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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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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

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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), 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 10×10 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 10×10 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 km² and
202 4,661,300 km², 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 km² 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 Saproxyllic 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

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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.

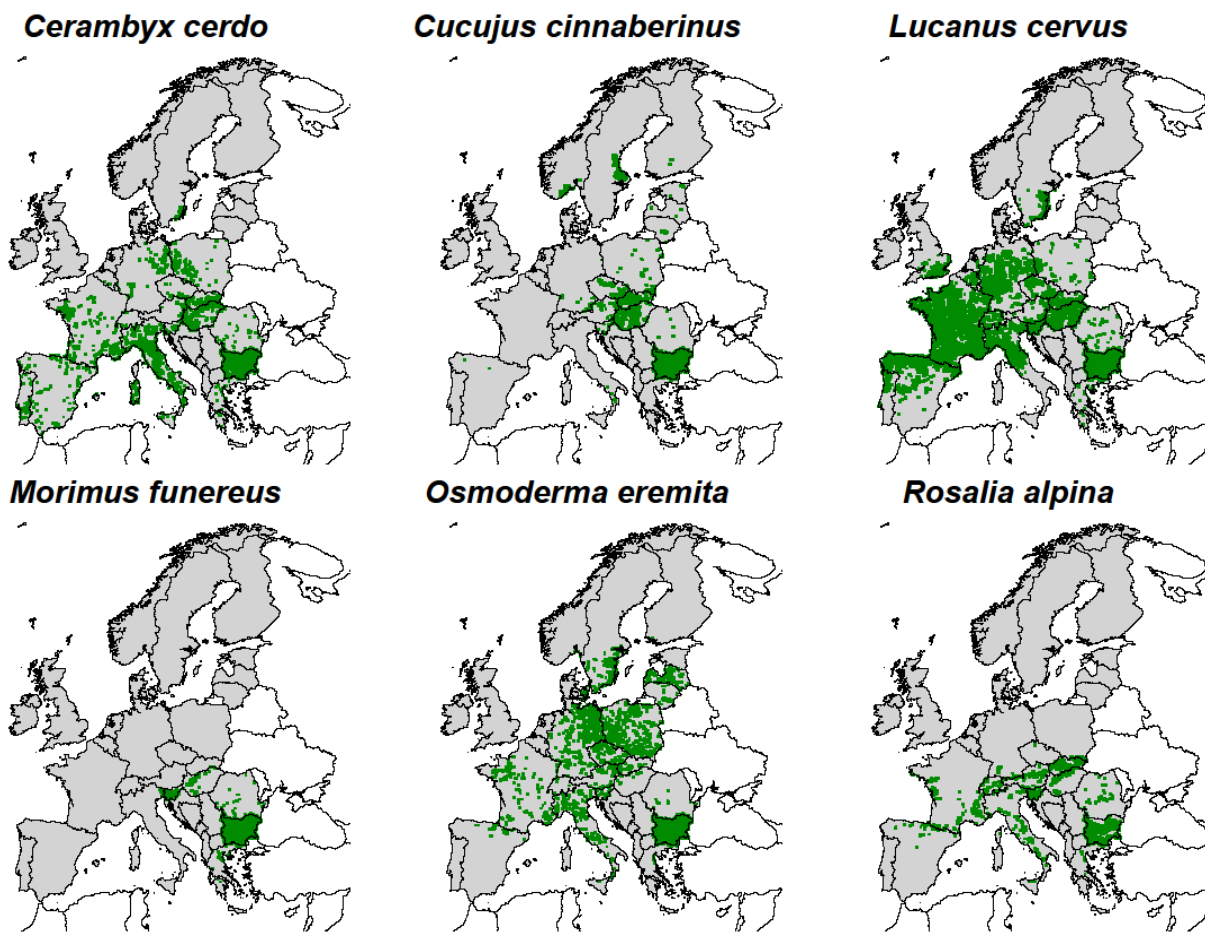
657 Table 1. Suitable areas (km²) for saproxylic beetles in Europe without considering species-
658 specific dispersal distances under future (2040-50) scenarios. Four land use change scenarios:
659 Libertarian Europe (A1), Eurosceptic Europe (A2), Social Democracy Europe (B1) and
660 European Localism (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 5th 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 (km²) 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 5th assessment - Coupled Model Intercomparison
678 Project Phase 5.

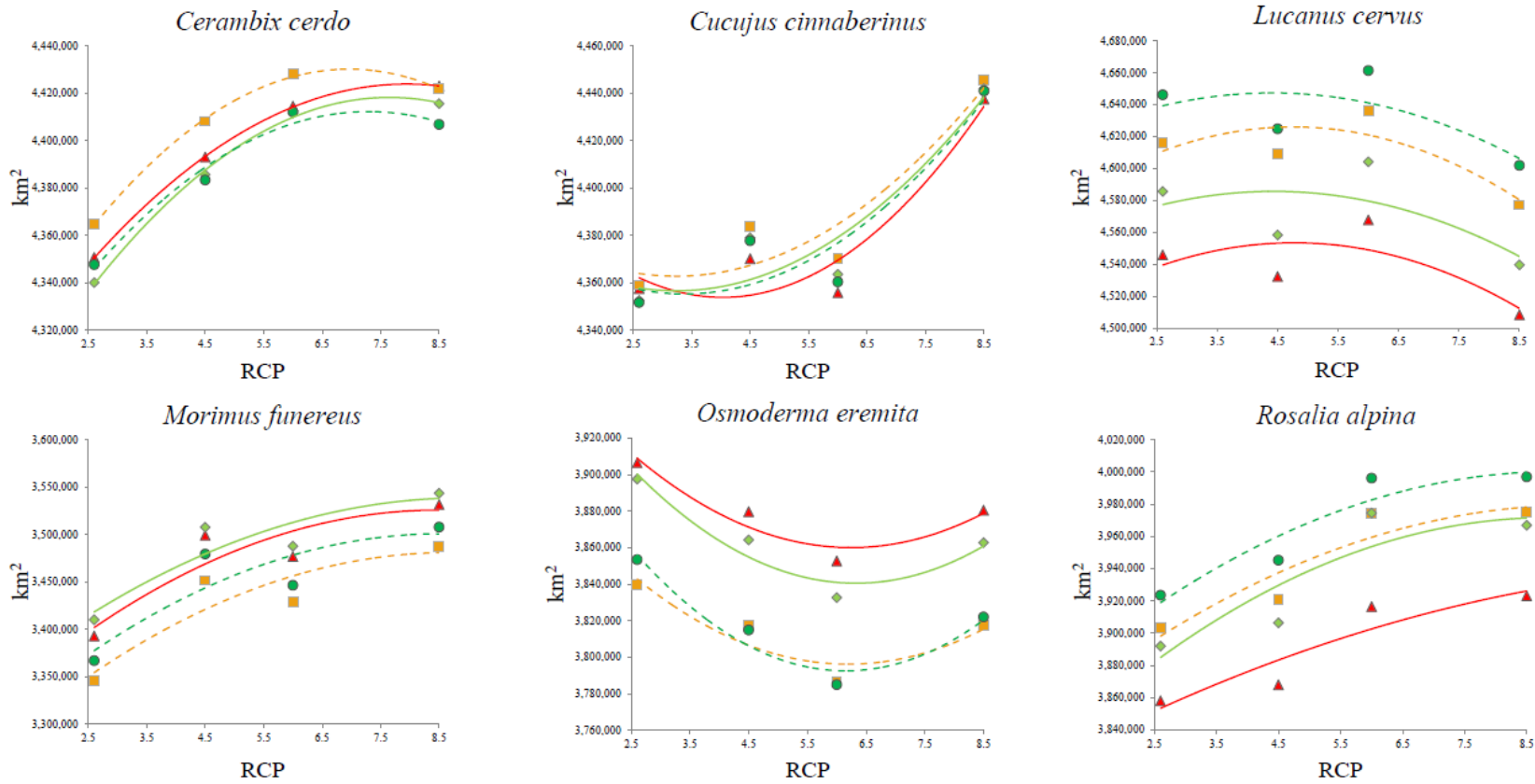
Species	RCP	A1	A2	B1	B2
<i>Cerambyx cerdo</i>	2.6	1,079,600	1,072,100	1,081,300	1,074,500
	4.5	1,083,500	1,083,000	1,087,200	1,076,100
	6	1,078,800	1,081,600	1,086,100	1,073,700
	8.5	1,090,000	1,089,700	1,091,500	1,086,500
<i>Cucujus cinnaberinus</i>	2.6	573,900	571,500	571,100	574,300
	4.5	578,300	577,700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



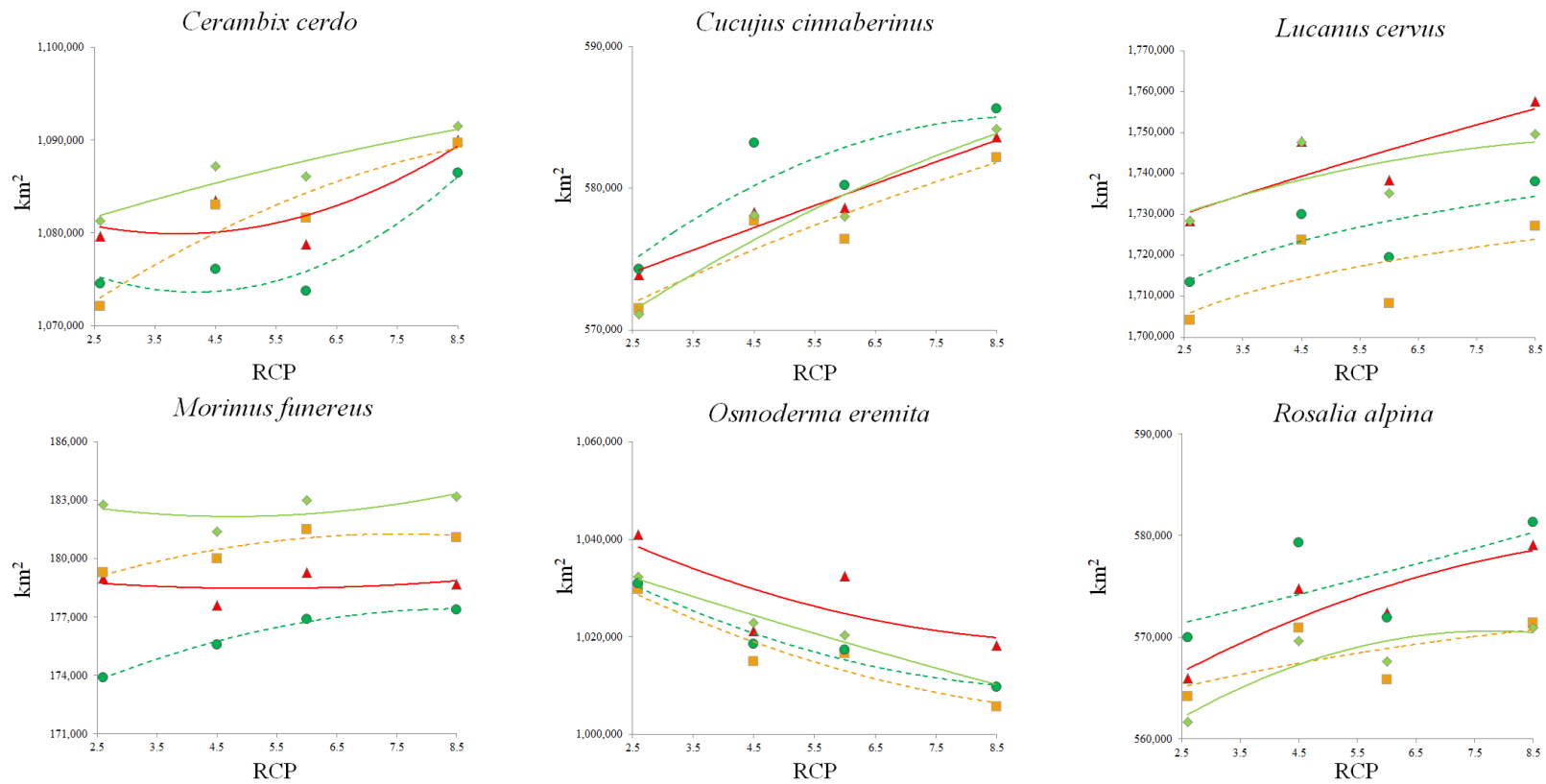
682

683 Figure 2. Response curves of suitable areas (km²), 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 5th assessment - Coupled Model Intercomparison Project Phase 5.



687

688 Figure 3. Response curves of suitable areas (km²), 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 5th assessment - Coupled Model Intercomparison Project Phase 5.



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693 **SUPPORTING INFORMATION**

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

695 section at the end of the article.