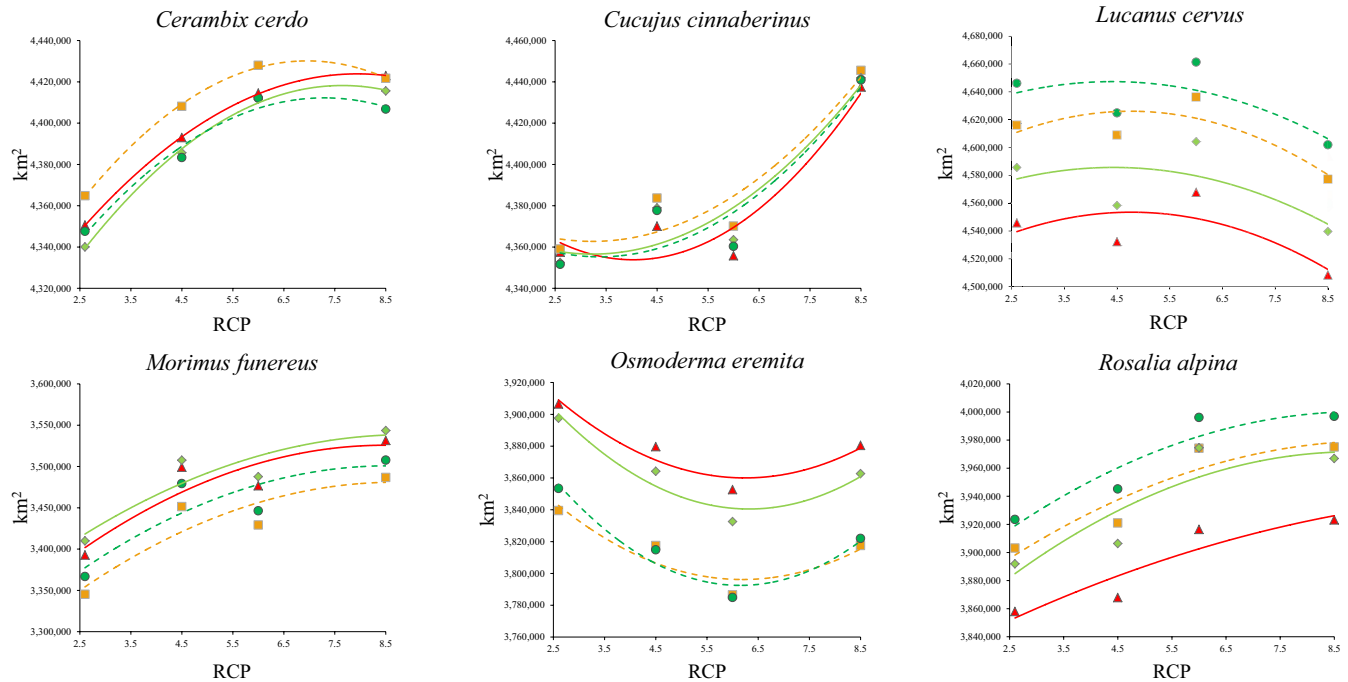


FIGURE 2 Response curves of suitable areas (km^2), generated without accounting for saproxylic beetles dispersal distances, in relation to four land use change scenarios (Stürck et al., 2015) and four Representative Concentration Pathways (RCP) derived by 11 general circulation models (GCMs) for the period 2040–2050 in Europe. Filled red for A1, dashed orange for A2, filled light green for B1 and dashed dark green for B2. Source: RCPs: Intergovernmental Panel on Climate Change 5th assessment—Coupled Model Intercomparison Project Phase 5. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/jbi.13804)]

cerdo, *C. cinnaberinus*, *L. cervus* and *R. alpina*, while in a decrease *O. eremita* (Figure 3). However, climate change would have a weak effect on the available suitable areas reached for *M. funereus* (Figure 3).

4 | DISCUSSION

Our results highlighted differences in the predicted distributions of saproxylic beetles given the differing effects that climate and land use can generate when accounting for or ignoring species dispersal abilities. Land use change was found to be the main constraint to species distributions when accounting for dispersal, whereas climate change when ignoring dispersal.

4.1 | Distribution of saproxylic species considering future climate and land use changes

Our modelled species' ranges will grow in the future due to the combined effects of changing temperatures and precipitations (due to greenhouse gas emissions increase) and an expansion of forested areas (occurring in all the land use scenarios considered). However, while climate change has a similar effect on most of the investigated species, the effect of land use change is more species specific. This is mainly due to the different landscape variables considered: the expansion of grasslands, the abandonment of grasslands resulting in forest expansion, the expansion of human

settlements, the intensification of forest management, and the resulting habitat diversity and the intensity of their exploitation (Stürck et al., 2015).

4.2 | Accessible versus available suitable areas under future climate and land use change scenarios

We found that none of the saproxylic beetles considered in this study will reach all of the suitable areas available in 2040–2050, due to the limited dispersal abilities characterizing these species. Flightless species with narrow geographic distributions would be able to occupy sometimes as little as 5% of the suitable area available to them in 2040–2050, as is the case with *M. funereus*. Conversely, widespread species might be able to cover as much as 38% of the suitable area available to them in 2040–2050, as is the case with *L. cervus*. Thus, species-specific dispersal abilities greatly limit the ability to colonize new suitable areas.

Without accounting for species-specific dispersal abilities, we generally found a strong effect of climate change when predicting future species distributions (except for *L. cervus* and *O. eremita*). Indeed, for most of our species, suitable areas would increase with increasing greenhouse gas emissions, indicating better climatic conditions for their occurrence in the future, supporting a general expansion of many species of saproxylic beetles to higher elevations and latitudes in Europe. However, suitable areas of *L. cervus* and *O. eremita* would be mainly affected by land use change: the future



TABLE 2 Suitable areas (km²) for saproxylic beetles in Europe accounting for species-specific dispersal distances under future (2040–2050) scenarios

| Species | RCP | A1 | A2 | B1 | B2 |
|-----------------------------|-----|-----------|-----------|-----------|-----------|
| <i>Cerambyx cerdo</i> | 2.6 | 1,079,600 | 1,072,100 | 1,081,300 | 1,074,500 |
| | 4.5 | 1,083,500 | 1,083,000 | 1,087,200 | 1,076,100 |
| | 6 | 1,078,800 | 1,081,600 | 1,086,100 | 1,073,700 |
| | 8.5 | 1,090,000 | 1,089,700 | 1,091,500 | 1,086,500 |
| <i>Cucujus cinnaberinus</i> | 2.6 | 573,900 | 571,500 | 571,100 | 574,300 |
| | 4.5 | 578,300 | 577,700 | 578,100 | 583,200 |
| | 6 | 578,600 | 576,400 | 578,000 | 580,200 |
| | 8.5 | 583,600 | 582,200 | 584,200 | 585,600 |
| <i>Lucanus cervus</i> | 2.6 | 1,728,200 | 1,704,100 | 1,728,200 | 1,713,300 |
| | 4.5 | 1,747,700 | 1,723,700 | 1,747,500 | 1,729,900 |
| | 6 | 1,738,300 | 1,708,100 | 1,735,000 | 1,719,400 |
| | 8.5 | 1,757,500 | 1,727,100 | 1,749,500 | 1,737,900 |
| <i>Morimus funereus</i> | 2.6 | 179,000 | 179,300 | 182,800 | 173,900 |
| | 4.5 | 177,600 | 180,000 | 181,400 | 175,600 |
| | 6 | 179,300 | 181,500 | 183,000 | 176,900 |
| | 8.5 | 178,700 | 181,100 | 183,200 | 177,400 |
| <i>Osmoderma eremita</i> | 2.6 | 1,041,000 | 1,029,800 | 1,032,300 | 1,030,900 |
| | 4.5 | 1,021,300 | 1,015,000 | 1,022,900 | 1,018,500 |
| | 6 | 1,032,400 | 1,016,600 | 1,020,300 | 1,017,300 |
| | 8.5 | 1,018,200 | 1,005,700 | 1,009,900 | 1,009,700 |
| <i>Rosalia alpina</i> | 2.6 | 566,000 | 564,200 | 561,700 | 570,000 |
| | 4.5 | 574,800 | 570,900 | 569,600 | 579,300 |
| | 6 | 572,400 | 565,800 | 567,600 | 571,900 |
| | 8.5 | 579,100 | 571,400 | 570,900 | 581,300 |

Note: Four land use change scenarios: Libertarian Europe (A1), Eurosceptic Europe (A2), Social Democracy Europe (B1) and European Localism (B2), representing strong (A1), high (A2), moderate (B1) and low (B2) economic interventions and growth (Stürck et al., 2015), and four Representative Concentration Pathways (RCP) derived by 11 general circulation models (GCMs), were combined to project species distribution in 2040–2050. RCPs represent four possible greenhouse gas emission trajectories: low (RCP 2.6), moderate (RCP 4.5), high (RCP 6) and strong (RCP 8.5) increases in global radiative forcing (Inlow et al., 2013).

Source: RCPs: Intergovernmental Panel on Climate Change 5th assessment—Coupled Model Intercomparison Project Phase 5.

scenarios “European localism” (B2—low economic interventions and growth) and “Libertarian” (A1—strong economic interventions and growth) predicted the maximum distribution expansion of these species respectively.

When accounting for species-specific dispersal abilities, we found a weak effect of climate change and a rather strong effect of land use change. Indeed, we found a clear, inverse relationship between the amount of suitable accessible areas and the degree of land use change for *C. cinnaberinus* and *R. alpina*, for which the scenario “European localism” (B2—low economic interventions and growth) predicted the highest expansion of suitable accessible areas. This land use change scenario, followed by “Social Democracy Europe” (B1—moderate economic interventions and growth), predicted the maximum expansion for *C. cerdo* and *M. funereus*. The main differences among these two scenarios concern the extent of grasslands, croplands (not included in the ENMs due

to multicollinearity, but see below), forests and the intensity of their exploitation (Table S3; Stürck et al., 2015). However, while the intensification of forest management, predicted for both the B1 and B2 scenarios, would present a threat for saproxylic beetles (Jonsson, Kruys, & Ranius, 2005; Jonsson et al., 2006), the increase in forest cover (more than 170,000 km² of current croplands would be abandoned and return naturally to forests or grasslands; Stürck et al., 2015) would increase the extent of suitable habitat for our target species. Moreover, the de-intensification of grasslands predicted for both the B1 (in combination with human settlement contraction) and B2 scenarios (i.e. reduction in livestock density to sustainable grazing) represents a positive change for saproxylic beetles (Russo et al., 2011).

Although, at a broad scale, climate change is expected to be the main constraint for many species distributions, here we found that this is only true for *C. cinnaberinus*, *R. alpina* and *C. cerdo* in the unrealistic scenario of

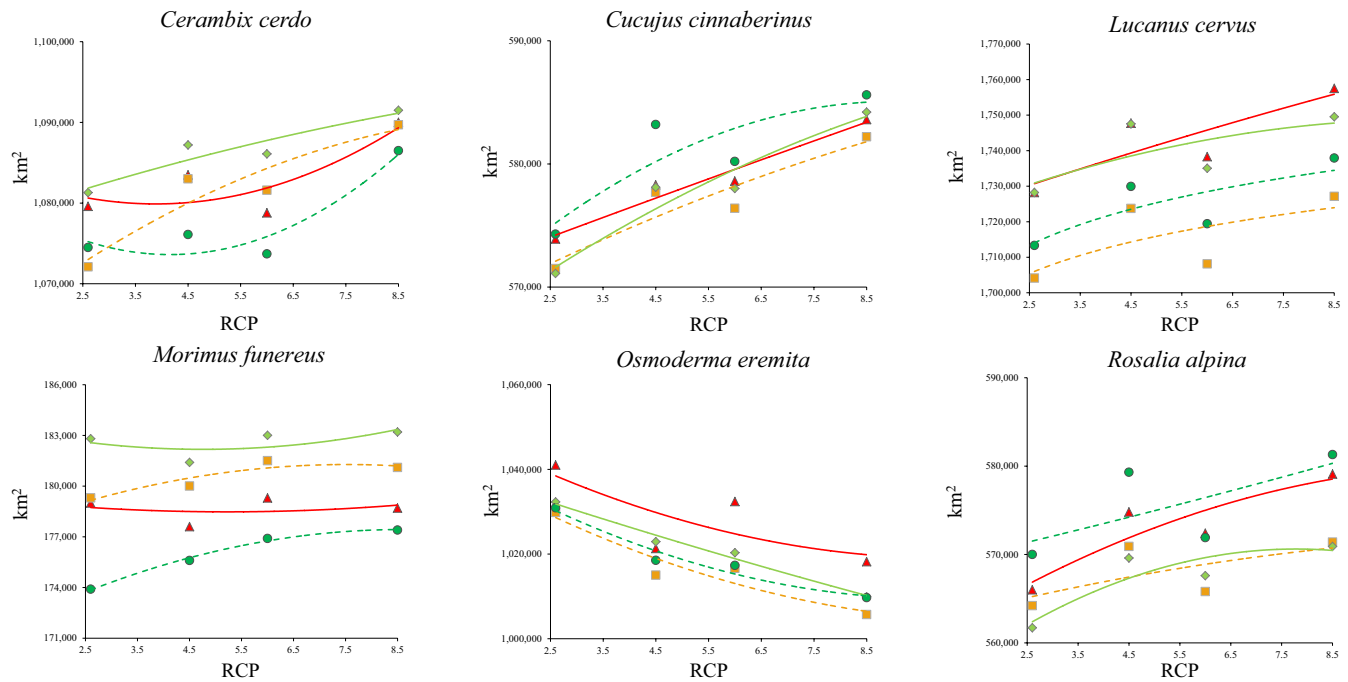


FIGURE 3 Response curves of suitable areas (km^2), accounting for saproxylic beetles dispersal distances, in relation to four land use change scenarios (Stürck et al., 2015) and four Representative Concentration Pathways (RCP) derived by 11 general circulation models (GCMs) for the period 2040–2050 in Europe. Filled red for A1, dashed orange for A2, filled light green for B1 and dashed dark green for B2. Source: RCPs: Intergovernmental Panel on Climate Change 5th assessment—Coupled Model Intercomparison Project Phase 5. [Colour figure can be viewed at wileyonlinelibrary.com]

unlimited dispersal. Conversely, we found that land use change affects all our modelled species. In particular, *L. cervus* and *O. eremita* distributions are affected by land use change in both the cases of limited and unlimited dispersal, whereas those of *C. cerdo*, *C. cinnaberinus*, *M. funereus* and *R. alpina* are affected by land use change only upon taking their dispersal abilities into account. The strong effect of land use change on these saproxylic beetles could be explained by the high dependence of these species on the amount, availability and distribution of deadwood, which, in turn, is closely linked to forest use (Bradford et al., 2014; Mazziotto et al., 2016).

4.3 | Caveats

We followed the approach of Jaeschke et al. (2013) for estimating yearly dispersal distance of saproxylic beetles. While we estimated yearly dispersal distance by dividing the maximum dispersal distance of each species by the number of years larvae would take to develop in the adult stage plus one, this likely resulted in overestimation of the distance these species are able to cover. Because of the lack of information on species traits for our target species, we assumed that the probability of colonization was 1 rather than 0. In doing so, we estimated the maximum dispersal probability without including any species traits in the model. Measuring the real dispersive capacity of a species is very complex (Trakhtenbrot, Nathan, Perry, & Richardson, 2005). In a variety of actively dispersing invertebrates, precise estimations of long-distance dispersal ability are based on morphological characteristics, such as body size or wingspan (Cizek, Fric, & Konvicka,

2006; Merckx & Van Dyck, 2002), or on life history traits (Sutherland, Harestad, Price, & Lertzman, 2000). However, in many cases, such qualitative proxies do not prove informative about dispersal ability due to the uncertainty involved in the identification of the dispersal distance mechanism (Trakhtenbrot et al., 2005). As such, often quantitative models are preferred (Trakhtenbrot et al., 2005). Some used data on variables affecting dispersal to predict the magnitude and frequency of long-distance dispersal, including changes in parameter values caused by human impacts threatening biodiversity (Trakhtenbrot et al., 2005). However, because of the high variability in behavioural and environmental factors (Higgins, Lavorel, & Revilla, 2003), these models tend to be case specific (e.g. Macdonald & Rushton, 2003; South & Kenward, 2001) and often are applied on passive dispersers (Nathan, Horn, Chave, & Levin, 2002) rather than active animals, such as our target species. For many active dispersers, including insects, phenomenological models are often used (Trakhtenbrot et al., 2005). These approaches can be applied if previous population demographic studies are available, for example, capture–mark–recapture studies that can provide presence/absence or dispersal distance data for the species studied (Kuras, Benes, Fric, & Konvicka, 2003). The quality and quantity of the necessary data needs to be thoroughly assessed to make accurate predictions for specific species in a landscape context (Whitmee & Orme, 2012). For most studies on species distribution these data are not available (Nathan, 2001).

Despite its limitations, we felt that the approach of Jaeschke et al. (2013) can be reasonably applied to our target species for two main reasons. First, the dispersal distances reported in this study



are most likely underestimated. Most field studies on saproxylic dispersal distance focus on one or few populations (Chiari et al., 2013; Torres-Vila, Mendiola-Díaz, & Sánchez-González, 2017), and are spatially limited (Drag, Hauck, Pokluda, Zimmermann, & Cizek, 2011; Rossi De Gasperis, Passacantilli, Redolfi De Zan, & Carpaneto, 2016) leading to an underestimation of the real distances an individual might be able to cover. This underestimation could be partially compensated by overestimation in our model. Second, although we may overestimate dispersal in our target species, our resulting spatial predictions are still very useful. In fact, they are more accurate than the unconstrained or no-dispersal scenarios often incorrectly assumed in most of the ENMs predicting the impact of climate change on species distributions (Araújo & Rahbek, 2006; Botkin et al., 2007; Broennimann et al., 2006).

While deadwood is the main resource affecting saproxylic beetle occurrence (Milberg, Bergman, Sancak, & Jansson, 2016; Stokland & Siitonen, 2012) and can influence microclimatic parameters (e.g. hollow trees, Pilskog, Birkemoe, Framstad, & Sverdrup-Thygeson, 2016; Ranius, 2002), we could not include deadwood-related variables in our analyses as deadwood amount and forest management intensity data are lacking at a continental scale (as well as a global scale). Actually, deadwood availability depends on forest management, which alter its distribution and abundance in a quite unpredictable way (i.e. much more than climate and land use; Della Rocca, Bogliani, Breienr, & Milanese, 2019). Thus, simulated future scenarios of deadwood amount/forest management intensity would be random and not based on accurate data and validations. Hence, assuming that climate and land use change are the main driving forces available to model species distribution (Guo, Lenoir, & Bonebrake, 2018; Hitch & Leberg, 2007; Walther et al., 2002), we can identify those areas where saproxylic species would exist should the deadwood required for their survival be present.

Finally, while the monitoring our target species is mandatory for EU Member States and regularly carried out in Switzerland and Norway, there are currently no standardized monitoring protocols at a continental scale (Campanaro et al., 2016). However, the methods used to sample our target species (e.g. attractive pheromones, baited traps, direct observations along transects) are the same within our study area (Campanaro et al., 2016; Maurizi et al., 2017) and thus comparable among different countries. Indeed, conservation actions at the continental scale within the EU are based on these data, collected from 28 countries.

5 | CONCLUSIONS

We developed this study with the observation that most of the published papers aiming to predict species distribution under global change often lack the inclusion of species-specific dispersal abilities. Surprisingly, this holds true also when dealing with species with low vagility for which the dispersal is obviously the main factor limiting their distribution (McCauley et al., 2014). Thus, in this study we showed the importance of dispersal ability in species distribution

modelling and how the effect of climate and land use change differed if dispersal abilities are taken into account or not. Moreover, we showed that combining climate and land use change scenarios with species-specific dispersal distances, resulted in more accurate and realistic projections of species distributions. Our findings are very important especially because poor dispersers suffer high risk of extinction (Beissinger, 2000) due to their limited ability to move away from unsuitable habitat or climatic conditions.

Saproxylic beetles are emblematic from this point of view. Through our approach we were able to accurately identify areas with fundamental species-specific resources, such as ancient woods, forest remnants, hedgerows and old deciduous tree and to provide tools for establishing protected areas and/or extending already existing ones. Concluding, we encourage researchers and conservationists to follow our approach when species dispersal information is available to avoid misleading and overestimated predictions, providing support for conservation actions on these species and their habitats.

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DATA AVAILABILITY STATEMENT

Species occurrence data used in this study are freely available at the following links: <http://cdr.eionet.europa.eu/>, <http://lepus.unine.ch/carto/>, <http://www.biodiversity.no/> and on Dryad online repository (<https://datadryad.org/stash/dataset/doi:10.5061/dryad.9zw3r229v>). GIS layers related to bioclimatic predictors for both current and future scenarios used in this study are available at <http://www.worldclim.org>. Current land use GIS layers are available at <https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012>, while future land use scenarios are freely available at <http://labs.kh.hercules-landscapes.eu/labs/themeLD.html>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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