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1 **Demographic, ecological, and life-history traits associated with**  
2 **bird population response to landscape fragmentation in Europe**

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4

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22

23 **Abstract**

24 *Context:* Human land-use transformation has fragmented natural landscapes around the world,  
25 with fragmentation currently being considered a global threat to biodiversity conservation.

26 Landscape fragmentation, however, does not affect all species similarly, suggesting that some  
27 species characteristics may render species more sensitive to fragmentation than others.

28 *Objectives:* The aim of this study was to test whether demographic, ecological, and life-  
29 history traits are associated with vulnerability to landscape fragmentation in European  
30 breeding bird species.

31 *Methods:* Effective mesh size per area unit was used as an index of landscape fragmentation.

32 Vulnerability to fragmentation for every bird species was estimated as population response to  
33 fragmentation per se (controlling for habitat loss due to fragmenting elements), with more  
34 vulnerable species showing a negative relationship between population density and  
35 fragmentation among countries, and less vulnerable species showing no (or even a positive)  
36 relationship. Comparative analyses controlled for similarity among species due to common  
37 phylogenetic descent.

38 *Results:* Response to fragmentation was more often positive than negative, and it was  
39 positively related to population size, migration distance, and body mass, and negatively  
40 related to age at first reproduction. The relationship between response to fragmentation and  
41 population size did not allow us to assess whether being less abundant was the cause or the  
42 consequence of being vulnerable to fragmentation. Response to fragmentation was not  
43 significantly related to other demographic, ecological, and life-history characteristics.

44 *Conclusions:* These results suggest that small-sized resident bird species with delayed  
45 maturity are particularly vulnerable to landscape fragmentation. Future conservation efforts  
46 should target these species.

47

48 **Keywords:** body size, European breeding birds, fragmentation vulnerability, generation time,  
49 landscape fragmentation, migration  
50

## 51 **Introduction**

52

53 Landscape fragmentation is the process by which habitat loss at the landscape scale results in  
54 the division of large, continuous tracts of natural habitat into smaller, spatially distinct  
55 fragments immersed within a dissimilar matrix (Collinge 2009; Didham 2010; Jaeger et al.  
56 2011). This process implies a loss of original habitat, an increase in the number of habitat  
57 patches, a reduction in mean patch size, and an increase in patch isolation (Tschardt et al.  
58 2002; Fahrig 2003; Ewers and Didham 2006; Didham et al. 2012). Landscapes have been  
59 profoundly fragmented across the world owing to the expansion and intensification of human  
60 land use (Wade et al. 2003; Haddad et al. 2015; Wilson et al. 2016). While there is consensus  
61 on the large negative effects of habitat loss on biodiversity, there is currently no agreement on  
62 the effects of fragmentation per se. Some reviews suggest that fragmentation per se has weak  
63 effects on biodiversity (Fahrig 2003), and these effects, when present, are more likely to be  
64 positive than negative (Fahrig 2017). In contrast, other studies show evidence for large  
65 negative effects arising from a reduction in the size of habitat patches and from an increase in  
66 both patch isolation and the amount of habitat edge (Didham 2010; Haddad et al. 2015).  
67 These discrepancies possibly stem from multiple and complex effects of fragmentation on  
68 ecosystems, with indirect and interaction effects being major drivers of ecological change,  
69 sometimes operating across long periods of time (Didham et al. 2012; Ibáñez et al. 2014).

70 Landscape fragmentation and other human-induced environmental changes do not  
71 affect all species similarly. While many are negatively affected (losers), there is also a number  
72 of species that benefit from these changes (winners) (McKinney and Lockwood 1999).  
73 Interestingly, losers and winners are not randomly distributed among taxa or among  
74 functional ecological groups, which suggests that there are traits which render some species  
75 particularly sensitive to fragmentation and thus more prone to extinction. Identifying these

76 traits and understanding the differential vulnerability to fragmentation among species may  
77 have implications for ecological and evolutionary theory, and also for development of  
78 effective conservation (Laurance 1991; Kotiaho et al. 2005). A large number of species traits  
79 have been proposed to be associated with sensitivity to habitat fragmentation (reviews in  
80 Tschardt et al. 2002; Henle et al. 2004; Ewers and Didham 2006). In general, they are the  
81 same traits that have been postulated to predispose species to population decline and  
82 extinction (reviews in McKinney 1997; Purvis et al. 2000; Fisher and Owens 2004; O'Grady  
83 et al. 2004; Zavaleta et al. 2009), but there are exceptions depending on the type of extrinsic  
84 threat that is causing population decline of a species (Owens and Bennett 2000). It should  
85 also be considered that the relationship between particular species traits and the response to  
86 fragmentation can be complex, because different traits may interact and reinforce each other  
87 (Davies et al. 2004; Wang et al. 2015).

88         The species characteristics that have been suggested to be associated with  
89 vulnerability to habitat fragmentation constitute three categories: demographic, ecological,  
90 and life-history traits. Among demographic traits we focus on population size (abundance),  
91 population trend, and heterogeneity of distribution. Population size (or population density) is  
92 one of the best predictors of sensitivity to fragmentation (e.g., Bolger et al. 1991; Foufopoulos  
93 and Ives 1999; Davies et al. 2000; Gonzalez and Chaneton 2002; Feeley et al. 2007; Wang et  
94 al. 2009), with less abundant species more likely declining in numbers and going extinct as a  
95 consequence of habitat fragmentation. On the other hand, species with more heterogeneous  
96 spatial distributions are predicted to be more susceptible to habitat fragmentation, because  
97 these species share characteristics generally associated with inability to cope with  
98 environmental change (Møller et al. 2010).

99         In relation to ecological traits, the main predictors of fragmentation sensitivity seem to  
100 be dispersal capacity and ecological plasticity, although migration may also play a role.

101 Theoretical models predict that species characterized by poor dispersal capacity will be more  
102 negatively affected by habitat fragmentation (Liao et al. 2013), a prediction confirmed by  
103 empirical studies (Ekroos et al. 2010; Öckinger et al. 2010; Benschoter et al. 2013; Benchimol  
104 and Peres 2015). However, different patterns have also been observed in some cases, possibly  
105 because of interactions with other traits such as home range, sociality, or population density  
106 (Thomas 2000; Van Houtan et al. 2007). More consistent results have been found on  
107 ecological plasticity, with specialist species showing higher vulnerability to fragmentation  
108 than generalist ones (e.g., Davies et al. 2004; Feeley et al. 2007; Devictor et al. 2008; Wang et  
109 al. 2015; Khimoun et al. 2016; Keinath et al. 2017). Regarding migration, sedentary species  
110 have been found to be more vulnerable to landscape changes than dispersive or migratory  
111 ones (Newbold et al. 2013; Pavlacky et al. 2015). However, migration behaviour can be both  
112 beneficial (e.g., avoiding harsh winter conditions) and detrimental (e.g., migration itself can  
113 be risky), and can interact with other species traits or with characteristics of the environment.

114 Life-history traits associated with low reproductive potential (low fecundity, long  
115 generation time) generally render species more vulnerable to habitat loss and fragmentation  
116 (Vance et al. 2003; Öckinger et al. 2010; Newbold et al. 2013; Pavlacky et al. 2015).  
117 Longevity, in contrast, has been suggested to decrease vulnerability to habitat fragmentation  
118 (Karr 1990) and other environmental changes (Morris et al. 2008). However, the role of  
119 longevity in fragmentation sensitivity is unclear (e.g., Henle et al. 2004), possibly because  
120 high longevity is also associated with low reproductive potential (Roff 1992), which, in turn,  
121 makes species more vulnerable to fragmentation. Large body size is simultaneously  
122 associated with traits making species more (e.g., low abundance and low reproductive  
123 potential) and less (e.g., high dispersal capacity) susceptible to habitat fragmentation, so the  
124 net effect is probably context dependent and difficult to predict. Although most empirical  
125 studies have found that larger species are more vulnerable to fragmentation (e.g., Feeley et al.

126 2007; Urquiza-Haas et al. 2009; Kormann et al. 2015; Pavlacky et al. 2015), in some cases  
127 smaller species were more vulnerable (Cosson et al. 1999; Boyle and Sigel 2015).

128         The aim of this study was to test the hypothesis that demographic, ecological, and life-  
129 history traits are associated with vulnerability to landscape fragmentation. Specifically, we  
130 predicted that vulnerable species would be characterized by small population size, negative  
131 population trend, high heterogeneity of spatial distribution, poor dispersal capacity, low  
132 ecological plasticity, non-migratory habits, low fecundity, long generation time, short  
133 longevity, and large body size. While some predictions seem to be robust according to the  
134 literature (e.g., regarding ecological plasticity), others are less clear because different studies  
135 have found contrasting results (e.g., regarding body size; see references above). Vulnerability  
136 to landscape fragmentation was estimated in terms of population response to fragmentation,  
137 with more vulnerable species having high and low population density in little and heavily  
138 fragmented areas, respectively, while less vulnerable species show no or even a positive  
139 relationship between population density and fragmentation. The hypothesis was tested in  
140 European breeding bird species because birds are one of the best studied classes of animals,  
141 particularly in Europe (so a large amount of information is available), and because Europe is  
142 the continent most affected by human-caused fragmentation (Wade et al. 2003). In addition,  
143 continent-wide programmes, such as the Pan-European Common Bird Monitoring Scheme,  
144 and international collaboration (e.g., Jaeger et al. 2011) provide the opportunity to estimate  
145 both bird population sizes and landscape fragmentation with standardized methodologies, thus  
146 making information from different European countries comparable.

147

148

## 149 **Materials and methods**

150



151 Landscape fragmentation index and response to fragmentation

152

153 An estimate of effective mesh density (i.e., the effective number of landscape patches per area  
154 unit) for each country was used as our index of landscape fragmentation. This estimate,  
155 obtained from Annex 1 in Jaeger et al. (2011), represented the number of times that the  
156 effective mesh size (calculated for the year 2009) fitted into an area of 1000 km<sup>2</sup>. Effective  
157 mesh size is based on the probability that two points chosen randomly in a region are not  
158 separated by any barriers, and it is calculated by multiplying this probability by the area of the  
159 region (Jaeger 2000; Jaeger et al. 2008). Both effective mesh size and density depend on  
160 which kind of landscape elements are considered to be barriers. Jaeger et al. (2011) defined a  
161 set of fragmenting elements, called fragmentation geometry, that included anthropogenic  
162 barriers (motorways and major roads, connecting roads, railway lines, and built-up areas) and  
163 natural barriers (lakes and major rivers) of non-mountainous land areas. This fragmentation  
164 geometry gave rise to an estimate of effective mesh density, i.e., a fragmentation index,  
165 representing anthropogenic and natural fragmentation of non-mountainous land areas.

166 We estimated response to fragmentation for each bird species as the partial correlation  
167 coefficient from a multiple regression across countries, with population size as the response  
168 variable, fragmentation index as the predictor, and country area, latitude, longitude,  
169 percentage of agricultural land, and percentage of country area covered by barriers as  
170 confounding variables. Inclusion of confounding variables in the regression analyses meant  
171 that estimates of response to fragmentation were controlled for these variables. Large positive  
172 values imply a strong and positive response to fragmentation: the more fragmented the  
173 landscape, the more abundant the species. In contrast, large negative values imply a strong  
174 and negative response to fragmentation: the more fragmented the landscape, the less abundant  
175 the species. Values around zero imply weak or no effect of landscape fragmentation on

176 abundance. Population sizes of bird species in European countries were obtained from  
177 BirdLife International (2004), and area of countries was the area for which bird population  
178 sizes had been estimated. Latitude and longitude for each country were estimated,  
179 respectively, as the latitude of the mid-point between the northernmost and the southernmost  
180 mainland points, and the longitude of the mid-point between the easternmost and the  
181 westernmost mainland points of every country. Percentage of agricultural land in each  
182 country was obtained from the Central Intelligence Agency (2016) World Factbook.  
183 Percentage of country area covered by barriers (i.e., by artificial areas and water bodies) was  
184 calculated from land cover information for the years 2006 and 2012 (the average of the two  
185 years) provided by the European Environment Agency (2017). Artificial areas included  
186 transport networks and infrastructures, urban fabric (housing, services, and recreation),  
187 industrial and commercial units, and mineral extraction sites. Water bodies included lakes,  
188 reservoirs, and water courses.

189         Controlling for the percentage of country area covered by barriers was important to  
190 control for habitat loss caused by the presence of barriers and to estimate response to  
191 fragmentation per se. Habitat loss is inherent to landscape fragmentation, because  
192 fragmentation is impossible without habitat loss (Didham et al. 2012), and this intrinsic  
193 dependence gives rise to a strong association between the two parameters (Fahrig 2003). As a  
194 result, if we studied vulnerability to landscape fragmentation without controlling for habitat  
195 loss due to fragmenting elements (barriers), it would be impossible to distinguish between the  
196 effect of fragmentation per se and the effect of habitat loss. As we were interested in the effect  
197 of fragmentation on biodiversity independent of amount of habitat, habitat loss due to  
198 fragmenting elements was controlled when estimating population response to fragmentation.  
199 Therefore, in the present study, we explicitly focused on the possible association between  
200 certain species-specific characteristics and vulnerability to landscape fragmentation per se.

201           It should be noted that habitat is, by definition, a species-specific concept, so habitat  
202 loss and fragmentation are also species-specific (Haila 2002). Ideally, fragmenting elements  
203 should have been defined for each species, because what represents a barrier for one species  
204 may not be a barrier for others. Similarly, population size of every species should have been  
205 estimated for each habitat type within each country, because some habitats are not suitable for  
206 some species. However, all this information is unavailable for most European bird species, so  
207 a species-centred approach (Betts et al. 2014) was not possible. We tried to compensate for  
208 the lack of species-specific detail by including in the study a large number of species and by  
209 covering a wide geographic area.

210           For further information on landscape fragmentation index and calculation of bird  
211 population response to landscape fragmentation, see Online Appendix S1. Fragmentation  
212 index, country area, latitude, longitude, percentage of agricultural land, and percentage of  
213 country area covered by barriers for each country are reported in Online Table S1. Population  
214 size for each bird species and country is reported in Online Table S2.

215

216

217 Demographic, ecological, and life-history characteristics of bird species

218

219 Population size (number of breeding pairs) of bird species in the Western Palearctic west of  
220 the Ural Mountains was obtained from Hagemeyer and Blair (1997). Population trend for  
221 every bird species in Europe during the period 1990-2000 was estimated using an assessment  
222 by BirdLife International (2004) on a seven-category scale: large increase (3), moderate  
223 increase (2), small increase (1), stable (0), small decline (-1), moderate decline (-2), and large  
224 decline (-3). Heterogeneity of distribution was estimated as the coefficient of variation in  
225 population density among European countries (for more details, see Møller et al. 2010).

226 Migration distance was estimated as breeding latitude minus wintering latitude, considering  
227 latitudes in the Southern Hemisphere as negative values. Breeding latitude was determined as  
228 the mean of the northernmost and southernmost latitudes of the breeding distribution to the  
229 nearest tenth of a degree. Similarly, wintering latitude was determined as the mean of the  
230 northernmost and southernmost latitudes of the wintering distribution. Breeding and wintering  
231 ranges were obtained from maps in Cramp and Perrins (1977-1994). Maximum dispersal  
232 distance was estimated as the minimum distance from the mainland to an island with a  
233 permanent breeding population, using information from distribution maps in Cramp and  
234 Perrins (1977-1994). This estimate of dispersal distance was preferred to others (e.g., natal  
235 dispersal; Paradis et al. 1998) because it was available for a much larger number of species.  
236 Ecological plasticity was estimated as the number of different habitats in which a species has  
237 been known to breed. Number of habitats was obtained from the habitat preferences listed by  
238 Cramp and Perrins (1977-1994) for each species, considering only habitats that appeared in  
239 their glossary (for more details, see Belliure et al. 2000; Møller and Garamszegi 2012). Body  
240 mass and life-history traits (fecundity, longevity, and generation time) for each bird species  
241 were obtained from Cramp and Perrins (1977-1994). Mean body mass was calculated as the  
242 mean of male and female body mass. Longevity was estimated as annual adult survival rate.  
243 Annual fecundity was calculated by multiplying clutch size (mean number of eggs) by  
244 maximum number of clutches per season. In the case of generation time, estimated as age at  
245 first reproduction, information was also obtained from Glutz von Blotzheim and Bauer (1985-  
246 1997). More information on bird species traits can be found in Online Appendix S1 and raw  
247 data are reported in Online Table S3.

248

249

250 Comparative methods

251  
252 Possible relationships between population response to landscape fragmentation and species-  
253 specific parameters were tested with phylogenetic generalized least square regression models  
254 (Martins and Hansen 1997; Pagel 1997, 1999) implemented in the R statistical environment  
255 (R Core Team 2014). To account for phylogenetic relationships among species in our  
256 analyses, we downloaded 1000 phylogenetic trees from <http://birdtree.org/> (Jetz et al. 2012)  
257 using the option “Ericson All Species”. Then, a majority rules consensus tree (Online  
258 Appendix S2) was estimated in the Mesquite environment (Maddison and Maddison 2015)  
259 and included in the models as a design matrix. The optimum degree of phylogenetic  
260 dependence was identified for each model, and the corresponding lambda parameter ( $\lambda$ )  
261 included in subsequent analyses. We performed weighted analyses using the number of  
262 countries from which response to fragmentation had been estimated minus seven as a weight  
263 (weight range = 1-19). Specifically, a matrix of 1/weight was added as an error term, and this  
264 term was multiplied by different values until the value providing the highest maximum  
265 likelihood was found. This method has been used and described in detail in previous studies  
266 (e.g., Garamszegi and Møller 2007).

267         Number of species with information for each parameter ranged from 137 in the case of  
268 heterogeneity of distribution to 261 species in the case of population size (Online Table S4).  
269 However, number of species with information for all ten parameters was only 73. To avoid a  
270 drastic reduction in sample size (and thus statistical power), we decided not to include all  
271 factors simultaneously in the same model, but to perform a forward stepwise selection of  
272 variables (see Online Table S4 for details). The final model included parameters related to  
273 response to fragmentation with  $P < 0.10$  because a threshold of 0.05 is considered too  
274 stringent and can fail to identify potentially important variables (Bendel and Afifi 1977).  
275 Although stepwise variable selection has been criticized on various grounds, e.g., because the

276 final model is sometimes not the best model (Whittingham et al. 2006), we assume this was  
277 not a problem in our case, since backward stepwise procedure selected exactly the same  
278 variables (Online Table S5). Akaike's (1974) information criterion was not used to select the  
279 best model because it implied a reduction in sample size to only 73 species. More information  
280 on statistical analysis can be found in Online Appendix S1.

281

282

## 283 **Results**

284

285 We expected most bird species to have a negative response to landscape fragmentation, but  
286 the response was significantly more often positive than negative (sign test;  $z = 4.33$ ,  $n = 261$ ,  
287  $P < 0.001$ ; Fig. 1). Most responses to fragmentation were close to zero or slightly positive,  
288 with relatively few species showing very large (either positive or negative) values (Fig. 1).

289 Demographic, ecological, and life-history characteristics that entered the final model  
290 were population size, migration distance, body mass, and age at first reproduction (Table 1  
291 and Online Tables S4 and S5). All these parameters were significantly related to bird  
292 population response to landscape fragmentation, with a positive relationship for population  
293 size, migration distance, and body mass, and a negative relationship for age at first  
294 reproduction (Table 1, Fig. 2). The relationship between response to fragmentation and age at  
295 first reproduction was just marginally significant (Table 1). All other species-specific  
296 characteristics (population trend, heterogeneity of distribution, dispersal distance, number of  
297 habitats, annual fecundity, and adult survival) were not significantly related to our estimate of  
298 response to fragmentation, and, hence, they were not included in the final model (Online  
299 Tables S4 and S5).

300

301

## 302 **Discussion**

303

304 Contrary to the general belief that landscape fragmentation per se (independent of amount of  
305 habitat) has detrimental effects on biodiversity (e.g., Haila 2002), we found that population  
306 response to fragmentation in European bird species was more often positive than negative.

307 This result agrees with previous studies suggesting that significant ecological responses to  
308 fragmentation are mostly positive (Fahrig 2017). Population response to fragmentation,  
309 however, varied greatly among species, and some (e.g., *Prunella collaris*, *Tetrao urogallus*,  
310 *Tichodroma muraria* or *Oenanthe oenanthe*, just to cite a few) responded strongly and  
311 negatively to fragmentation, i.e., they were particularly vulnerable to the breaking apart of  
312 habitat. At least for these species, fragmentation might be an important issue to take into  
313 account should conservation measures be needed.

314 The relationships between population response to landscape fragmentation and the  
315 species parameters studied here suggest that European birds responded more negatively to  
316 fragmentation (i.e., showed lower population densities in more fragmented countries) in  
317 scarce, small, resident species with delayed maturation (Table 1). In the case of population  
318 size, the positive relationship might imply higher vulnerability to fragmentation in less  
319 abundant species, a conclusion reached in numerous studies (see Introduction). Another  
320 possible, non-mutually exclusive interpretation of the result is that species particularly  
321 vulnerable to fragmentation for reasons other than small population size experienced more  
322 pronounced decreases in abundance in highly fragmented countries. In that case, small  
323 population size would be a consequence and not the cause of vulnerability to fragmentation.  
324 In this study, population sizes of bird species in Europe were estimated in the 1990s  
325 (Hagemeijer and Blair 1997), while population sizes for every European country, the base for

326 calculating response to fragmentation, were estimated between 1990 and 2002 (BirdLife  
327 International 2004), that is, simultaneously or slightly later. Consequently, there was little  
328 time for new fragmentation between the two sets of avian censuses, and limited opportunities  
329 for population size causing different population trends depending on the level of landscape  
330 fragmentation in every country. Although some effects of population size on the response to  
331 fragmentation cannot be ruled out, the small population size in some bird species in the 1990s  
332 was probably the consequence of humans transforming, and thus fragmenting, the European  
333 landscape intensively for many decades (or even centuries) before the data were collected.  
334 The timing of bird censuses in this study was not appropriate for testing the possible effect of  
335 population size on vulnerability to landscape fragmentation.

336         Regarding migratory habits, our study suggests that sedentary bird species are more  
337 vulnerable to landscape fragmentation than migratory ones, as in tropical forest birds  
338 (Newbold et al. 2013; Pavlacky et al. 2015). It should be noted that resident bird species stay  
339 all year round in Europe, so they are affected by habitat fragmentation in Europe both during  
340 breeding and non-breeding, while migratory species are affected by fragmentation in Europe  
341 only during reproduction. During the last third of the 20th century, long-distance migrants  
342 declined in Europe to a larger extent than short-distance migrants or residents, and different  
343 processes have been suggested to drive this differential decline (Sanderson et al. 2006). Our  
344 results clearly suggest that landscape fragmentation in Europe is not responsible for the more  
345 negative trends of long-distance migrants, so other explanations should be invoked. When all  
346 existing birds are considered, migratory species are overall less likely to be threatened with  
347 extinction than sedentary species (Şekercioğlu 2007). The higher vulnerability to habitat  
348 fragmentation shown by sedentary species in this study might help explain this pattern.

349         The mechanism behind the higher vulnerability of sedentary species to fragmentation  
350 is unknown, but we can speculate that roads (or any parameter associated with road density)



351 had a more negative effect for sedentary than migratory bird species. Roads and traffic  
352 generally have a negative effect on animal abundance (review in Fahrig and Rytwinski 2009),  
353 mainly because they reduce the amount of habitat, increase mortality due to collision with  
354 vehicles, limit access to resources, and subdivide populations into smaller units (Jaeger et al.  
355 2005). In general, all these effects might be more detrimental for sedentary species because  
356 they spend all year in Europe. However, it is also possible that detrimental effects of roads are  
357 more intense in winter, when resources (e.g., food) are scarce and reduce body condition,  
358 survival, and abundance of birds, at least at middle and high latitudes (Doherty and Grubb  
359 2002; Carrascal et al. 2012; Morosinotto et al. 2017). For example, birds might need a larger  
360 home range during winter (e.g., Morganti et al. 2017), but less suitable habitat would be  
361 available in high road-density areas. Similarly, certain areas of high-quality habitat might be  
362 crucial for winter survival, thus attracting birds during this time of the year (e.g., Smith et al.  
363 2014), but they might also be areas with high road density, with the consequent increase in  
364 traffic-related mortality. This could happen for example if valley bottoms concentrate most  
365 roads, but also a high proportion of birds in winter.

366         Our study suggests that small bird species are more vulnerable to landscape  
367 fragmentation than large ones, a result consistent with previous research on vertebrates in  
368 tropical forests (Cosson et al. 1999; Boyle and Sigel 2015). As explained in the Introduction,  
369 the relationship between body size and response to fragmentation was difficult to predict,  
370 because body size is simultaneously associated with traits making species more or less  
371 susceptible to fragmentation, so the net effect is probably context dependent. The simplest  
372 explanation for our result would be that body size is generally positively associated with  
373 dispersal distance (Jenkins et al. 2007) and survival (McCarthy et al. 2008; Collingham et al.  
374 2014), two traits that presumably make species less vulnerable to fragmentation (see  
375 Introduction). However, dispersal distance and adult survival were not significantly related to

376 response to fragmentation in this study, thus suggesting that the relationship between body  
377 size and response to fragmentation was not mediated by these traits. In addition, large bird  
378 species are less sensitive to low winter temperatures or temporal food scarcity (Peters 1983),  
379 environmental conditions that might be associated with habitat fragmentation (e.g.,  
380 fragmented habitats might have less refuge or food). Body size is related to almost every  
381 demographic, ecological, physiological or life-history trait of a species (Peters 1983), so it is  
382 difficult to disentangle the precise mechanisms behind the relationship between body size and  
383 response to fragmentation. Finally, bird abundance decreased dramatically in Europe during  
384 the last decades of the 20th century, but this reduction in abundance mostly affected small  
385 species, while large ones remained relatively stable or even increased in population size  
386 (Inger et al. 2015). According to our results, landscape fragmentation in Europe during the  
387 late 20th century (or any process associated with fragmentation) might be one of the factors  
388 responsible for the more negative population trends of small bird species.

389         Among life-history traits, only age at first reproduction (a proxy for generation time)  
390 was significantly related to response to fragmentation, with a more negative response in  
391 delayed breeders, as expected. Although the relationship was marginally significant, and thus  
392 should be interpreted with caution, this result is consistent with a previous study showing that  
393 tropical forest bird species with longer generation time are more negatively affected by human  
394 land use (Newbold et al. 2013). The most straightforward explanation for our result would be  
395 that long generation time implies low reproductive potential and probably less capacity to  
396 recover from perturbations and population crashes. However, other life-history traits generally  
397 considered prime indicators of reproductive potential (e.g., annual fecundity) were not  
398 significantly related to response to fragmentation, and thus other mechanisms have to be  
399 invoked. The relationship between response to fragmentation and generation time was not  
400 mediated by body size (larger bird species generally show longer generation time; Sæther

401 1987), because body mass was controlled in the analysis (Table 1). It has previously been  
402 shown that bird species with longer generation time suffer a higher extinction risk when the  
403 main source of extinction is human persecution or introduced predators (Owens and Bennett  
404 2000). In our case, landscape fragmentation might entail an increase in predation-related  
405 mortality, thus having a more negative effect in species with longer generation time. For  
406 example, roads might enhance access of pets (cats, dogs) or hunters to natural habitats, and  
407 traffic itself can cause mortality due to collisions with vehicles (Fahrig and Rytwinski 2009).  
408 In addition, more fragmented landscapes usually contain more edge for a given amount of  
409 habitat, often resulting in increased predation by natural predators (Chalfoun et al. 2002).

410       According to theoretical models (e.g., Fahrig 1998; With and King 1999), populations  
411 under certain conditions are expected to show thresholds in their response to landscape  
412 fragmentation. These thresholds might reflect a non-linear relationship between the degree of  
413 fragmentation and population size (e.g., an accelerated rate of population decline after a  
414 critical fragmentation level is passed) or could result from an increasing effect of  
415 fragmentation on population size below some level of habitat amount. However, empirical  
416 research on birds has found mixed support for the existence of landscape-scale thresholds, as  
417 some studies detected them (e.g., Betts et al. 2007), but others did not (e.g., Villard et al.  
418 1999). If we assume that thresholds were relevant in our study, species showing high  
419 vulnerability to fragmentation might be species whose thresholds have been reached. Thus, as  
420 landscape fragmentation increases (or suitable habitat is lost) a disproportionately greater  
421 proportion of species would be considered vulnerable to fragmentation. For the many bird  
422 species in this study showing a positive response to fragmentation, a threshold could be the  
423 level of fragmentation above which (or the level of habitat amount below which) the response  
424 to fragmentation becomes negative.

425           Some species characteristics were predicted to be associated with vulnerability to  
426 habitat fragmentation, but this study does not support such associations. This happened for  
427 example for dispersal capacity or heterogeneity of spatial distribution, although probably the  
428 most striking case is ecological plasticity. Previous studies (many of them on birds) have  
429 consistently found higher sensitivity to habitat fragmentation in specialist than in generalist  
430 species (see Introduction). However, most of these studies, particularly those on birds (e.g.,  
431 Feeley et al. 2007; Devictor et al. 2008; Wang et al. 2015), did not investigate the effects of  
432 fragmentation per se, but the effects of habitat patch size or isolation, which are inherently  
433 confounded with effects of amount of habitat (Fahrig 2003, 2017). Moreover, both ecological  
434 plasticity and vulnerability to fragmentation have been estimated in different ways in this and  
435 previous studies, which might affect the results. Finally, the temporal framework of this study  
436 might also have played a role, because it is known that time lag is very important for  
437 understanding the impact of fragmentation on animal populations (Bennett and Saunders  
438 2010). While some species characteristics might only be related to vulnerability to  
439 fragmentation when long-term effects are studied, it is possible that other characteristics  
440 appear to be related in the short term.

441           To summarize, this study suggests that small-sized resident bird species with delayed  
442 maturation are particularly vulnerable to landscape fragmentation in Europe, considering  
443 fragmentation as the breaking apart of habitat independent of amount of habitat. Vulnerability  
444 to fragmentation was also related to small population size, but it is unclear if being less  
445 abundant is the cause or the consequence of vulnerability to fragmentation. Other species  
446 characteristics such as dispersal distance, habitat specialization, annual fecundity or adult  
447 survival were not significantly related to susceptibility to fragmentation. These results could  
448 be useful for understanding and predicting, and maybe also mitigating, the effects of  
449 landscape fragmentation on biodiversity.

450 **References**

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684

685 **Electronic Supplementary Material**

686

687 **Appendix S1** Additional information on Materials and methods

688

689 **Appendix S2** Consensus phylogenetic tree in Phylip format used to test for relationships  
690 between bird population response to landscape fragmentation and a number of demographic,  
691 ecological, and life-history characteristics of bird species

692

693 **Table S1** Fragmentation index, area, latitude, longitude, percentage of agricultural land, and  
694 percentage of country area covered by barriers for the countries included in the study

695

696 **Table S2** Population size for each bird species within each country

697

698 **Table S3** Demographic, ecological, and life-history characteristics of the bird species  
699 included in the study

700

701 **Table S4** Forward stepwise procedure used to determine the final model (set of species-  
702 specific characteristics) that best predicted the estimates of bird population response to  
703 landscape fragmentation

704

705 **Table S5** Backward stepwise procedure used to determine the final model (set of species-  
706 specific characteristics) that best predicted the estimates of bird population response to  
707 landscape fragmentation

708

709 **Table 1** Phylogenetic generalized least square regression model on factors related to bird  
710 population response to anthropogenic and natural fragmentation of non-mountainous land  
711 areas. The final model only included parameters related to response to fragmentation with  $P <$   
712 0.10 after a forward stepwise procedure. A backward stepwise procedure provided the same  
713 final model. Phylogenetic relations among species and number of countries used to estimate  
714 response to fragmentation in each species were controlled in the analyses (see Comparative  
715 methods for details). Both the dependent variable and its residuals were approximately  
716 normally distributed (Kolmogorov-Smirnov test for normality;  $P > 0.05$  in the two tests), thus  
717 justifying the use of a linear model approach. The model had the statistics:  $F = 6.35$ ,  $\text{adj-}r^2 =$   
718 0.088,  $n = 224$ ,  $P < 0.001$ ,  $\lambda = 0.000$   
719

Factors	Estimate (SE)	$t$	$P$
Population size	0.079 (0.029)	2.75	0.0065
Migration distance	0.032 (0.008)	4.14	< 0.001
Body mass	0.095 (0.041)	2.31	0.022
Age at first reproduction	-0.064 (0.032)	-1.99	0.047

720



721 **Figure legends**

722

723 **Figure 1** Frequency distribution of response to landscape fragmentation (anthropogenic and  
724 natural fragmentation of non-mountainous land areas) in 261 European bird species. Mean  
725 (SD) = 0.094 (0.396), median = 0.177, skewness = -0.444

726

727 **Figure 2** Relationships between relative estimates of bird population response to  
728 anthropogenic and natural fragmentation of non-mountainous land areas and (a) relative  
729 population size, (b) relative migration distance, (c) relative body mass, and (d) relative age at  
730 first reproduction in European bird species. Relative estimates of response to fragmentation  
731 were estimated as the residuals from a model with response to fragmentation as the response  
732 variable and (a) migration distance, body mass, and age at first reproduction, (b) population  
733 size, body mass, and age at first reproduction, (c) population size, migration distance, and age  
734 at first reproduction, and (d) population size, migration distance, and body mass as predictors.  
735 Relative population size was estimated as the residuals from a model with population size as  
736 the response variable and migration distance, body mass, and age at first reproduction as  
737 predictors. Relative migration distance was estimated as the residuals from a model with  
738 migration distance as the response variable and population size, body mass, and age at first  
739 reproduction as predictors. Relative body mass was estimated as the residuals from a model  
740 with body mass as the response variable and population size, migration distance, and age at  
741 first reproduction as predictors. Relative age at first reproduction was estimated as the  
742 residuals from a model with age at first reproduction as the response variable and population  
743 size, migration distance, and body mass as predictors. All variables except age at first  
744 reproduction and response to fragmentation were transformed before the analyses (Appendix  
745 S1). Lines are best-fit regressions (a:  $y = -0.018 + 0.073 x$ ; b:  $y = -0.002 + 0.032 x$ ; c:  $y =$

746  $0.022 + 0.078 x$ ; d:  $y = 0.017 - 0.051 x$ ). All models and regressions took into account the  
747 number of countries used to estimate response to fragmentation (bubble size indicates this  
748 number; range = 8-26) and similarities among species due to common phylogenetic descent  
749 (see Comparative methods for details)

Figure 1

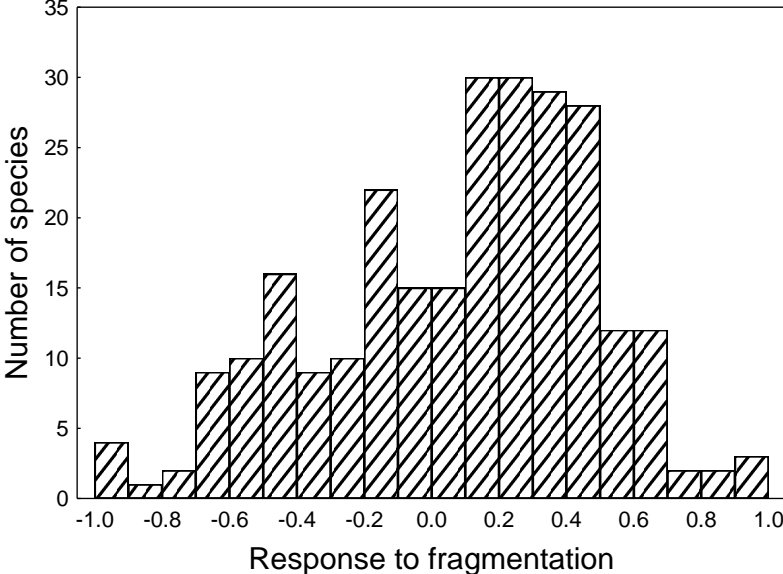
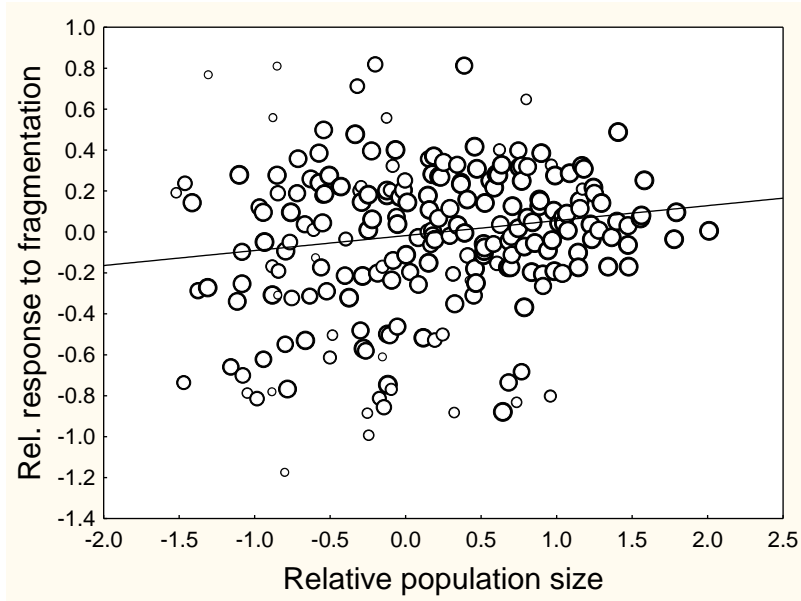
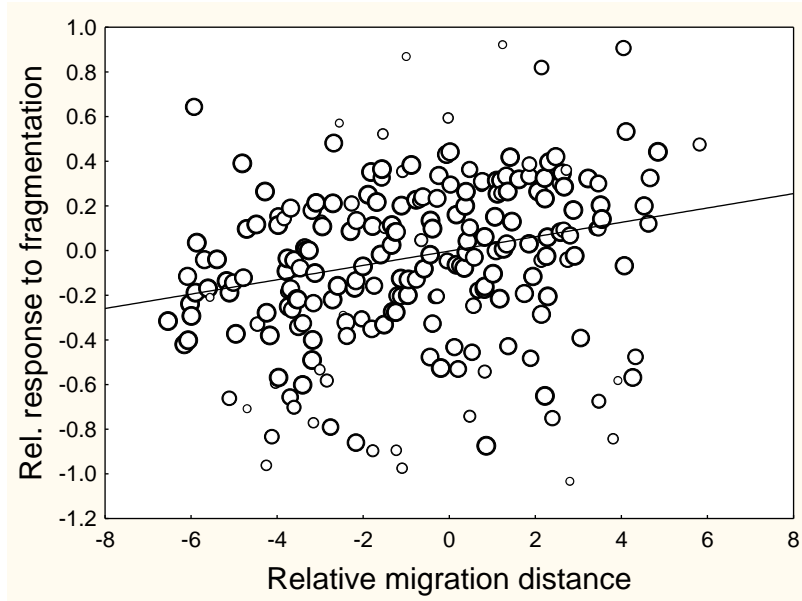


Figure 2

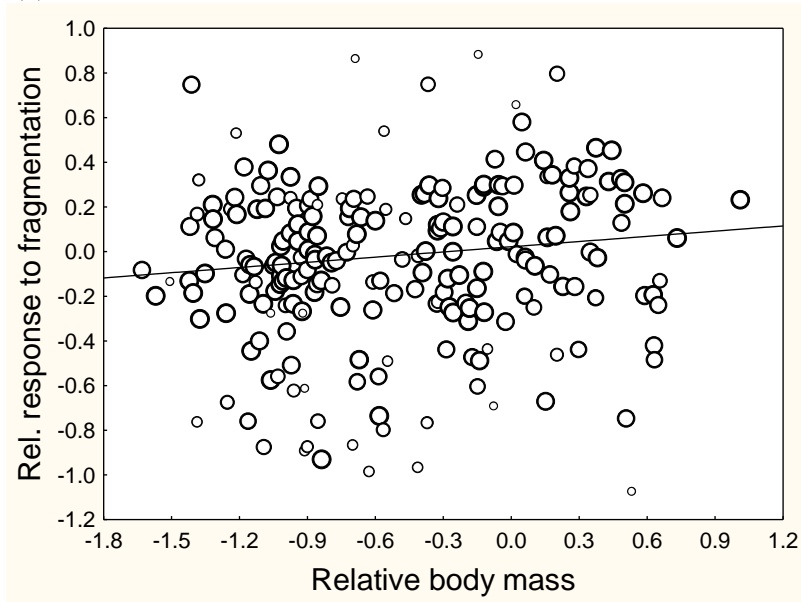
(a)



(b)



(c)



(d)

