RESEARCH ARTICLE

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

José Javier Cuervo · Anders Pape Møller

Abstract

Context Human land-use transformation has fragmented natural landscapes around the world, with fragmentation currently being considered a global threat to biodiversity conservation. Landscape fragmentation, however, does not affect all species similarly, suggesting that some species characteristics may render species more sensitive to fragmentation than others.

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

Methods Effective mesh size per area unit was used as an index of landscape fragmentation. Vulnerability to fragmentation for every bird species was estimated as population response to fragmentation per se (controlling for habitat loss due to fragmenting elements), with more vulnerable species showing a negative relationship between population density and fragmentation among countries, and less vulnerable species showing no (or even a positive) relationship. Comparative analyses controlled for similarity among species due to common phylogenetic descent.

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

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

J. J. Cuervo (✉)
Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Calle José Gutiérrez Abascal 2, 28006 Madrid, Spain
e-mail: jjcuervo@mncn.csic.es

A. P. Møller
Ecologie Systématique Evolution, Université Paris-Sud, CNRS, AgroParisTech, Université Paris-Saclay, 91405 Orsay Cedex, France

 Springer

Introduction

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

Landscape fragmentation and other human-induced environmental changes do not affect all species similarly. While many are negatively affected (losers), there is also a number of species that benefit from these changes (winners) (McKinney and Lockwood 1999). Interestingly, losers and winners are not randomly distributed among taxa or among functional ecological groups, which suggests that there are traits which render some species particularly sensitive to fragmentation and thus more prone to extinction. Identifying these traits and understanding the differential vulnerability to fragmentation among species may have implications for ecological and evolutionary theory, and also for development of effective conservation (Laurance 1991; Kotiaho et al. 2005). A large number of species traits have been proposed to be associated with sensitivity to habitat fragmentation (reviews in

Tscharntke et al. 2002; Henle et al. 2004; Ewers and Didham 2006). In general, they are the same traits that have been postulated to predispose species to population decline and extinction (reviews in McKinney 1997; Purvis et al. 2000a, b; Fisher and Owens 2004; O'Grady et al. 2004; Zavaleta et al. 2009), but there are exceptions depending on the type of extrinsic threat that is causing population decline of a species (Owens and Bennett 2000). It should also be considered that the relationship between particular species traits and the response to fragmentation can be complex, because different traits may interact and reinforce each other (Davies et al. 2004; Wang et al. 2015).

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

In relation to ecological traits, the main predictors of fragmentation sensitivity seem to be dispersal capacity and ecological plasticity, although migration may also play a role. Theoretical models predict that species characterized by poor dispersal capacity will be more negatively affected by habitat fragmentation (Liao et al. 2013), a prediction confirmed by empirical studies (Ekroos et al. 2010; Öckinger et al. 2010; Benscoter et al. 2013; Benchimol and Peres 2015). However, different patterns have also been observed in some cases, possibly because of interactions with other traits such as home range, sociality, or population density (Thomas 2000; Van Houtan et al. 2007). More consistent results have been found on ecological plasticity, with specialist species showing higher vulnerability to fragmentation than generalist ones

(e.g., Davies et al. 2004; Feeley et al. 2007; Devictor et al. 2008; Wang et al. 2015; Khimoun et al. 2016; Keinath et al. 2017). Regarding migration, sedentary species have been found to be more vulnerable to landscape changes than dispersive or migratory ones (Newbold et al. 2013; Pavlacky et al. 2015). However, migration behaviour can be both beneficial (e.g., avoiding harsh winter conditions) and detrimental (e.g., migration itself can be risky), and can interact with other species traits or with characteristics of the environment.

Life-history traits associated with low reproductive potential (low fecundity, long generation time) generally render species more vulnerable to habitat loss and fragmentation (Vance et al. 2003; Öckinger et al. 2010; Newbold et al. 2013; Pavlacky et al. 2015). Longevity, in contrast, has been suggested to decrease vulnerability to habitat fragmentation (Karr 1990) and other environmental changes (Morris et al. 2008). However, the role of longevity in fragmentation sensitivity is unclear (e.g., Henle et al. 2004), possibly because high longevity is also associated with low reproductive potential (Roff 1992), which, in turn, makes species more vulnerable to fragmentation. Large body size is simultaneously associated with traits making species more (e.g., low abundance and low reproductive potential) and less (e.g., high dispersal capacity) susceptible to habitat fragmentation, so the net effect is probably context dependent and difficult to predict. Although most empirical studies have found that larger species are more vulnerable to fragmentation (e.g., Feeley et al. 2007; Urquiza-Haas et al. 2009; Kormann et al. 2015; Pavlacky et al. 2015), in some cases smaller species were more vulnerable (Cosson et al. 1999; Boyle and Sigel 2015).

The aim of this study was to test the hypothesis that demographic, ecological, and life-history traits are associated with vulnerability to landscape fragmentation. Specifically, we predicted that vulnerable species would be characterized by small population size, negative population trend, high heterogeneity of spatial distribution, poor dispersal capacity, low ecological plasticity, non-migratory habits, low fecundity, long generation time, short longevity, and large body size. While some predictions seem to be robust according to the literature (e.g., regarding ecological plasticity), others are less clear because different studies have found contrasting results (e.g., regarding

body size; see references above). Vulnerability to landscape fragmentation was estimated in terms of population response to fragmentation, with more vulnerable species having high and low population density in little and heavily fragmented areas, respectively, while less vulnerable species show no or even a positive relationship between population density and fragmentation. The hypothesis was tested in European breeding bird species because birds are one of the best studied classes of animals, particularly in Europe (so a large amount of information is available), and because Europe is the continent most affected by human-caused fragmentation (Wade et al. 2003). In addition, continent-wide programmes, such as the Pan-European Common Bird Monitoring Scheme, and international collaboration (e.g., Jaeger et al. 2011) provide the opportunity to estimate both bird population sizes and landscape fragmentation with standardized methodologies, thus making information from different European countries comparable.

Materials and methods

Landscape fragmentation index and response to fragmentation

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

anthropogenic and natural fragmentation of non-mountainous land areas.

We estimated response to fragmentation for each bird species as the partial correlation coefficient from a multiple regression across countries, with population size as the response variable, fragmentation index as the predictor, and country area, latitude, longitude, percentage of agricultural land, and percentage of country area covered by barriers as confounding variables. Inclusion of confounding variables in the regression analyses meant that estimates of response to fragmentation were controlled for these variables. Large positive values imply a strong and positive response to fragmentation: the more fragmented the landscape, the more abundant the species. In contrast, large negative values imply a strong and negative response to fragmentation: the more fragmented the landscape, the less abundant the species. Values around zero imply weak or no effect of landscape fragmentation on abundance. Population sizes of bird species in European countries were obtained from BirdLife International (2004), and area of countries was the area for which bird population sizes had been estimated. Latitude and longitude for each country were estimated, respectively, as the latitude of the mid-point between the northernmost and the southernmost mainland points, and the longitude of the mid-point between the easternmost and the westernmost mainland points of every country. Percentage of agricultural land in each country was obtained from the Central Intelligence Agency (2016) World Fact-book. Percentage of country area covered by barriers (i.e., by artificial areas and water bodies) was calculated from land cover information for the years 2006 and 2012 (the average of the 2 years) provided by the European Environment Agency (2017). Artificial areas included transport networks and infrastructures, urban fabric (housing, services, and recreation), industrial and commercial units, and mineral extraction sites. Water bodies included lakes, reservoirs, and water courses.

Controlling for the percentage of country area covered by barriers was important to control for habitat loss caused by the presence of barriers and to estimate response to fragmentation per se. Habitat loss is inherent to landscape fragmentation, because fragmentation is impossible without habitat loss (Didham et al. 2012), and this intrinsic dependence gives rise to a strong association between the two parameters

(Fahrig 2003). As a result, if we studied vulnerability to landscape fragmentation without controlling for habitat loss due to fragmenting elements (barriers), it would be impossible to distinguish between the effect of fragmentation per se and the effect of habitat loss. As we were interested in the effect of fragmentation on biodiversity independent of amount of habitat, habitat loss due to fragmenting elements was controlled when estimating population response to fragmentation. Therefore, in the present study, we explicitly focused on the possible association between certain species-specific characteristics and vulnerability to landscape fragmentation per se.

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

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

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

Population size (number of breeding pairs) of bird species in the Western Palearctic west of the Ural Mountains was obtained from Hagemeijer and Blair (1997). Population trend for every bird species in Europe during the period 1990–2000 was estimated using an assessment by BirdLife International (2004) on a seven-category scale: large increase (3), moderate increase (2), small increase (1), stable (0), small

decline (− 1), moderate decline (− 2), and large decline (− 3). Heterogeneity of distribution was estimated as the coefficient of variation in population density among European countries (for more details, see Møller et al. 2010). Migration distance was estimated as breeding latitude minus wintering latitude, considering latitudes in the Southern Hemisphere as negative values. Breeding latitude was determined as the mean of the northernmost and southernmost latitudes of the breeding distribution to the nearest tenth of a degree. Similarly, wintering latitude was determined as the mean of the northernmost and southernmost latitudes of the wintering distribution. Breeding and wintering ranges were obtained from maps in Cramp and Perrins (1977–1994). Maximum dispersal distance was estimated as the minimum distance from the mainland to an island with a permanent breeding population, using information from distribution maps in Cramp and Perrins (1977–1994). This estimate of dispersal distance was preferred to others (e.g., natal dispersal; Paradis et al. 1998) because it was available for a much larger number of species. Ecological plasticity was estimated as the number of different habitats in which a species has been known to breed. Number of habitats was obtained from the habitat preferences listed by Cramp and Perrins (1977–1994) for each species, considering only habitats that appeared in their glossary (for more details, see Belliure et al. 2000; Møller and Garamszegi 2012). Body mass and life-history traits (fecundity, longevity, and generation time) for each bird species were obtained from Cramp and Perrins (1977–1994). Mean body mass was calculated as the mean of male and female body mass. Longevity was estimated as annual adult survival rate. Annual fecundity was calculated by multiplying clutch size (mean number of eggs) by maximum number of clutches per season. In the case of generation time, estimated as age at first reproduction, information was also obtained from Glutz von Blotzheim and Bauer (1985–1997). More information on bird species traits can be found in Online Appendix S1 and raw data are reported in Online Table S3.

Comparative methods

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

Number of species with information for each parameter ranged from 137 in the case of heterogeneity of distribution to 261 species in the case of population size (Online Table S4). However, number of species with information for all ten parameters was only 73. To avoid a drastic reduction in sample size (and thus statistical power), we decided not to include all factors simultaneously in the same model, but to perform a forward stepwise selection of variables (see Online Table S4 for details). The final model included parameters related to response to fragmentation with $P < 0.10$ because a threshold of 0.05 is considered too stringent and can fail to identify potentially important variables (Bendel and Afifi 1977). Although stepwise variable selection has been criticized on various grounds, e.g., because the final model is sometimes not the best model (Whittingham et al. 2006), we assume this was not a problem in our case, since backward stepwise procedure selected exactly the same variables (Online Table S5). Akaike's (1974) information criterion was not used to select the best model because it implied a reduction in sample size to only 73 species. More information on statistical analysis can be found in Online Appendix S1.

Results

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

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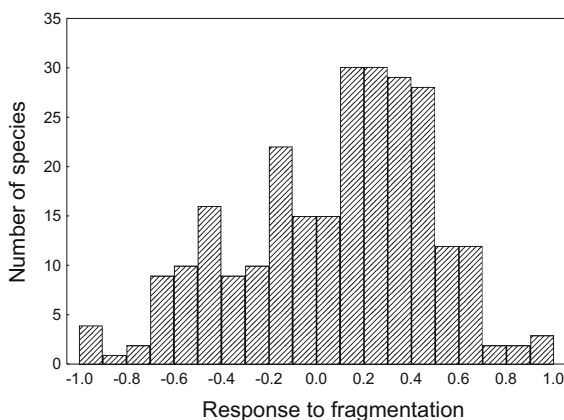

Fig. 1 Frequency distribution of response to landscape fragmentation (anthropogenic and natural fragmentation of non-mountainous land areas) in 261 European bird species. Mean (SD) = 0.094 (0.396), median = 0.177, skewness = − 0.444

Discussion

Contrary to the general belief that landscape fragmentation per se (independent of amount of habitat) has detrimental effects on biodiversity (e.g., Haila 2002), we found that population response to fragmentation in European bird species was more often positive than negative. This result agrees with previous studies suggesting that significant ecological responses to fragmentation are mostly positive (Fahrig 2017). Population response to fragmentation, however, varied greatly among species, and some (e.g., *Prunella collaris*, *Tetrao urogallus*, *Tichodroma muraria* or *Oenanthe oenanthe*, just to cite a few) responded strongly and negatively to fragmentation, i.e., they were particularly vulnerable to the breaking apart of habitat. At least for these species, fragmentation might be an important issue to take into account should conservation measures be needed.

The relationships between population response to landscape fragmentation and the species parameters studied here suggest that European birds responded more negatively to fragmentation (i.e., showed lower population densities in more fragmented countries) in scarce, small, resident species with delayed maturation (Table 1). In the case of population size, the positive relationship might imply higher vulnerability to fragmentation in less abundant species, a conclusion reached in numerous studies (see "Introduction" section). Another possible, non-mutually exclusive interpretation of the result is that species particularly vulnerable to fragmentation for reasons other than small population size experienced more pronounced decreases in abundance in highly fragmented countries. In that case, small population size would be a consequence and not the cause of vulnerability to fragmentation. In this study, population sizes of bird species in Europe were estimated in the 1990s (Hagemeijer and Blair 1997), while population sizes for every European country, the base for calculating response to fragmentation, were estimated between 1990 and 2002 (BirdLife International 2004), that is, simultaneously or slightly later. Consequently, there was little time for new fragmentation between the two sets of avian censuses, and limited opportunities for population size causing different population trends depending on the level of landscape fragmentation in every country. Although some effects of population size on the response to fragmentation cannot be ruled

Table 1 Phylogenetic generalized least square regression model on factors related to bird population response to anthropogenic and natural fragmentation of non-mountainous land areas

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

The final model only included parameters related to response to fragmentation with $P < 0.10$ after a forward stepwise procedure. A backward stepwise procedure provided the same final model. Phylogenetic relations among species and number of countries used to estimate response to fragmentation in each species were controlled in the analyses (see "Comparative methods" section for details). Both the dependent variable and its residuals were approximately normally distributed (Kolmogorov–Smirnov test for normality; $P > 0.05$ in the two tests), thus justifying the use of a linear model approach. The model had the statistics: $F = 6.35$, adj-$r^2 = 0.088$, $n = 224$, $P < 0.001$, $\lambda = 0.000$

out, the small population size in some bird species in the 1990s was probably the consequence of humans transforming, and thus fragmenting, the European landscape intensively for many decades (or even centuries) before the data were collected. The timing of bird censuses in this study was not appropriate for testing the possible effect of population size on vulnerability to landscape fragmentation.

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

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

Our study suggests that small bird species are more vulnerable to landscape fragmentation than large ones, a result consistent with previous research on vertebrates in tropical forests (Cosson et al. 1999; Boyle and Sigel 2015). As explained in the Introduction, the
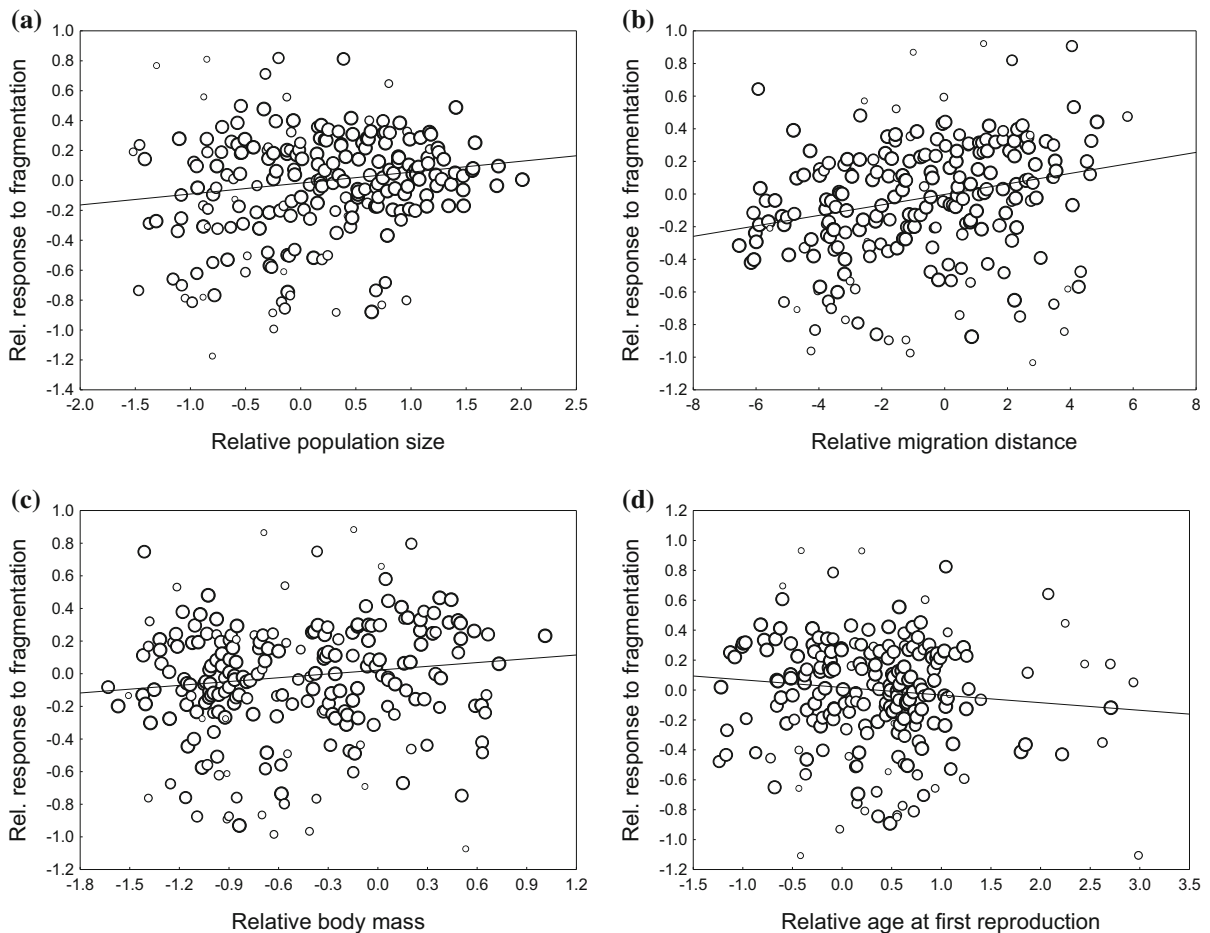
(a)

(b)

(c)

(d)

Fig. 2 Relationships between relative estimates of bird population response to anthropogenic and natural fragmentation of non-mountainous land areas and **a** relative population size, **b** relative migration distance, **c** relative body mass, and **d** relative age at first reproduction in European bird species. Relative estimates of response to fragmentation were estimated as the residuals from a model with response to fragmentation as the response variable and **a** migration distance, body mass, and age at first reproduction, **b** population size, body mass, and age at first reproduction, **c** population size, migration distance, and age at first reproduction, and **d** population size, migration distance, and body mass as predictors. Relative population size was estimated as the residuals from a model with population size as the response variable and migration distance, body mass, and age at first reproduction as predictors. Relative migration distance was estimated as the residuals from a model with migration distance as the response variable and population size,

body mass, and age at first reproduction as predictors. Relative body mass was estimated as the residuals from a model with body mass as the response variable and population size, migration distance, and age at first reproduction as predictors. Relative age at first reproduction was estimated as the residuals from a model with age at first reproduction as the response variable and population size, migration distance, and body mass as predictors. All variables except age at first reproduction and response to fragmentation were transformed before the analyses (Appendix S1). Lines are best-fit regressions (**a** y = − 0.018 + 0.073 x; **b** y = − 0.002 + 0.032 x; **c** y = 0.022 + 0.078 x; **d** y = 0.017 − 0.051 x). All models and regressions took into account the number of countries used to estimate response to fragmentation (bubble size indicates this number; range 8–26) and similarities among species due to common phylogenetic descent (see "Comparative methods" section for details)

relationship between body size and response to fragmentation was difficult to predict, because body size is simultaneously associated with traits making species more or less susceptible to fragmentation, so the net effect is probably context dependent. The

simplest explanation for our result would be that body size is generally positively associated with dispersal distance (Jenkins et al. 2007) and survival (McCarthy et al. 2008; Collingham et al. 2014), two traits that presumably make species less vulnerable to

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

Among life-history traits, only age at first reproduction (a proxy for generation time) was significantly related to response to fragmentation, with a more negative response in delayed breeders, as expected. Although the relationship was marginally significant, and thus should be interpreted with caution, this result is consistent with a previous study showing that tropical forest bird species with longer generation time are more negatively affected by human land use (Newbold et al. 2013). The most straightforward explanation for our result would be that long generation time implies low reproductive potential and probably less capacity to recover from perturbations and population crashes. However, other life-history traits generally considered prime indicators of reproductive potential (e.g., annual fecundity) were not significantly related to response to fragmentation, and thus other mechanisms have to be invoked. The relationship between response to fragmentation and generation time was not mediated by body size (larger bird species generally show longer generation time; Sæther 1987), because body mass was controlled in the analysis (Table 1). It has previously been shown that bird species with longer generation time suffer a

higher extinction risk when the main source of extinction is human persecution or introduced predators (Owens and Bennett 2000). In our case, landscape fragmentation might entail an increase in predation-related mortality, thus having a more negative effect in species with longer generation time. For example, roads might enhance access of pets (cats, dogs) or hunters to natural habitats, and traffic itself can cause mortality due to collisions with vehicles (Fahrig and Rytwinski 2009). In addition, more fragmented landscapes usually contain more edge for a given amount of habitat, often resulting in increased predation by natural predators (Chalfoun et al. 2002).

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

Some species characteristics were predicted to be associated with vulnerability to habitat fragmentation, but this study does not support such associations. This happened for example for dispersal capacity or heterogeneity of spatial distribution, although probably the most striking case is ecological plasticity. Previous studies (many of them on birds) have consistently found higher sensitivity to habitat fragmentation in specialist than in generalist species (see "Introduction" section). However, most of these studies, particularly those on birds (e.g., Feeley et al.

2007; Devictor et al. 2008; Wang et al. 2015), did not investigate the effects of fragmentation per se, but the effects of habitat patch size or isolation, which are inherently confounded with effects of amount of habitat (Fahrig 2003, 2017). Moreover, both ecological plasticity and vulnerability to fragmentation have been estimated in different ways in this and previous studies, which might affect the results. Finally, the temporal framework of this study might also have played a role, because it is known that time lag is very important for understanding the impact of fragmentation on animal populations (Bennett and Saunders 2010). While some species characteristics might only be related to vulnerability to fragmentation when long-term effects are studied, it is possible that other characteristics appear to be related in the short term.

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

References

Akaike H (1974) A new look at statistical model identification. IEEE Trans Autom Control 19:716–723

Belliure J, Sorci G, Møller AP, Clobert J (2000) Dispersal distances predict subspecies richness in birds. J Evol Biol 13:480–487

Benchimol M, Peres CA (2015) Predicting local extinctions of Amazonian vertebrates in forest islands created by a mega dam. Biol Conserv 187:61–72

Bendel RB, Afifi AA (1977) Comparison of stopping rules in forward "stepwise" regression. J Am Stat Assoc 72:46–53

Bennett AF, Saunders DA (2010) Habitat fragmentation and landscape change. In: Sodhi NS, Ehrlich PR (eds) Conservation biology for all. Oxford University Press, Oxford, pp 88–106

Benscoter AM, Reece JS, Noss RF, Brandt LA, Mazzotti FJ, Romañach SS, Watling JI (2013) Threatened and endangered subspecies with vulnerable ecological traits also have high susceptibility to sea level rise and habitat fragmentation. PLoS ONE 8:e70647

Betts MG, Forbes GJ, Diamond AW (2007) Thresholds in songbird occurrence in relation to landscape structure. Conserv Biol 21:1046–1058

Betts MG, Fahrig L, Hadley AS, Halstead KE, Bowman J, Robinson WD, Wiens JA, Lindenmayer DB (2014) A species-centered approach for uncovering generalities in organism responses to habitat loss and fragmentation. Ecography 37:517–527

BirdLife International (2004) Birds in Europe: population estimates, trends and conservation status. BirdLife Conservation Series No 12. BirdLife International, Wageningen

Bolger DT, Alberts AC, Soulé ME (1991) Occurrence patterns of bird species in habitat fragments: sampling, extinction, and nested species subsets. Am Nat 137:155–166

Boyle WA, Sigel BJ (2015) Ongoing changes in the avifauna of La Selva Biological Station, Costa Rica: twenty-three years of Christmas Bird Counts. Biol Conserv 188:11–21

Carrascal LM, Seoane J, Villén-Pérez S (2012) Temperature and food constraints in wintering birds: an experimental approach in montane Mediterranean oakwoods. Community Ecol 13:221–229

Central Intelligence Agency (2016) CIA world factbook. Central Intelligence Agency, Washington, DC. https://www.cia.gov/library/publications/the-world-factbook. Accessed 2 August 2017

Chalfoun AD, Thompson FR, Ratnaswamy MJ (2002) Nest predators and fragmentation: a review and meta-analysis. Conserv Biol 16:306–318

Collinge SK (2009) Ecology of fragmented landscapes. Johns Hopkins University Press, Baltimore

Collingham YC, Huntley B, Altwegg R, Barnard P, Beveridge OS, Gregory RD, Mason LR, Oschadleus HD, Simmons RE, Willis SG, Green RE (2014) Prediction of mean adult survival rates of southern African birds from demographic and ecological covariates. Ibis 156:741–754

Cosson JF, Ringuet S, Claessens O, de Massary JC, Dalecky A, Villiers JF, Granjon L, Pons JM (1999) Ecological changes in recent land-bridge islands in French Guiana, with emphasis on vertebrate communities. Biol Conserv 91:213–222

Cramp S, Perrins CM (eds) (1977–1994) Handbook of the birds of Europe, the Middle East and North Africa: the birds of the Western Palearctic, vols 1–9. Oxford University Press, Oxford

Davies KF, Margules CR, Lawrence JF (2000) Which traits of species predict population declines in experimental forest fragments? Ecology 81:1450–1461

Davies KF, Margules CR, Lawrence JF (2004) A synergistic effect puts rare, specialized species at greater risk of extinction. Ecology 85:265–271

Devictor V, Julliard R, Jiguet F (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117:507–514

Didham RK (2010) Ecological consequences of habitat fragmentation. In: Encyclopedia of life sciences. Wiley: Chichester

Didham RK, Kapos V, Ewers RM (2012) Rethinking the conceptual foundations of habitat fragmentation research. Oikos 121:161–170

Doherty PF, Grubb TC (2002) Survivorship of permanent-resident birds in a fragmented forested landscape. Ecology 83:844–857

Ekroos J, Heliölä J, Kuussaari M (2010) Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. J Appl Ecol 47:459–467

European Environment Agency (2017) Land cover country fact sheets 2012. European Environment Agency, Copenhagen. https://www.eea.europa.eu/themes/landuse/land-cover-country-fact-sheets/land-cover-country-fact-sheets. Accessed 27 September 2018

Ewers RM, Didham RK (2006) Confounding factors in the detection of species responses to habitat fragmentation. Biol Rev 81:117–142

Fahrig L (1998) When does fragmentation of breeding habitat affect population survival? Ecol Model 105:273–292

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fahrig L (2017) Ecological responses to habitat fragmentation per se. Annu Rev Ecol Evol Syst 48:1–23

Fahrig L, Rytwinski T (2009) Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc 14:21

Feeley KJ, Gillespie TW, Lebbin DJ, Walter HS (2007) Species characteristics associated with extinction vulnerability and nestedness rankings of birds in tropical forest fragments. Anim Conserv 10:493–501

Fisher DO, Owens IPF (2004) The comparative method in conservation biology. Trends Ecol Evol 19:391–398

Foufopoulos J, Ives AR (1999) Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. Am Nat 153:1–25

Garamszegi LZ, Møller AP (2007) Prevalence of avian influenza and host ecology. Proc R Soc B 274:2003–2012

Glutz von Blotzheim UN, Bauer KM (eds) (1985–1997). Handbuch der Vögel Mitteleuropas, vols 1–14. AULA-Verlag, Wiesbaden

Gonzalez A, Chaneton EJ (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented microecosystem. J Anim Ecol 71:594–602

Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD, Cook WM, Damschen EI, Ewers RM, Foster BL, Jenkins CN, King AJ, Laurance WF, Levey DJ, Margules CR, Melbourne BA, Nicholls AO, Orrock JL, Son D-X, Townshend JR (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052

Hagemeijer WJM, Blair MJ (1997) The EBCC atlas of European breeding birds: their distribution and abundance. T & AD Poyser, London

Haila Y (2002) A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. Ecol Appl 12:321–334

Henle K, Davies KF, Kleyer M, Margules C, Settele J (2004) Predictors of species sensitivity to fragmentation. Biodivers Conserv 13:207–251

Ibáñez I, Katz DSW, Peltier D, Wolf SM, Connor Barrie BT (2014) Assessing the integrated effects of landscape fragmentation on plants and plant communities: the challenge of multiprocess-multiresponse dynamics. J Ecol 102:882–895

Inger R, Gregory R, Duffy JP, Stott I, Voríšek P, Gaston KJ (2015) Common European birds are declining rapidly while less abundant species' numbers are rising. Ecol Lett 18:28–36

Jaeger JAG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landsc Ecol 15:115–130

Jaeger JAG, Bertiller R, Schwick C, Müller K, Steinmeier C, Ewald KC, Ghazoul J (2008) Implementing landscape fragmentation as an indicator in the Swiss Monitoring System of Sustainable Development (MONET). J Environ Manage 88:737–751

Jaeger JAG, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, von Toschanowitz KT (2005) Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecol Model 185:329–348

Jaeger JAG, Soukup T, Madriñán LF, Schwick C, Kienast F (2011) Landscape fragmentation in Europe. Joint EEA-FOEN report. EEA Report No. 2/2011. European Environment Agency, Copenhagen; Swiss Federal Office for the Environment, Bern. http://www.eea.europa.eu/publications/landscape-fragmentation-in-europe. Accessed 8 May 2014

Jenkins DG, Brescacin CR, Duxbury CV, Elliott JA, Evans JA, Grablow KR, Hillegass M, Lyon BN, Metzger GA, Olandese ML, Pepe D, Silvers GA, Suresch HN, Thompson TN, Trexler CM, Williams GE, Williams NC, Williams SE (2007) Does size matter for dispersal distance? Glob Ecol Biogeogr 16:415–425

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO (2012) The global diversity of birds in space and time. Nature 491:444–448

Karr JR (1990) Avian survival rates and the extinction process on Barro Colorado Island, Panama. Conserv Biol 4:391–397

Keinath DA, Doak DF, Hodges KE, Prugh LR, Fagan W, Şekercioğlu ÇH, Buchart SHM, Kauffman M (2017) A global analysis of traits predicting species sensitivity to habitat fragmentation. Glob Ecol Biogeogr 26:115–127

Khimoun A, Eraud C, Ollivier A, Arnoux E, Rocheteau V, Bely M, Lefol E, Delpuech M, Carpentier M-L, Leblond G, Levesque A, Charbonnel A, Faivre B, Garnier S (2016) Habitat specialization predicts genetic response to fragmentation in tropical birds. Mol Ecol 25:3831–3844

Kormann U, Rösch V, Batáry P, Tscharntke T, Orci KM, Samu F, Scherber C (2015) Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. Divers Distrib 21:1204–1217

Kotiaho JS, Kaitala V, Komonen A, Päivinen J (2005) Predicting the risk of extinction from shared ecological characteristics. Proc Natl Acad Sci USA 102:1963–1967

Laurance WF (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conserv Biol 5:79–89

Liao J, Li Z, Hiebeler DE, El-Bana M, Deckmyn G, Nijs I (2013) Modelling plant population size and extinction thresholds from habitat loss and habitat fragmentation: effects of neighbouring competition and dispersal strategy. Ecol Model 268:9–17

Maddison WP, Maddison DR (2015) Mesquite: a modular system for evolutionary analysis, version 3.04. http://mesquiteproject.org. Accessed 26 October 2018

Martins EP, Hansen TF (1997) Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. Am Nat 149:646–667

McCarthy MA, Citroen R, McCall SC (2008) Allometric scaling and Bayesian priors for annual survival of birds and mammals. Am Nat 172:216–222

McKinney ML (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. Annu Rev Ecol Syst 28:495–516

McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol Evol 14:450–453

Møller AP, Garamszegi LZ (2012) Between individual variation in risk-taking behavior and its life history consequences. Behav Ecol 23:843–853

Møller AP, Soler JJ, Vivaldi MM (2010) Spatial heterogeneity in distribution and ecology of Western Palearctic birds. Ecology 91:2769–2782

Morganti M, Assandri G, Aguirre JI, Ramírez A, Caffi M, Pulido F (2017) How residents behave: home range flexibility and dominance over migrants in a Mediterranean passerine. Anim Behav 123:293–304

Morosinotto C, Villers A, Varjonen R, Korpimäki E (2017) Food supplementation and predation risk in harsh climate: interactive effects on abundance and body condition of tit species. Oikos 126:863–873

Morris WF, Pfister CA, Tuljapurkar S, Haridas CV, Boggs CL, Boyce MS, Bruna EM, Church DR, Coulson T, Doak DF, Forsyth S, Gaillard J-M, Horvitz CC, Kalisz S, Kendall BE, Knight TM, Lee CT, Menges ES (2008) Longevity can buffer plant and animal populations against changing climatic variability. Ecology 89:19–25

Newbold T, Scharlemann JPW, Butchart SHM, Şekercioğlu ÇH, Alkemade R, Booth H, Purves DW (2013) Ecological traits affect the response of tropical forest bird species to land-use intensity. Proc R Soc B 280:20122131

Öckinger E, Schweiger O, Crist TO, Debinski DM, Krauss J, Kuussaari M, Petersen JD, Pöyry J, Settele J, Summerville KS, Bommarco R (2010) Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecol Lett 13:969–979

O'Grady JJ, Reed DH, Brook BW, Frankham R (2004) What are the best correlates of predicted extinction risk? Biol Conserv 118:513–520

Owens IPF, Bennett PM (2000) Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proc Natl Acad Sci USA 97:12144–12148

Pagel M (1997) Inferring evolutionary processes from phylogenies. Zool Scr 26:331–348

Pagel M (1999) Inferring the historical patterns of biological evolution. Nature 401:877–884

Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. J Anim Ecol 67:518–536

Pavlacky DC, Possingham HP, Goldizen AW (2015) Integrating life history traits and forest structure to evaluate the vulnerability of rainforest birds along gradients of deforestation and fragmentation in eastern Australia. Biol Conserv 188:89–99

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Purvis A, Agapow P-M, Gittleman JL, Mace GM (2000a) Nonrandom extinction and the loss of evolutionary history. Science 288:328–330

Purvis A, Jones KE, Mace GM (2000b) Extinction. BioEssays 22:1123–1133

Roff DA (1992) The evolution of life histories: theory and analysis. Chapman & Hall, New York

Sæther B-E (1987) The influence of body-weight on the covariation between reproductive traits in European birds. Oikos 48:79–88

Sanderson FJ, Donald PF, Pain DJ, Burfield IJ, van Bommel FPJ (2006) Long-term population declines in Afro-Palearctic migrant birds. Biol Conserv 131:93–105

Şekercioğlu ÇH (2007) Conservation ecology: area trumps mobility in fragment bird extinctions. Curr Biol 17:R283–R286

Smith KT, Kirol CP, Beck JL, Blomquist FC (2014) Prioritizing winter habitat quality for greater sage-grouse in a landscape influenced by energy development. Ecosphere 5:15

R Core Team (2014) R: a language and environment for statistical computing, version 3.1.0. R Foundation for Statistical Computing, Vienna

Thomas CD (2000) Dispersal and extinction in fragmented landscapes. Proc R Soc B 267:139–145

Tscharntke T, Steffen-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: a mini review. Ecol Res 17:229–239

Urquiza-Haas T, Peres CA, Dolman PM (2009) Regional scale effects of human density and forest disturbance on large-bodied vertebrates throughout the Yucatán Peninsula, Mexico. Biol Conserv 142:134–148

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO, Lovejoy TE (2007) Dispersal of Amazonian birds in continuous and fragmented forest. Ecol Lett 10:219–229

Vance MD, Fahrig L, Flather CH (2003) Effect of reproductive rate on minimum habitat requirements of forest-breeding birds. Ecology 84:2643–2653

Villard M-A, Trzcinski MK, Merriam G (1999) Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. Conserv Biol 13:774–783

Wade TG, Riitters KH, Wickham JD, Jones KB (2003) Distribution and causes of global forest fragmentation. Conserv Ecol 7:7

Wang Y, Thornton DH, Ge D, Wang S, Ding P (2015) Ecological correlates of vulnerability to fragmentation in forest birds on inundated subtropical land-bridge islands. Biol Conserv 191:251–257

Wang Y, Zhang J, Feeley KJ, Jiang P, Ding P (2009) Life-history traits associated with fragmentation vulnerability of lizards in the Thousand Island Lake, China. Anim Conserv 12:329–337

Whittingham MJ, Stephens PA, Bradbury RB, Freckleton RP (2006) Why do we still use stepwise modelling in ecology and behaviour? J Anim Ecol 75:1182–1189

Wilson MC, Chen X-Y, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF, Liu J, Pimm SL, Robinson SK, Russo SE, Si X, Wilcove DS, Wu J, Yu M (2016) Habitat fragmentation and biodiversity conservation: key findings and future challenges. Landsc Ecol 31:219–227

With KA, King AW (1999) Extinction thresholds for species in fractal landscapes. Conserv Biol 13:314–326

Zavaleta E, Pasari J, Moore J, Hernández D, Suttle KB, Wilmers CC (2009) Ecosystem responses to community disassembly. Ann N Y Acad Sci 1162:311–333