



ALMA MATER STUDIORUM  
UNIVERSITÀ DI BOLOGNA

## ARCHIVIO ISTITUZIONALE DELLA RICERCA

### Alma Mater Studiorum Università di Bologna Archivio istituzionale della ricerca

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

This is the final peer-reviewed author's accepted manuscript (postprint) of the following publication:

*Published Version:*

Della Rocca F., Milanese P. (2020). Combining climate, land use change and dispersal to predict the distribution of endangered species with limited vagility. JOURNAL OF BIOGEOGRAPHY, 47(7), 1427-1438 [10.1111/jbi.13804].

*Availability:*

This version is available at: <https://hdl.handle.net/11585/927452> since: 2024-05-15

*Published:*

DOI: <http://doi.org/10.1111/jbi.13804>

*Terms of use:*

Some rights reserved. The terms and conditions for the reuse of this version of the manuscript are specified in the publishing policy. For all terms of use and more information see the publisher's website.

This item was downloaded from IRIS Università di Bologna (<https://cris.unibo.it/>).  
When citing, please refer to the published version.

(Article begins on next page)

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

3

4 Running title: **Integrating climate, land use change and dispersal**

5

6 DELLA ROCCA FRANCESCA<sup>1</sup>, MILANESI PIETRO<sup>2</sup>

7

8 <sup>1</sup> *Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, Via*  
9 *Ferrata 1, 27100 Pavia, Italy. [fdellarocca@gmail.com](mailto:fdellarocca@gmail.com)*

10 <sup>2</sup> *Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland.*

11

12 Corresponding author: Francesca Della Rocca [fdellarocca@gmail.com](mailto:fdellarocca@gmail.com)

13

14 **ACKNOWLEDGEMENTS**

15 We thank Prof. Francesco Bracco, manager of the Riserva Naturale Integrale Bosco Siro  
16 Negri, who supported part of this research through funds from the Italian Ministry of the  
17 Environment and Protection of Land and Sea. We thank the European Environment  
18 Information and Observation Network (EIONET) for making their data publicly available;  
19 Peter Verburg, who kindly provided the land use change scenario maps for the year 2040, and  
20 Stephanie Witczak for revising and improving this manuscript. The comments of the Editor-in  
21 Chief Jon Sadler, the Associate Editor Jenny McGuire, as well as those of Jakub Horák and an  
22 anonymous reviewer greatly helped improving this paper.

23 **ABSTRACT**

24 **Aim.** To investigate the effects of both climate and land use change on the distribution of  
25 endangered beetle species with limited vagility, accounting for and ignoring species-specific  
26 dispersal when projecting species distribution.

27 **Location.** Europe.

28 **Time period.** 2007-2012; 2040-2050.

29 **Taxon.** Saproxyllic beetles.

30 **Methods.** Using current (2007-2012) species occurrences, we predicted the distribution of six  
31 endangered saproxyllic beetles under a range of future (2040-50) climate and land use change  
32 scenarios in Europe by using ecological niche models.

33 **Results.** Our results showed that, while all the species considered would increase their  
34 distribution, areas both accessible and suitable would range between only 5% and 38% of the  
35 total potential available area, depending on the species and the future scenarios considered.

36 **Main conclusion.** We strongly encourage researchers and conservationists to combine  
37 climate and land use change with dispersal when projecting species distribution under future  
38 scenarios. This should avoid misleading predictions and overestimation, as climate and land  
39 use change generate differing effects depending on the inclusion or exclusion of species  
40 dispersal abilities.

41

42 **KEYWORDS:** ecological niche models, future scenarios, global change, macroecology, *n*-  
43 dimensional hypervolume, saproxyllic beetles, species traits.

44

45 **1. INTRODUCTION**

46 Many rare species are dispersal-limited, exhibiting a low probability of colonizing new sites  
47 and establishing viable populations (Baur, 2014). The current and future distributions of these  
48 species are highly influenced by human-related environmental change, such as climate and

49 land use change, creating insurmountable barriers to their dispersal across space and time  
50 (Jaeschke et al., 2013). Although both climate and land use change are considered dominant  
51 drivers of biodiversity at a global scale (Barbet-Massin et al., 2012; Pimm et al., 2014), only  
52 the former has been widely used as a predictor for modelling future species distributions (e.g.  
53 Markovic et al., 2014; Titeux et al., 2016). Indeed, during the last 25 years, more than 85% of  
54 published research in this field explored the impact of future climate change alone on  
55 biodiversity (Titeux et al., 2016). Moreover, in the few studies that considered the impact of  
56 land use change on species distribution (Radinger et al., 2016; Milanesi et al., 2017a), the  
57 combined effect with climate change was rarely investigated (Mantyka-Pringle et al., 2014;  
58 Radinger et al., 2016). Since species range shift varies depending on site-specific climate-land  
59 use combinations, neglecting the effect of land use change could lead to biased predictions of  
60 species distributions under future conditions. Especially, this holds true for species with  
61 limited dispersal capacities, for which even minimal land use changes can dramatically impact  
62 their colonization capacity (Velo-Antón et al., 2013; McCauley et al., 2014).

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

72       Taking into account these limitations, in this study we (i) investigated the effect(s) of  
73 climate and land use change on species with short-distance dispersal abilities and (ii) defined  
74 areas that should be accessible to them in the future. We used the current (2007-2012)

75 occurrences of six endangered saproxylic beetles, widely considered to be umbrella species  
76 for biodiversity conservation (Ranius, 2002; Buse et al., 2007; Russo et al., 2011; Campanaro  
77 et al., 2011; Solano et al., 2013; Bełcik et al., 2019), to develop ENMs using current climate  
78 and land use conditions. We then projected the distributions of our target species under future  
79 scenarios to estimate species potential occurrences in the years 2040-50 (based on four  
80 different climate and land use change scenarios). Finally, taking into account the species-  
81 specific dispersal abilities of our target species, we limited their distributions in 2040-50 to  
82 areas accessible to them across Europe.

83

## 84 2. METHODS

### 85 2.1 Study area and species data

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

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

95 We obtained species occurrence data for the period 2007-2012 from (i) the European  
96 Environment Information and Observation NETwork (EIONET, 2013) Central Data  
97 Repository server (<http://cdr.eionet.europa.eu/>), (ii) the Swiss Biological Records Center  
98 (<http://lepus.unine.ch/carto/>) and (iii) the Norwegian Taxonomy Initiative  
99 (<http://www.biodiversity.no/>). All species occurrences were resampled at the same spatial

100 resolution of EIONET data (10 × 10 km grid cell size; Fig. 1), resulting in a total of 4,310

101 cells for *C. cerdo*, 3,561 for *C. cinnaberinus*, 11,535 for *L. cervus*, 2,211 for *M. funereus*,  
102 5,248 for *O. eremita* and 2,628 for *R. alpina*. We tested for overestimation of saproxylic  
103 species occurrences calculating a modified version of the Multivariate Environmental  
104 Similarity Surface (mMESS, Milanesi et al., 2017b). We find consistent results (Fig. S1-6)  
105 and thus, we included all data collected in the further analysis.

106

## 107 2.2 Species ecological requirement

108 The species considered in this study (Table S1) are highly susceptible to both climate and  
109 land use changes (Gough et al., 2015). In fact, being highly specialized wood-living beetles,  
110 their survival is, above all, linked to the availability of suitable forest habitat. As such, their  
111 ability to respond to climate change is mainly influenced by habitat degradation (Filz et al.,  
112 2013; Ball-Damerow et al., 2014). Moreover, the study species are characterized by low  
113 dispersal distances (Schiegg, 2001), and inhabit most of the European deciduous old-growth  
114 forests currently threatened by large-scale human disturbance (Wirth et al., 2009; Stokland et  
115 al., 2012).

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

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

125 *L. cervus* is widely spread across Europe and is associated with mature deciduous  
126 forests. It can be found especially in lowland and medium-altitude oak woodlands, where the

127 saproxylic larvae feed on rotten deadwood at ground level (Campanaro et al., 2011). This  
128 species may also be common in urban habitats (e.g. city parks, private gardens; Hawes, 2008;  
129 Harvey et al., 2011).

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

135 *O. eremita* is a genus that includes many species. Based on genetic studies (Audisio et  
136 al. 2007, 2009), there is now consensus that *Osmoderma eremita* is just one of four species  
137 occurring in Europe. However, in our analysis, we considered all these species as belonging to  
138 *Osmoderma eremita*. It is generally associated with hollow veteran trees (Ranius & Hedin,  
139 2001; Svensson et al., 2011), of the ecotonal areas and clearings of mature forests, agricultural  
140 and urban landscapes (Maurizi et al., 2017).

141 *R. alpina* lives mainly in the mountainous regions of central and southern Europe and is  
142 associated with beech forests, but also maples and elms (Bosso et al., 2013; Lachat et al.,  
143 2013). It prefers open and semi-open woodlands (Russo et al., 2011), reproducing mainly in  
144 mature, dead (or declining), and sun-exposed trees (Campanaro et al., 2017a).

145

## 146 2.3 Predictor variables

147 For the period 2007-2012, we considered a total of 28 predictors of species occurrence,  
148 accounting for the assumed habitat characteristics of the target species, and for which  
149 continuous spatial data were available for the entire study area (Table S2). We considered two  
150 topographic variables (ASTER GDEM; [gdem.ersdac.jspacesystems.or.jp](http://gdem.ersdac.jspacesystems.or.jp)), seven land use  
151 variables (CORINE Land Cover 2012; [https://land.copernicus.eu/pan-european/corine-land-](https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012)  
152 [cover/clc-2012](https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012)) and the Euclidean distances to human settlements (Table S2). Moreover, we

153 considered 19 bioclimatic variables (<http://www.worldclim.org>; Table S2). All predictors  
154 were resampled at a  $10 \times 10$  km grid cell size.

155 For the period 2040-50, we considered four different scenarios of climate and land use  
156 change. Specifically, thanks to recent advances in the development of socioeconomic  
157 storylines and their potential effect on future land use patterns, we used four land use change  
158 scenarios addressing both changes in land cover and land use intensity, reflecting  
159 socioeconomic, cultural, political, and technological changes in the EU (Stürck et al., 2015;  
160 data provided by the authors). These scenarios, namely Libertarian Europe (A1), Eurosceptic  
161 Europe (A2), Social Democracy Europe (B1) and European Localism (B2), represent strong,  
162 high, moderate and low economic interventions and growth, respectively (see Table S3 and  
163 Stürck et al., 2015 for details on the scenarios).

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

175

## 176 2.4 Data analysis

177 To avoid multi-collinearity among predictors, we estimated the variance inflation factor (VIF)  
178 for each predictor. Thus, in the further analysis we retained 13 (ecologically relevant;



179 Thomaes et al., 2008; Bosso et al., 2013; Campanaro et al., 2017b) out of 28 predictors due to  
180 VIF values lower than three (i.e. poorly correlated with other predictors; Zuur et al., 2010;  
181 Table S2).

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

193 Similar to Jaeschke et al. (2013), we identified suitable areas accessible to our target  
194 species in the future multiplying the yearly dispersal distance of each species (Table S1) for  
195 the total number of years ( $n=33$ , from 2013 to 2045, average of 2040-50). The resulting  
196 distances were divided by the number of years larvae would take to develop in the adult stage  
197 (Table S1) plus one and then used to define accessible areas around current occurrences.

198

### 199 **3. RESULTS**

200 Without taking into account species-specific dispersal abilities, we found that suitable areas  
201 for the saproxylic beetles for the period 2040-50 would vary between 3,345,200 km<sup>2</sup> and  
202 4,661,300 km<sup>2</sup>, corresponding to the scenario A2 – RCP 2.6 for *M. funereus* and scenario B2  
203 – RCP 6 for *L. cervus*, respectively (Table 1). Specifically, suitable conditions for *C. cerdo*  
204 would occur all over Europe, mainly in the central-eastern part of the continent, while those

205 for *C. cinnaberinus* would occur in many areas of central-eastern Europe (excluding  
206 Switzerland). For *L. cervus* suitable areas would be mainly located from eastern to western  
207 Europe (excluding the southern part of the European continent), while those of *O. eremita*  
208 would be in central-eastern Europe, including Sweden and Finland. Finally, suitable areas for  
209 *M. funereus* would be widely located across central-eastern Europe, while *R. alpina* would be  
210 distributed throughout Europe, though most concentrated in France, Lithuania and Latvia.

211 When examining the suitable areas available for the six modelled species (generated  
212 without accounting for dispersal abilities) we found a higher impact of climate change relative  
213 to land use change on the distribution of *C. cerdo*, *C. cinnaberinus*, *M. funereus* and *R.*  
214 *alpina*. For these species we found a direct relationship between climate change increase and  
215 the availability of suitable areas (Fig. 2). Conversely, the suitable area of *L. cervus* and *O.*  
216 *eremita* is more susceptible to land use change than climate change, reaching the maximum  
217 extent in land use change scenarios B2 and A1, respectively (Fig. 2)

218 When we combined climate and land use change with species-specific dispersal  
219 abilities, we found that from 2040-50 accessible suitable areas for the six saproxylic beetles  
220 would range between only 5.05% and 38.98% of the total available suitable areas calculated  
221 previously (Table 2; Table S5). When considering dispersal abilities, *C. cerdo* would reach  
222 24% of its suitable area available from 2040-50 (Fig. S7), while *C. cinnaberinus* would reach  
223 only 13% (Fig. S8), mainly located in Eastern Europe, Fennoscandian and Baltic countries. *L.*  
224 *cervus* would reach the largest percentage of its suitable area available from 2040-50 in  
225 relation to the other species considered, corresponding to 36 – 38% (Fig. S9), while *M.*  
226 *funereus* would reach only 5% of its suitable area for this timeframe (Fig. S10), mainly  
227 located in Slovenia, Hungary, Bulgaria, Southern Romania and Northern Greece. Finally, *O.*  
228 *eremita* would reach 26% of its suitable areas available in 2040-50 (Fig. S11), mainly located  
229 in central Europe, while *R. alpina* would reach 14% of its suitable area available during this

230 timeframe (Fig. S12), mainly located in the mountainous and hilly areas of Southern Europe  
231 (excluding Bosnia, Montenegro, Albania and Kosovo).

232         When including species-specific dispersal abilities we generally found a higher impact  
233 of land use change on the distribution of all six saproxylic beetles compared to when dispersal  
234 abilities were excluded (Fig. 3). Specifically, the highest percentage of accessible suitable  
235 areas for *C. cerdo* and *M. funereus* would be reached in the context of land use change  
236 scenario B1 while for *C. cinnaberinus* and *R. alpina*, it would be land use change scenario B2  
237 (Fig. 3). Finally, for *L. cervus* and *O. eremita*, the highest percentage of available suitable area  
238 reached corresponds to the A1 land use change scenario (Fig 3). Generally, an increase in  
239 greenhouse gas emissions corresponds to an increase in the available suitable areas for *C.*  
240 *cerdo*, *C. cinnaberinus*, *L. cervus* and *R. alpina*, while in a decrease *O. eremita* (Fig 3).  
241 However, climate change would have a weak effect on the available suitable areas reached for  
242 *M. funereus* (Fig. 3).

243

#### 244 **4. DISCUSSION**

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

249

##### 250 4.1 Distribution of saproxylic species considering future climate and land use changes

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

256 expansion of grasslands, the abandonment of grasslands resulting in forest expansion, the  
257 expansion of human settlements, the intensification of forest management, and the resulting  
258 habitat diversity and the intensity of their exploitation (Stürck et al., 2015).

259

#### 260 4.2 Accessible vs. available suitable areas under future climate and land use change scenarios

261 We found that none of the saproxylic beetles considered in this study will reach all of the  
262 suitable areas available in 2040-50, due to the limited dispersal abilities characterizing these  
263 species. Flightless species with narrow geographic distributions would be able to occupy  
264 sometimes as little as 5% of the suitable area available to them in 2040-50, as is the case with  
265 *M. funereus*. Conversely, widespread species might be able to cover as much as 38% of the  
266 suitable area available to them in 2040-50, as is the case with *L. cervus*. Thus, species-specific  
267 dispersal abilities greatly limit the ability to colonize new suitable areas.

268 Without accounting for species-specific dispersal abilities, we generally found a strong  
269 effect of climate change when predicting future species distributions (except for *L. cervus* and  
270 *O. eremita*). Indeed, for most of our species, suitable areas would increase with increasing  
271 greenhouse gas emissions, indicating better climatic conditions for their occurrence in the  
272 future, supporting a general expansion of many species of saproxylic beetles to higher  
273 elevations and latitudes in Europe. However, suitable areas of *L. cervus* and *O. eremita* would  
274 be mainly affected by land use change: the future scenarios “European localism” (B2 – low  
275 economic interventions and growth) and “Libertarian” (A1 – strong economic interventions  
276 and growth) predicted the maximum distribution expansion of these species, respectively.

277 When accounting for species-specific dispersal abilities, we found a weak effect of  
278 climate change and a rather strong effect of land use change. Indeed, we found a clear, inverse  
279 relationship between the amount of suitable accessible areas and the degree of land use  
280 change for *C. cinnaberinus* and *R. alpina*, for which the scenario “European localism” (B2 –  
281 low economic interventions and growth) predicted the highest expansion of suitable

282 accessible areas. This land use change scenario, followed by “Social Democracy Europe” (B1  
283 – moderate economic interventions and growth), predicted the maximum expansion for *C.*  
284 *cerdo* and *M. funereus*. The main differences among these two scenarios concern the extent of  
285 grasslands, croplands (not included in the ENMs due to multi-collinearity, but see below),  
286 forests and the intensity of their exploitation (Table S3; Stürck et al., 2015). However, while  
287 the intensification of forest management, predicted for both the B1 and B2 scenarios, would  
288 present a threat for saproxylic beetles (Jonsson et al., 2005; 2006), the increase in forest cover  
289 (more than 170,000 km<sup>2</sup> of current croplands would be abandoned and return naturally to  
290 forests or grasslands; Stürck et al., 2015) would increase the extent of suitable habitat for our  
291 target species. Moreover, the de-intensification of grasslands predicted for both the B1 (in  
292 combination with human settlement contraction) and B2 scenarios (i.e. reduction of livestock  
293 density to sustainable grazing) represent a positive change for saproxylic beetles (Russo et al.,  
294 2011).

295         Although, at a broad scale, climate change is expected to be the main constraint for  
296 many species distributions, here we found that this is only true for *C. cinnaberinus*, *R. alpina*  
297 and *C. cerdo* in the unrealistic scenario of unlimited dispersal. Conversely, we found that land  
298 use change affects all our modelled species. In particular, *L. cervus* and *O. eremita*  
299 distributions are affected by land use change in both the cases of limited and unlimited  
300 dispersal, while those of *C. cerdo*, *C. cinnaberinus*, *M. funereus* and *R. alpina* are affected by  
301 land use change only upon taking their dispersal abilities into account. The strong effect of  
302 land use change on these saproxylic beetles could be explained by the high dependence of  
303 these species on the amount, availability and distribution of deadwood, which, in turn, is  
304 closely linked to forest use (Bradford et al., 2014; Mazziotta et al., 2016).

305

306 4.3 Caveats

307 We followed the approach of Jaeschke et al. (2013) for estimating yearly dispersal distance of  
308 saproxylic beetles. While we estimated yearly dispersal distance by dividing the maximum  
309 dispersal distance of each species by the number of years larvae would take to develop in the  
310 adult stage plus one, this likely resulted in overestimation of the distance these species are  
311 able to cover. Because of the lack of information on species-traits for our target species, we  
312 assumed that the probability of colonization was 1 rather than 0. In doing so, we estimated the  
313 maximum dispersal probability without including any species-traits in the model. Measuring  
314 the real dispersive capacity of a species is very complex (Trakhtenbrot et al., 2005). In a  
315 variety of actively dispersing invertebrates, precise estimations of long-distance dispersal  
316 ability are based on morphological characteristics, such as body size or wingspan (Merckx &  
317 VanDyck, 2002; Cizek, et al., 2006), or on life-history traits (Sutherland et al., 2000).  
318 However, in many cases, such qualitative proxies do not prove informative about dispersal  
319 ability, due to the uncertainty involved in the identification of the dispersal distance  
320 mechanism (Trakhtenbrot et al., 2005). As such, often quantitative models are preferred  
321 (Trakhtenbrot et al., 2005). Some used data on variables affecting dispersal to predict the  
322 magnitude and frequency of long-distance dispersal, including changes in parameter values  
323 caused by human impacts threatening biodiversity (Trakhtenbrot et al., 2005). However,  
324 because of the high variability in behavioural and environmental factors (Higgins et al.,  
325 2003), these models tend to be case-specific (e.g. South & Kenward, 2001; Macdonald &  
326 Rushton, 2003) and often are applied on passive dispersers (Nathan et al., 2002) rather than  
327 active animals, such as our target species. For many active dispersers, including insects,  
328 phenomenological models are often used (Trakhtenbrot et al., 2005). These approaches can be  
329 applied if previous population demographic studies are available, for example, capture-mark-  
330 recapture studies that can provide presence/absence or dispersal distance data for the species  
331 studied (Kuras et al., 2003). The quality and quantity of the necessary data needs to be  
332 thoroughly assessed to make accurate predictions for specific species in a landscape context

333 (Whitmee & Orme, 2012). For most studies on species distribution these data are not  
334 available (Nathan, 2002).

335         Despite its limitations, we felt that the approach of Jaeschke et al. (2013) can be  
336 reasonably applied to our target species for two main reasons. First, the dispersal distances  
337 reported in this study are most likely underestimated. Most field studies on saproxylic  
338 dispersal distance focus on one or few populations (Chiari et al., 2013; Torres-Vila et al.,  
339 2017), and are spatially limited (Rossi De Gasperis et al., 2016; Drag et al., 2011) leading to  
340 an underestimation of the real distances an individual might be able to cover. This  
341 underestimation could be partially compensated by overestimation in our model. Second,  
342 although we may overestimate dispersal in our target species, our resulting spatial predictions  
343 are still very useful. In fact, they are more accurate than the unconstrained or no-dispersal  
344 scenarios often incorrectly assumed in most of the ENMs predicting the impact of climate  
345 change on species distributions (Araújo & Rahbek, 2006; Broennimann et al., 2006; Botkin et  
346 al., 2007).

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

359 Finally, while the monitoring our target species is mandatory for EU Member States and  
360 regularly carried out in Switzerland and Norway, there are currently no standardized  
361 monitoring protocols at a continental scale (Campanaro et al., 2016). However, the methods  
362 used to sample our target species (e.g. attractive pheromones, baited traps, direct observations  
363 along transects) are the same within our study area (Campanaro et al., 2016; Maurizi et al.,  
364 2017) and thus comparable among different countries. Indeed, conservation actions at the  
365 continental scale within the EU are based on these data, collected from 28 countries.

366

## 367 **5. CONCLUSIONS**

368 We developed this study with the observation that most of the published papers aiming to  
369 predict species distribution under global change often lack the inclusion of species-specific  
370 dispersal abilities. Surprisingly, this holds true also when dealing with species with low  
371 vagility for which the dispersal is obviously the main factor limiting their distribution  
372 (McCauley et al., 2014). Thus, in this study we showed the importance of dispersal ability in  
373 species distribution modeling and how the effect of climate and land use change differed if  
374 dispersal abilities are taken into account or not. Moreover, we showed that combining climate  
375 and land use change scenarios with species-specific dispersal distances, resulted in more  
376 accurate and realistic projections of species distributions. Our findings are very important  
377 especially because poor dispersers suffer of high risk of extinction (Beissinger, 2000) due to  
378 their limited ability to move away from unsuitable habitat or climatic conditions.

379 Saproxylic beetles are emblematic from this point of view. Through our approach we were  
380 able to accurately identify areas with fundamental species-specific resources, such as ancient  
381 woods, forest remnants, hedgerows and old deciduous tree and to provide tools for  
382 establishing protected areas and/or extending already existing ones. Concluding, we  
383 encourage researchers and conservationists to follow our approach when species dispersal



384 information is available to avoid misleading and overestimated predictions, providing support  
385 for conservation actions on these species and their habitats.

386

#### 387 **DATA AVAILABILITY STATEMENT**

388 Species occurrence data used in this study is freely available at the following links:

389 <http://cdr.eionet.europa.eu/>, <http://lepus.unine.ch/carto/> and <http://www.biodiversity.no/>.

390 GIS layers related to bioclimatic predictors for both current and future scenarios used in this  
391 study are available at <http://www.worldclim.org>. Current land use GIS layers are available at  
392 <https://land.copernicus.eu/pan-european/corine-land-cover/clc-2012>, while future land use  
393 scenarios are freely available at <http://labs.kh.hercules-landscapes.eu/labs/themeLD.html>.

394

#### 395 **REFERENCES**

396 Araújo, M.B. & Rahbek, C. (2006). How does climate change affect biodiversity? *Science*,  
397 **313**, 1396–1397.

398 Audisio, P., Brustel, H., Carpaneto, G.M., Coletti, G., Mancini, E., Piattella, E., Trizzino, M.,  
399 Dutto, M., Antonini, G. & De Biase, A. (2007) Updating the taxonomy and distribution of  
400 the European *Osmoderma*, and strategies for their conservation (Coleoptera, Scarabaeidae,  
401 *Cetoniinae*). *Fragmenta Entomologica*, **39**, 273–290.

402 Audisio, P., Brustel, H., Carpaneto, G. M., Coletti, G., Mancini, E., Trizzino, M., Antonini, G.  
403 & De Biase, A. (2009). Data on molecular taxonomy and genetic diversification of the  
404 European Hermit beetles, a species complex of endangered insects (Coleoptera:  
405 Scarabaeidae, *Cetoniinae*, *Osmoderma*). *Journal of Zoological Systematics and*  
406 *Evolutionary Research*, **47**, 88-95.

407 Ball-Damerow, J.E., M’Gonigle, L.K. & Resh, V.H. (2014). Changes in occurrence, richness,  
408 and biological traits of dragonflies and damselflies (*Odonata*) in California and Nevada  
409 over the past century. *Biodiversity and Conservation*, **23**, 2107–2126.

410 Barbet-Massin, M., Thuiller, W. & Jiguet, F. (2012). The fate of European breeding birds  
411 under climate, land-use and dispersal scenarios. *Global change biology*, **18**, 881–890.

412 Baur, B. (2014). Dispersal-limited species—a challenge for ecological restoration. *Basic and*  
413 *Applied Ecology*, **15**, 559–564.

414 Beissinger, S.R. (2000). Ecological mechanisms of extinction. *Proceedings of National*  
415 *Academy of Science USA*, **97**, 11688–11689.

416 Bełcik, M., Goczał, J., & Ciach, M. (2019). Large-scale habitat model reveals a key role of  
417 large trees and protected areas in the metapopulation survival of the saproxylic specialist  
418 *Cucujus cinnaberinus*. *Biodiversity and Conservation*, 1-21.

419 Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2014). The n-dimensional  
420 hypervolume. *Global Ecology and Biogeography*, **23**, 595–609.

421 Blonder, B., Morrow, C.B., Maitner, B., Harris, D.J., Lamanna, C., Violle, C., Enquist, B.J. &  
422 Kerkhoff, A.J. (2017a). New approaches for delineating n-dimensional hypervolumes.  
423 *Methods in Ecology and Evolution*, **9**, 305–319.

424 Blonder, B., Lamanna, C., Violle, C. & Enquist, B.J. (2017b). Using *n*-dimensional  
425 hypervolumes for species distribution modelling: A response to Qiao et al. (). *Global*  
426 *Ecology and Biogeography*, **26**, 1071–1075.

427 Bosso, L., Rebelo, H., Garonna, A.P. & Russo, D. (2013). Modelling geographic distribution  
428 and detecting conservation gaps in Italy for the threatened beetle *Rosalia alpina*. *Journal*  
429 *for Nature Conservation*, **21**, 72–80.

430 Botkin, D.B., Saxe, H., Araujo, M.B., Betts, R., Bradshaw, R.H.W., Cedhagen, T., Chesson,  
431 P., Dawson, T.P., Etterson, J.R., Faith, D.P., Ferrier, S., Guisan, A., Hansen, A.S., Hilbert,  
432 D.W., Loehle, C., Margules, C., New, M., Sobel, M.J. & Stockwell, D.R.B. (2007).  
433 Forecasting the effects of global warming on biodiversity. *Bioscience*, **57**, 227–236.

434 Bradford, M.A., Warren II, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E.,  
435 Wieder, W.R., Wood, S.A. & King, J.R. (2014). Climate fails to predict wood  
436 decomposition at regional scales. *Nature Climate Change*, **4**, 625.

437 Broennimann, O., Thuiller, W., Hughes, G., Midgley, G.F., Alke-made, J.R.M. & Guisan, A.  
438 (2006). Do geographic distribution, niche property and life form explain plants'  
439 vulnerability to global change? *Global Change Biology*, **12**, 1079–1093.

440 Buse, J., Schröder, B. & Assmann, T. (2007). Modelling habitat and spatial distribution of an  
441 endangered longhorn beetle—a case study for saproxylic insect conservation. *Biological*  
442 *Conservation*, **137**, 372–381.

443 Campanaro, A., Toni, I., Hadersen, S. & Grasso, D.A. (2011). Monitoring of *Lucanus cervus*  
444 by means of remains of predation (*Coleoptera: Lucanidae*). *Entomologia generalis*, **33**, 79–  
445 89.

446 Campanaro, A., Zapponi, L., Hadersen, S., Méndez, M., Al Fulaij, N., Audisio, P., Bardiani,  
447 M., Carpaneto, G.M., Corezzola, S., Della Rocca, F. & Harvey, D. (2016). A European  
448 monitoring protocol for the stag beetle, a saproxylic flagship species. *Insect conservation*  
449 *and diversity*, **9**, 574–584.

450 Campanaro, A., RedolfideZan, L., Hadersen, S., Antonini, G., Chiari, S., Cini, A., Mancini,  
451 E., Mosconi, F., Gasperis, S.R. de & Solano, E. (2017a). Guidelines for the monitoring of  
452 *Rosalia alpina*. *Nature Conservation*, **20**, 165.

453 Campanaro, A., Hadersen, S., Zan, L.R. de, Antonini, G., Bardiani, M., Maura, M., Maurizi,  
454 E., Mosconi, F., Zauli, A. & Bologna, M.A. (2017b). Analyses of occurrence data of  
455 protected insect species collected by citizens in Italy. *Nature Conservation*, **20**, 265.

456 Carpaneto, G.M., Baviera, C., Biscaccianti, A.B., Brandmayr, P., Mazzei, A., Mason, F.,  
457 Battistoni, A., Teofili, C., Rondinini, C. & Fattorini, S. (2015). A Red List of Italian  
458 Saproxylic Beetles: taxonomic overview, ecological features and conservation issues  
459 (*Coleoptera*). *Fragmenta entomologica*, **47**, 53–126.

460 Chiari, S., Carpaneto, G.M., Zauli, A., Zirpoli, G.M., Audisio, P. & Ranius, T. (2013).  
461 Dispersal patterns of a saproxylic beetle, *Osmoderma eremita*, in Mediterranean  
462 woodlands. *Insect Conservation and Diversity*, **6**, 309–318.

463 Cizek, L., Fric, Z. & Konvicka, M. (2006). Host plant defences and voltinism in European  
464 butterflies. *Ecological Entomology*, **31**, 337– 344.

465 De Marco, D.E., Montemurro, M.A. & Cannas, S.A. (2011). Comparing short and long-  
466 distance dispersal: modelling and field case studies. *Ecography*, **34**, 671–682.

467 Della Rocca, F., Bogliani, G., Breienr, F.T. & Milanese, P. (2019). Identifying hotspots for  
468 rare species under climate change scenarios: improving saproxylic beetle conservation in  
469 Italy. *Biodiversity and Conservation*, **28**, 433–449.

470 Drag, L., Hauck, D., Pokluda, P., Zimmermann, K. & Cizek, L. (2011). Demography and  
471 dispersal ability of a threatened saproxylic beetle: a mark-recapture study of the *Rosalia*  
472 Longicorn (*Rosalia alpina*). *PLoS One*, **6**, e21345.

473 Engler, R. & Guisan, A. (2009). MigClim: predicting plant distribution and dispersal in a  
474 changing climate. *Diversity and Distributions*, **15**, 590–601.

475 Filz, K.J., Wiemers, M., Herrig, A., Weitzel, M. & Schmitt, T. (2013). A question of  
476 adaptability: Climate and habitat change lower trait diversity in butterfly communities in  
477 south-western Germany. *European Journal of Entomology*, **110**, 633–642.

478 Franklin, J. (2010). Moving beyond static species distribution models in support of  
479 conservation biogeography. *Diversity and Distributions*, **16**, 321–330.

480 Gough, L.A., Sverdrup-Thygeson, A., Milberg, P., Pilskog, H.E., Jansson, N., Jonsell, M. &  
481 Birkemoe, T. (2015). Specialists in ancient trees are more affected by climate than  
482 generalists. *Ecology and evolution*, **5**, 5632–5641.

483 Guo, F., Lenoir, J. & Bonebrake, T.C. (2018). Land-use change interacts with climate to  
484 determine elevational species redistribution. *Nature communications*, **9**, 1315.

485 Hardersen, S., Bardiani, M., Chiari, S., Maura, M., Maurizi, E., Roversi, P.F., Mason, F. &  
486 Bologna, M.A. (2017). Guidelines for the monitoring of *Morimus asper funereus* and  
487 *Morimus asper asper*. *Nature Conservation*, **20**, 205.

488 Harvey, D.J., Gange, A.C., Hawes, C.J. & Rink, M. (2011). Bionomics and distribution of the  
489 stag beetle, *Lucanus cervus* (L.) across Europe. *Insect Conservation and Diversity*, **4**, 23–  
490 38.

491 Hawes, C. J. (2008). The stag beetle *Lucanus cervus* (Linnaeus, 1758) (Coleoptera: Lucanidae):  
492 a mark-release-recapture study undertaken in one United Kingdom residential garden. *Rev.*  
493 *Écol. (Terre Vie)*, **63**, 139–146.

494 Higgins, S.I., Lavorel, S. & Revilla, E. (2003). Estimating plant migration rates under habitat  
495 loss and fragmentation. *Oikos*, **101**, 354–366.

496 Hitch, A.T. & Leberg, P.L. (2007). Breeding distributions of North American bird species  
497 moving north as a result of climate change. *Conservation Biology*, **21**, 534–539.

498 Horák, J., Chobot, K., Kohutka, A. & Gebauer, R. (2008). Possible factors influencing the  
499 distribution of a threatened saproxylic beetle *Cucujus cinnaberinus* (Scopoli 1763)  
500 (Coleoptera: Cucujidae). *The Coleopterists Bulletin*, **62**, 437–440.

501 Horák, J. & Chobot, K. (2009). Worldwide distribution of saproxylic beetles of the genus  
502 *Cucujus* Fabricius, 1775 (Coleoptera: Cucujidae). *Saproxylic beetles—Their role and*  
503 *diversity in European woodland and tree habitats*. Pensoft Publishers, Sofia–Moscow, 189–  
504 206.

505 Horák, J., Vávrová, E. & Chobot, K. (2010). Habitat preferences influencing populations,  
506 distribution and conservation of the endangered saproxylic beetle *Cucujus cinnaberinus*  
507 (Coleoptera: Cucujidae) at the landscape level. *European Journal of Entomology*, **107**, 81–  
508 88.

509 Horák, J. (2011). Response of saproxylic beetles to tree species composition in a secondary  
510 urban forest area. *Urban Forestry & Urban Greening*, **10**, 213–222.

511 Kuras, T., Benes, J., Fric, Z. & Konvicka, M. (2003). Dispersal patterns of endemic alpine  
512 butterflies with contrasting population structures: *Erebia epiphron* and *E. sudetica*.  
513 *Population Ecology*, **45**, 115-123.

514 Ihlow, F., Courant, J., Secondi, J., Herrel, A., Rebelo, R., Measey, G.J., Lillo, F., de Villiers,  
515 F.A., Vogt, S. & de Busschere, C. (2016). Impacts of climate change on the global invasion  
516 potential of the African clawed frog *Xenopus laevis*. *PLoS One*, **11**, e0154869.

517 Jaeschke, A., Bittner, T., Reineking, B. & Beierkuhnlein, C. (2013). Can they keep up with  
518 climate change?—Integrating specific dispersal abilities of protected *Odonata* in species  
519 distribution modelling. *Insect Conservation and Diversity*, **6**, 93–103.

520 Jonsson, B.G., Kruys, N. & Ranius, T. (2005). Ecology of species living on dead wood—  
521 lessons for dead wood management. *Silva Fennica*, **39**, 289–309.

522 Jonsson, M., Ranius, T., Ekvall, H., Bostedt, G., Dahlberg, A., Ehnström, B., Nordén, B. &  
523 Stokland, J.N. (2006). Cost-effectiveness of silvicultural measures to increase substrate  
524 availability for red-listed wood-living organisms in Norway spruce forests. *Biological*  
525 *Conservation*, **127**, 443–462.

526 Jurc, M., Ogris, N., Pavlin, R. & Borkovic, D. (2008). Forest as a habitat of saproxylic beetles  
527 on natura 2000 sites in slovenia. *Rev. Écol.(Terre Vie)*, **63**, 61–74.

528 Lachat, T., Ecker, K., Duelli, P. & Wermelinger, B. (2013). Population trends of *Rosalia*  
529 *alpina* (L.) in Switzerland: a lasting turnaround? *Journal of Insect Conservation*, **17**, 653–  
530 662.

531 Larsson, M.C. & Svensson, G.P. (2011). Monitoring spatiotemporal variation in abundance  
532 and dispersal by a pheromone-kairomone system in the threatened saproxylic beetles  
533 *Osmoderma eremita* and *Elater ferrugineus*. *Journal of Insect Conservation*, **15**, 891– 902.

534 Macdonald, D.W. & Rushton, S. (2003). Modelling space use and dispersal of mammals in  
535 real landscapes: a tool for conservation. *Journal of Biogeography*, **30**, 607.

536 Mantyka-Pringle, C.S., Martin, T.G., Moffatt, D.B., Linke, S. & Rhodes, J.R. (2014).  
537 Understanding and predicting the combined effects of climate change and land-use change  
538 on freshwater macroinvertebrates and fish. *Journal of Applied Ecology*, **51**, 572–581.

539 Markovic, D., Carrizo, S., Freyhof, J., Cid, N., Lengyel, S., Scholz, M., Kasperdius, H. &  
540 Darwall, W. (2014). Europe's freshwater biodiversity under climate change: distribution  
541 shifts and conservation needs. *Diversity and Distributions*, **20**, 1097–1107.

542 Maurizi, E., Campanaro, A., Chiari, S., Maura, M., Mosconi, F., Sabatelli, S., Zauli, A.,  
543 Audisio, P. & Carpaneto, G.M. (2017). Guidelines for the monitoring of *Osmoderma*  
544 *eremita* and closely related species. *Nature Conservation*, **20**, 79.

545 Mazziotta, A., Triviño, M., Tikkanen, O.-P., Kouki, J., Strandman, H. & Mönkkönen, M.  
546 (2016). Habitat associations drive species vulnerability to climate change in boreal forests.  
547 *Climatic change*, **135**, 585–595.

548 Merckx, T. & Van Dyck, H. (2002). Interrelations among habitat use, behavior, and flight-  
549 related morphology in two cooccurring Satyrine butterflies, *Maniola jurtina* and *Pyronia*  
550 *tithonus*. *Journal of Insect Behavior*, **15**, 541– 561.

551 McCauley, S.J., Davis, C.J., Werner, E.E. & Robeson, M.S. (2014). Dispersal, niche breadth  
552 and population extinction: colonization ratios predict range size in North American  
553 dragonflies. *Journal of Animal Ecology*, **83**, 858–865.

554 Milanesi, P., Breiner, F.T., Puopolo, F. & Holderegger, R. (2017a). European human-  
555 dominated landscapes provide ample space for the recolonization of large carnivore  
556 populations under future land change scenarios. *Ecography*, **40**, 1359–1368.

557 Milanesi, P., Herrando, S., Pla, M., Villero, D. & Keller, V. (2017b). Towards continental  
558 bird distribution models: environmental variables for the second European breeding bird  
559 atlas and identification of priorities for further surveys. *Vogelwelt*, **137**, 53–60.

560 Milberg, P., Bergman, K., Sancak, K. & Jansson, N. (2016). Assemblages of saproxylic  
561 beetles on large downed trunks of oak. *Ecology and evolution*, **6**, 1614–1625.

562 Nathan, R. (2001). Dispersal biogeography. Encyclopedia of biodiversity (ed. by S.A. Levin),  
563 pp. 127-152. Academic Press, San Diego.

564 Nobis, M.P. & Normand, S. (2014). KISSMig—a simple model for R to account for limited  
565 migration in analyses of species distributions. *Ecography*, **37**, 1282–1287.

566 Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura,  
567 M. & Araújo, M.B. (2011). *Ecological Niches and Geographic Distributions (MPB-49)*.  
568 Princeton University Press.

569 Pilskog, H.E., Birkemoe, T., Framstad, E. & Sverdrup-Thygeson, A. (2016). Effect of habitat  
570 size, quality, and isolation on functional groups of beetles in hollow oaks. *Journal of Insect*  
571 *Science*, **26**, 1–8.

572 Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H.,  
573 Roberts, C.M. & Sexton, J.O. (2014). The biodiversity of species and their rates of  
574 extinction, distribution, and protection. *Science*, **344**, 1246752.

575 Radinger, J., Hölker, F., Horký, P., Slavík, O., Dendoncker, N. & Wolter, C. (2016).  
576 Synergistic and antagonistic interactions of future land use and climate change on river fish  
577 assemblages. *Global change biology*, **22**, 1505–1522.

578 Ranius, T. & Hedin, J. (2001). The dispersal rate of a beetle, *Osmoderma eremita*, living in  
579 tree hollows. *Oecologia*, **126**, 363–370.

580 Ranius, T. (2002). *Osmoderma eremita* as an indicator of species richness of beetles in tree  
581 hollows. *Biodiversity and Conservation*, **11**, 931–941.

582 Redolfi de Zan, L., Bardiani, M., Antonini, G., Campanaro, A., Chiari, S., Mancini, E.,  
583 Maura, M., Sabatelli, S., Solano, E. & Zauli, A. (2017). Guidelines for the monitoring of  
584 *Cerambyx cerdo*. *Nature Conservation*, **20**, 129.

585 Rossi de Gasperis, S., Passacantilli, C., Redolfi De Zan, L. & Carpaneto, G.M. (2016).  
586 Overwintering ability and habitat preference of *Morimus asper*: a two-year mark-recapture



587 study with implications for conservation and forest management. *Journal of Insect*  
588 *Conservation*, **20**, 821–835.

589 Russo, D., Cistrone, L. & Garonna, A.P. (2011). Habitat selection by the highly endangered  
590 long-horned beetle *Rosalia alpina* in Southern Europe: a multiple spatial scale assessment.  
591 *Journal of Insect Conservation*, **15**, 685–693.

592 Sama, G. (1988). Fauna d'Italia XXVI. *Coleoptera Cerambycidae. Catalogo topografico e*  
593 *sinonimico, Calderini, Bologna.*

594 Sama, G. (2009). Fauna Europaea: *Cerambycidae. Fauna Europaea: Coleoptera. Fauna*  
595 *Europaea version, 2.*

596 Schiegg, K. (2000). Are there saproxylic beetle species characteristic of high dead wood  
597 connectivity? *Ecography*, **23**, 579–587.

598 Smolik, M.G., Dullinger, S., Essl, F., Kleinbauer, I., Leitner, M., Peterseil, J., Stadler, L. &  
599 Vogl, G. (2010). Integrating species distribution models and interacting particle systems to  
600 predict the spread of an invasive alien plant. *Journal of Biogeography*, **37**, 411–422.

601 Soberón, J. & Peterson, A.T. (2005). Interpretation of models of fundamental ecological  
602 niches and species' distributional areas. *Biodiversity Informatics*, **2**, 1–10.

603 Solano, E., Mancini, E., Ciucci, P., Mason, F., Audisio, P. & Antonini, G. (2013). The EU  
604 protected taxon *Morimus funereus* Mulsant, 1862 (Coleoptera: Cerambycidae) and its  
605 western Palaearctic allies: Systematics and conservation outcomes. *Conservation Genetics*.  
606 **14** (3), 683–694.

607 South, A.B. & Kenward, R.E. (2001). Mate finding, dispersal distances and population  
608 growth in invading species: a spatially explicit model. *Oikos*, **95**, 53–5.

609 Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P. (2000). Scaling of natal  
610 dispersal distances in terrestrial birds and mammals. *Conservation Ecology*, **4**, 16.

611 Stokland, J.N. & Siitonen, J. (2012). Mortality factors and decay succession. *Biodiversity in*  
612 *dead wood. Cambridge University Press, Cambridge*, 110–149.

613 Stokland, J.N., Siitonen, J. & Jonsson, B.G. (2012). Threatened saproxylic species.  
614 *Biodiversity in dead wood. Cambridge University Press, Cambridge, 356-379.*

615 Stürck, J., Levers, C., van der Zanden, Emma Henriëtta, Schulp, C.J.E., Verkerk, P.J.,  
616 Kuemmerle, T., Helming, J., Lotze-Campen, H., Tabeau, A. & Popp, A. (2015). Simulating  
617 and delineating future land change trajectories across Europe. *Regional Environmental*  
618 *Change*, 1–17.

619 Svensson, G.P., Sahlin, U., Brage, B. & Larsson, M.C. (2011). Should I stay or should I go?  
620 Modelling dispersal strategies in saproxylic insects based on pheromone capture and radio  
621 telemetry: a case study on the threatened hermit beetle *Osmoderma eremita*. *Biodiversity*  
622 *and Conservation*, **20**, 2883–2902.

623 Thomaes, A., Kervyn, T. & Maes, D. (2008). Applying species distribution modelling for the  
624 conservation of the threatened saproxylic Stag Beetle (*Lucanus cervus*). *Biological*  
625 *Conservation*, **141**, 1400–1410.

626 Titeux, N., Henle, K., Mihoub, J., Regos, A., Geijzendorffer, I.R., Cramer, W., Verburg, P.H.  
627 & Brotons, L. (2016). Biodiversity scenarios neglect future land-use changes. *Global*  
628 *change biology*, **22**, 2505–2515.

629 Torres-Vila, L.M., Mendiola-Diaz, F.J. & Sánchez-González, Á. (2017). Dispersal differences  
630 of a pest and a protected Cerambyx species (*Coleoptera: Cerambycidae*) in oak open  
631 woodlands: a mark–recapture comparative study. *Ecological Entomology*, **42**, 18–32.

632 Trakhtenbrot, A., Nathan, R., Perry, G. & Richardson, D.M. (2005). The importance of long-  
633 distance dispersal in biodiversity conservation. *Diversity and Distributions*, **11**, 173-181.

634 Vasudev, D., Fletcher, R.J., Goswami, V.R. & Krishnadas, M. (2015). From dispersal  
635 constraints to landscape connectivity: lessons from species distribution modeling.  
636 *Ecography*, **38**, 967–978.

- 637 Velo-Antón, G., Parra, J.L., Parra-Olea, G. & Zamudio, K.R. (2013). Tracking climate change  
638 in a dispersal-limited species: reduced spatial and genetic connectivity in a montane  
639 salamander. *Molecular ecology*, **22**, 3261–3278.
- 640 Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-  
641 M., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate  
642 change. *Nature*, **416**, 389.
- 643 Whitmee, S. & Orme, D. (2012). Predicting dispersal distance in mammals: A trait-based  
644 approach. *Journal of Animal Ecology*, **82**, 211–221.
- 645 Wirth, C., Messier, C., Bergeron, Y., Frank, D. & Fankhänel, A. (2009). Old-Growth Forest  
646 Definitions: a Pragmatic View. *Old-Growth Forests*, 11–33.
- 647 Zuur, A.F., Ieno, E.N. & Elphick, C.S. (2010). A protocol for data exploration to avoid  
648 common statistical problems. *Methods in Ecology and Evolution*, **1**, 3–14.

649

## 650 **BIOSKETCH**

651 **Francesca Della Rocca** is an Adjunct Professor at the Department of Biology and  
652 Biotechnology, University of Pavia, and is broadly interested in the biogeography of  
653 endangered saproxylic beetles. **Pietro Milanesi** is a postdoc at the Swiss Ornithological  
654 Institute in spatial statistical modelling and is mainly interested in macroecology. Author  
655 contributions: FDR and PM conceived and designed this study, analyzed the data and wrote  
656 the first drafts of this manuscript, and alternately commented and revised the manuscript.

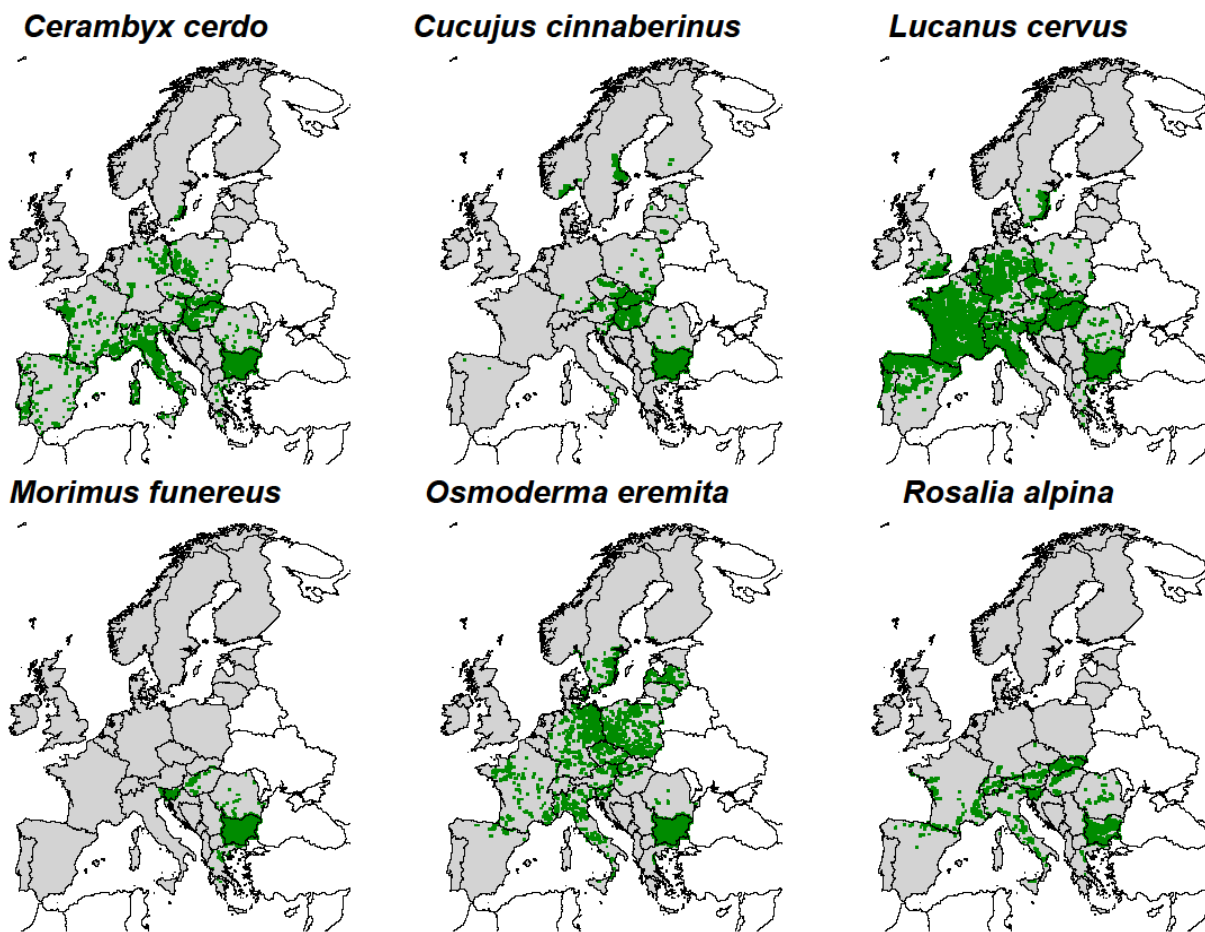
657 Table 1. Suitable areas (km<sup>2</sup>) for saproxylic beetles in Europe without considering species-  
658 specific dispersal distances under future (2040-50) scenarios. Four land use change scenarios:  
659 Libertarian Europe (A1), Eurosceptic Europe (A2), Social Democracy Europe (B1) and  
660 European Localism (B2), representing strong (A1), high (A2), moderate (B1) and low (B2)  
661 economic interventions and growth (Stürck *et al.*, 2015), and four Representative  
662 Concentration Pathways (RCP) derived by 11 general circulation models (GCMs), were  
663 combined to project species distribution in 2040-50. RCPs represent four possible greenhouse  
664 gas emission trajectories: low (RCP 2.6), moderate (RCP 4.5), high (RCP 6) and strong (RCP  
665 8.5) increases in global radiative forcing (Ihlow *et al.*, 2016). Source RCPs:  
666 Intergovernmental Panel on Climate Change 5<sup>th</sup> assessment - Coupled Model Intercomparison  
667 Project Phase 5.

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

668 Table 2. Suitable areas (km<sup>2</sup>) for saproxylic beetles in Europe accounting for species-specific  
669 dispersal distances under future (2040-50) scenarios. Four land use change scenarios:  
670 Libertarian Europe (A1), Eurosceptic Europe (A2), Social Democracy Europe (B1) and  
671 European Localism (B2), representing strong (A1), high (A2), moderate (B1) and low (B2)  
672 economic interventions and growth (Stürck *et al.*, 2015), and four Representative  
673 Concentration Pathways (RCP) derived by 11 general circulation models (GCMs), were  
674 combined to project species distribution in 2040-50. RCPs represent four possible greenhouse  
675 gas emission trajectories: low (RCP 2.6), moderate (RCP 4.5), high (RCP 6) and strong (RCP  
676 8.5) increases in global radiative forcing (Ihlow *et al.*, 2016). Source RCPs:  
677 Intergovernmental Panel on Climate Change 5<sup>th</sup> assessment - Coupled Model Intercomparison  
678 Project Phase 5.

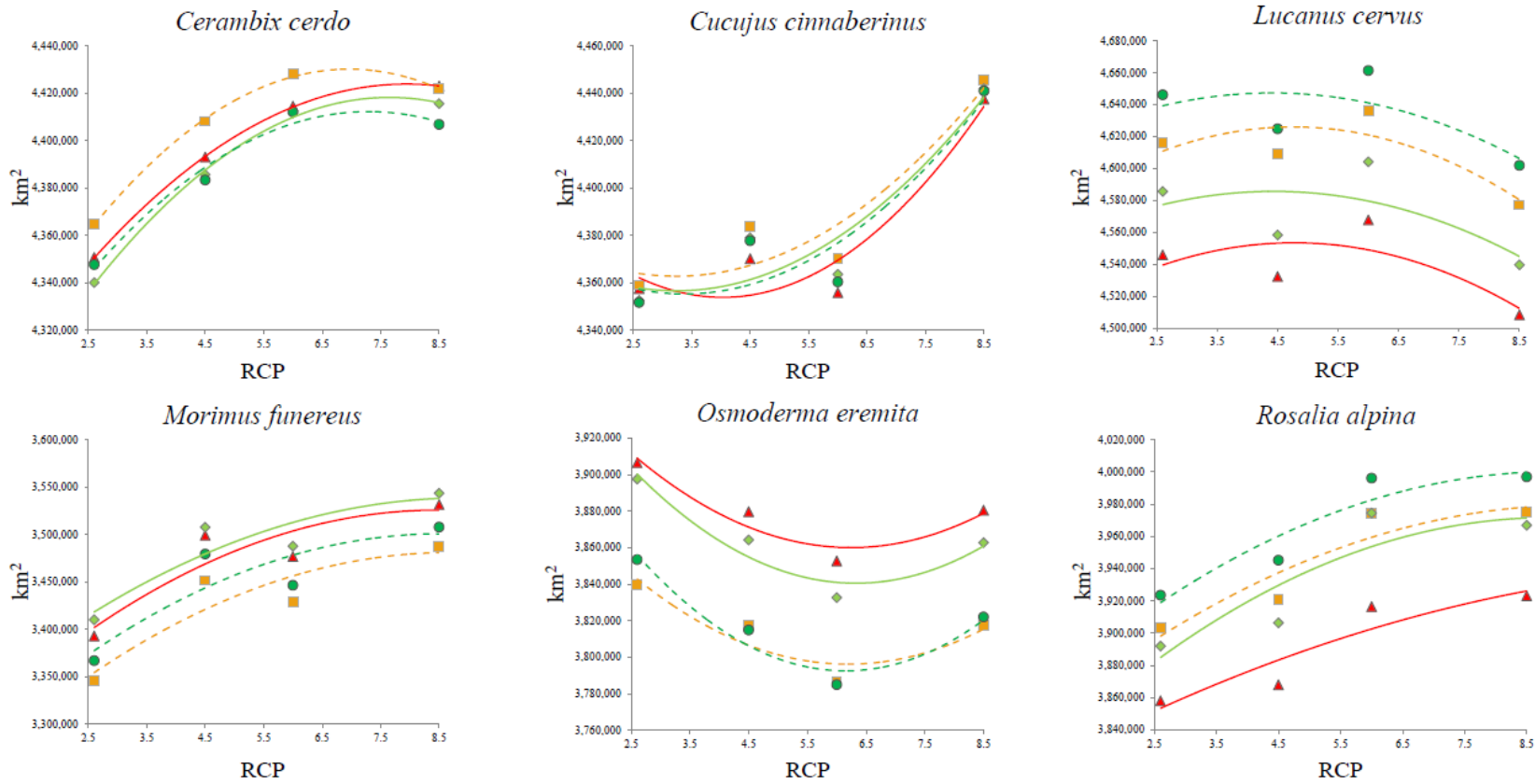
Species	RCP	A1	A2	B1	B2
<i>Cerambyx cerdo</i>	2.6	1,079,600	1,072,100	1,081,300	1,074,500
	4.5	1,083,500	1,083,000	1,087,200	1,076,100
	6	1,078,800	1,081,600	1,086,100	1,073,700
	8.5	1,090,000	1,089,700	1,091,500	1,086,500
<i>Cucujus cinnaberinus</i>	2.6	573,900	571,500	571,100	574,300
	4.5	578,300	577,700	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

679 Figure 1. Study area (in grey) and current species ranges, according to European Environment Information and Observation Network (EIONET)  
680 Central Data Repository server, Swiss Biological Records Center and Norwegian Taxonomy Initiative, of the six saproxylic species considered (in  
681 green).



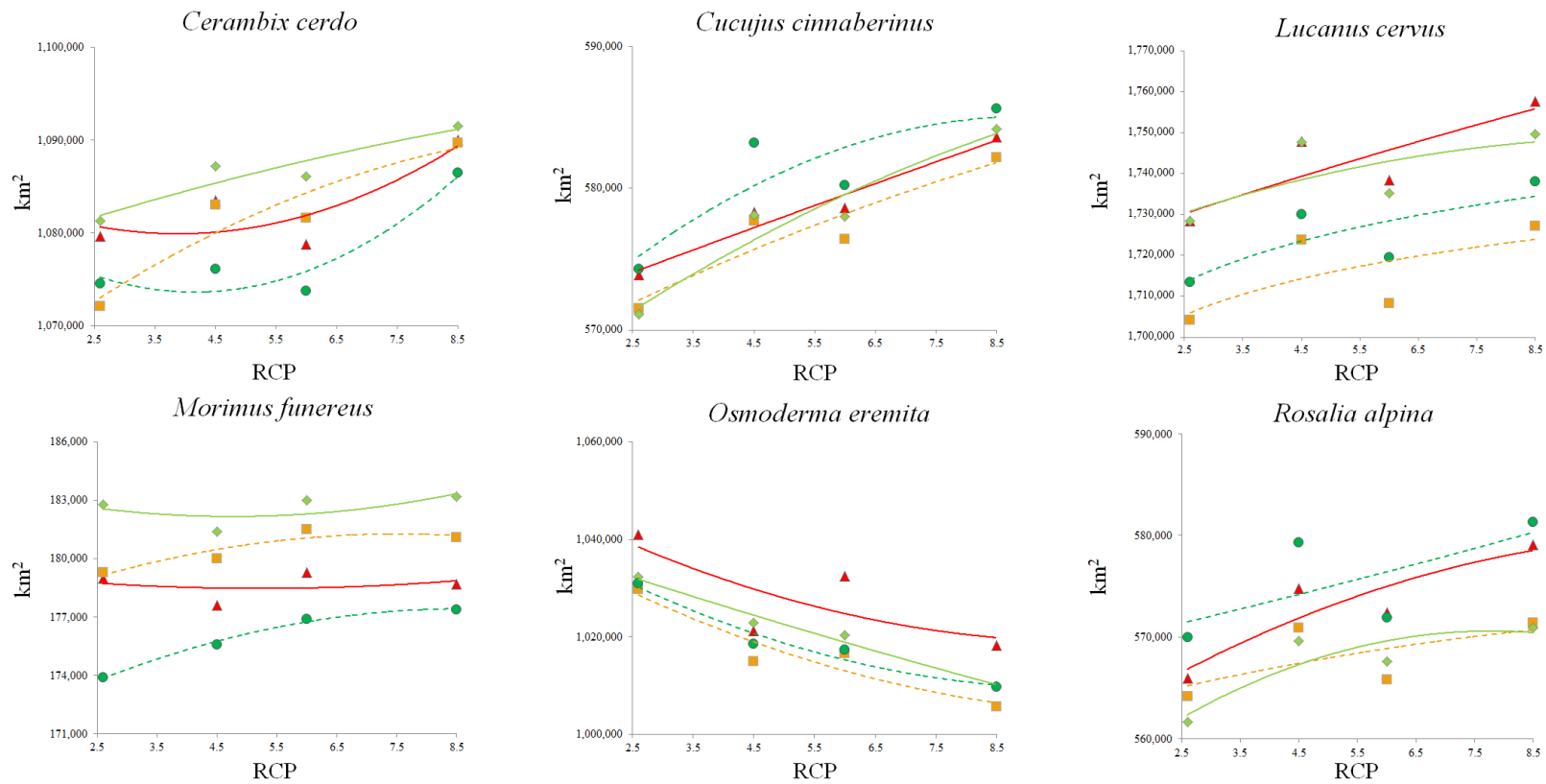
682

683 Figure 2. Response curves of suitable areas (km<sup>2</sup>), generated without accounting for saproxylic beetles dispersal distances, in relation to four land  
 684 use change scenarios (Stürck *et al.*, 2015) and four Representative Concentration Pathways (RCP) derived by 11 general circulation models (GCMs)  
 685 for the period 2040-50 in Europe. Filled red for A1, dashed orange for A2, filled light green for B1 and dashed dark green for B2. Source RCPs:  
 686 Intergovernmental Panel on Climate Change 5<sup>th</sup> assessment - Coupled Model Intercomparison Project Phase 5.



687

688 Figure 3. Response curves of suitable areas (km<sup>2</sup>), accounting for saproxylic beetles dispersal distances, in relation to four land use change scenarios  
 689 (Stürck *et al.*, 2015) and four Representative Concentration Pathways (RCP) derived by 11 general circulation models (GCMs) for the period 2040-  
 690 50 in Europe. Filled red for A1, dashed orange for A2, filled light green for B1 and dashed dark green for B2. Source RCPs: Intergovernmental  
 691 Panel on Climate Change 5<sup>th</sup> assessment - Coupled Model Intercomparison Project Phase 5.



692



693 **SUPPORTING INFORMATION**

694 Additional supporting information may be found online, in the Supporting Information

695 section at the end of the article.