Review article

Under-representation of avian studies in landscape genetics

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Landscape genetics is a rapidly growing discipline that examines how heterogeneous landscapes and other environmental factors influence population genetic variation. We conducted a systematic review of the landscape genetic literature which demonstrates that birds are severely under-represented relative to their species diversity and general publication prevalence. Most avian studies were on species that have relatively low dispersal ability, and we suggest that this reflects an assumed high vagility of birds that precludes spatial genetic variation relatable to landscape heterogeneity. However, spatial genetic variation exists in several bird species with very high dispersal ability, but this has not been considered in the context of landscape features. Genetic patterns may also relate to landscape due to breeding habitat selection and territorial behaviour, despite the fact that species may be able to move throughout different landscape elements with minimal movement costs. Habitat loss and fragmentation are continuing globally and are strongly related to declines in bird populations. Landscape genetic studies provide a means to understand, predict and mitigate the effects of anthropogenic landscape change on birds. This review promotes the need for landscape genetic studies of birds, such that a greater understanding of the drivers of their genetic structuring can be developed and generalizations can be made from landscape genetic studies that apply more broadly across taxa.

Keywords: birds, dispersal distance, geographical bias, model taxa, taxonomic bias.

Landscape genetics examines the relationships between landscape and environmental heterogeneity and the spatial genetic variation of populations (Manel *et al.* 2003). Landscape genetics has been pivotal in addressing areas such as identifying specific barriers to dispersal, quantifying the impact of habitat fragmentation or landscape change on population genetic diversity and connectivity, and predicting spread of disease or invasive species (Storfer *et al.* 2007). New knowledge generated in these areas is critical for understanding, predicting and mitigating the effects of anthropogenic landscape change on species of conservation concern, and landscape genetic studies of birds commonly address these questions (e.g. Bruggeman *et al.* 2010, Alda *et al.* 2011, Amos *et al.* 2012, Table S1). Growth of this discipline largely is due to increasingly powerful molecular tools (e.g. Next Generation Sequencing), greater availability and quality of landscape data (e.g. remote sensing), and a burgeoning array of complex multivariate statistical techniques that broaden the variety of questions that landscape genetics is equipped to answer (Bolliger *et al.* 2014). However, the rapid growth of this field has led to a number of problems, including confusion over its definition (Storfer *et al.* 2007), poor choices of analytical methods (Balkenhol *et al.* 2009, Cushman & Landguth 2010, Wang 2010,

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2011) and, potentially, taxonomic bias (Pawar 2003) in research outputs and outcomes. This last problem is the focus of this review.

Taxonomic bias is prevalent in ecological and behavioural research (Bonnet *et al.* 2002, Clark & May 2002) and compromises our ability to develop generalized theory. For conservation, knowledge of the landscape features that influence population connectivity is highly desirable because maintaining population connectivity is important for the resilience of any single population to localized perturbation (Hanski 1998) and to combat inbreeding depression (Schwartz & Mills 2005). However, with the exception of a summary of landscape genetic research across very broadly defined taxa (Storfer *et al.* 2010), and a review specifically considering the use of resistance surfaces (models that represent the resistance a landscape to movement of individuals from a given population; Zeller *et al.* 2012), no review to date has sought to examine the prevalence of landscape genetic research across taxonomic groups, which is central to our ability to assess the generalizability of findings.

Previous studies of taxonomic bias in ecology have found birds, and endotherms generally, to be over-represented in the literature. For instance, Stahlschmidt (2011) found that 58% of papers on parental care were studies of birds. In contrast, the perceived high vagility of birds relative to other taxa may discourage the application of landscape genetic research (negative taxonomic bias) due to expectations of low spatial genetic variability, as well as the difficulty of sampling mobile species with large ranges. However, spatial genetic variation in birds may be driven by breeding habitat selection, site fidelity or territoriality. In such cases, dispersal is a behavioural process of decision-making with respect to landscape, not merely a product of constrained landscape permeability conferred by limited vagility. These factors are present and even prevalent among bird species (Jones 2001) but are not often entertained as drivers of landscape genetic patterns.

We present a systematic review of the landscape genetic literature to quantify the prevalence of studies within each tetrapod Class relative to its species diversity and prevalence in the general zoological literature. We test for taxonomic bias in studies of landscape genetics and investigate its potential causes, such as geographical biases or assumptions about high vagility precluding spatial genetic structure.

METHODS

We conducted a literature search using the Institute for Scientific Information (ISI) Web of Science (Thompson Reuters, New York, NY, USA) Core Collection (see Appendix 1 for included citation indexes), including all articles published from 2003 until the time of the search (9 April 2015). The keywords *'landscape genetic*'* (note the use of inverted commas in the search) were used, retrieving only papers that included both of these terms. Not all landscape genetic studies use this terminology, nor will all papers retrieved necessarily be strictly landscape genetic papers. However, as these caveats are likely to apply equally across all taxa, our search terms provide an unbiased picture of relative taxon prevalence in landscape genetics. Additional search terms would have expanded the search results, but with a diminishing proportion of relevant landscape genetic papers. We appreciate that this search may not be exhaustive, but it does represent high-intensity sampling of all available information, akin to ecological studies with many replicates. This review does not include any landscape genetic papers found using other methods, for example citations from within papers identified from the database search, in order to maintain consistency in the search parameters used and to prevent exaggeration of bias due to self-citation by authors with specific taxonomic research interests.

The search yielded 962 articles, which were then screened further. Reviews and purely methodological papers were removed, as were other papers that were clearly not landscape genetic studies according to the title and abstract. Because this review focuses on wild populations of tetrapods, we also excluded studies of plants, fishes, microorganisms, invertebrates and domestic animals. Two studies investigating multiple taxa across tetrapod Classes were also excluded. Subsequently, 289 articles (Table S1) remained for allocation to the four tetrapod Classes: mammals, birds, amphibians and reptiles.

We conducted a chi-square analysis to determine whether numbers of landscape genetic papers per tetrapod Class deviated significantly from what would be expected if they were published in proportion to species diversity, based on a global species database (IUCN 2014). We also examined the geographical distribution of landscape genetic studies to see whether any taxonomic bias could be

related to the geographical distribution of species or research efforts across different regions. Geographical location (continent) was defined according to the location of the main study population. Four studies of marine mammals were excluded from the geographical analysis owing to ambiguity assigning their location. Finally, we assessed publication bias relative to the number of general zoological papers published per taxon. The ProQuest Zoological Record Plus database was searched across the same time interval (2003 to 9 April 2015). This database codes papers by taxonomic groups, enabling counting of papers published by higher taxon (e.g. search term *SU(aves)*).

To investigate the possibility that bird species may be chosen for landscape genetics according to their dispersal ability, the articles on avian landscape genetics were searched for instances where the maximum dispersal distance of the study species was stated (in almost all cases where dispersal type was reported, this was natal dispersal; Table S2), or a reference was made directly to a source of this information. Dispersal distance information is usually relevant to landscape genetic studies and is often reported where it is available, so independent literature searches for dispersal distance data for each study species were not undertaken. Avian dispersal distances from landscape genetic studies were then contrasted with dispersal distances reported from the avian population genetic literature. Because manually sorting the numerous population genetic papers into taxonomic groups would be prohibitively time-consuming, an advanced search was conducted using the ProQuest Zoological Record Plus database using the following terms: *SU(aves) AND ('population genetic*') NOT ('landscape genetic*')*.

Maximum dispersal distance information was reported in 15 of the 48 avian landscape genetic articles. In two additional cases, dispersal ability of the study species was indicated (Amos *et al.* 2012, 2014), but each of these studies featured a suite of 10 species that vary considerably in their putative mobility, with no specific dispersal distance estimate available. These papers were therefore excluded in further analyses. The Zoological Record Plus search returned 2147 avian population genetic articles (Table S3). We selected papers at random from this list until we had found an equivalent number of papers containing maximum dispersal distance information to compare with the landscape genetic papers; we examined 210 papers before 15 were found. From each of these population genetic papers, we recorded the study species and maximum dispersal distance of that species. An exhaustive search for dispersal distances across the entire avian population genetic literature was beyond the scope of our study, the effort required being that of an independent review itself. We believe a balanced sample of 15 vs. 15 is sufficiently robust, and we conducted a Fisher's exact test to validate this comparison.

Inclusion of the term *'landscape genomic*'* was later considered in a Zoological Record Plus search, to gauge whether the avian landscape genetics field had been under-represented in our initial searches owing to the increasing use of genomic approaches. Up to April 2015, two additional papers were found for birds, one for mammals, one for reptiles and none for amphibians. While this search method differed from the main Web of Science search and thus could not be pooled with those results, this search indicates that the inclusion of these terms in the original search would have had negligible impact on its results.

RESULTS AND DISCUSSION

The frequency of landscape genetic studies of tetrapods has increased over time, particularly in mammals and amphibians (Fig. 1). The distribution of landscape genetic literature between mammals, birds, amphibians and reptiles was significantly different to that expected based on known species diversity worldwide ($\chi^2 = 308.05$, df = 3, $P < 0.001$; Fig. 2, Table 1). Mammals were over-represented, with 153 (52.9%) landscape genetic papers compared with an expected 48 (16.6%). Birds and reptiles were under-represented, having 34 (11.8%) and 28 (9.7%) papers published, in contrast to expected numbers of 91 (31.3%) and 87 (30.2%), respectively. Chi-square results for each taxon are reported in Table S4. This under-representation of avian landscape genetic studies is even more marked given that the general zoological literature is positively biased towards avian studies (see below).

The geographical distribution of landscape genetic studies was consistent with previous studies of geographical bias in ecology (Pysek *et al.* 2008). Most have been conducted in North America ($n = 142$), followed by Europe ($n = 63$), Africa ($n = 17$), Asia ($n = 19$), Australasia ($n = 26$) and South America ($n = 18$) (Fig. 3). In Australasia
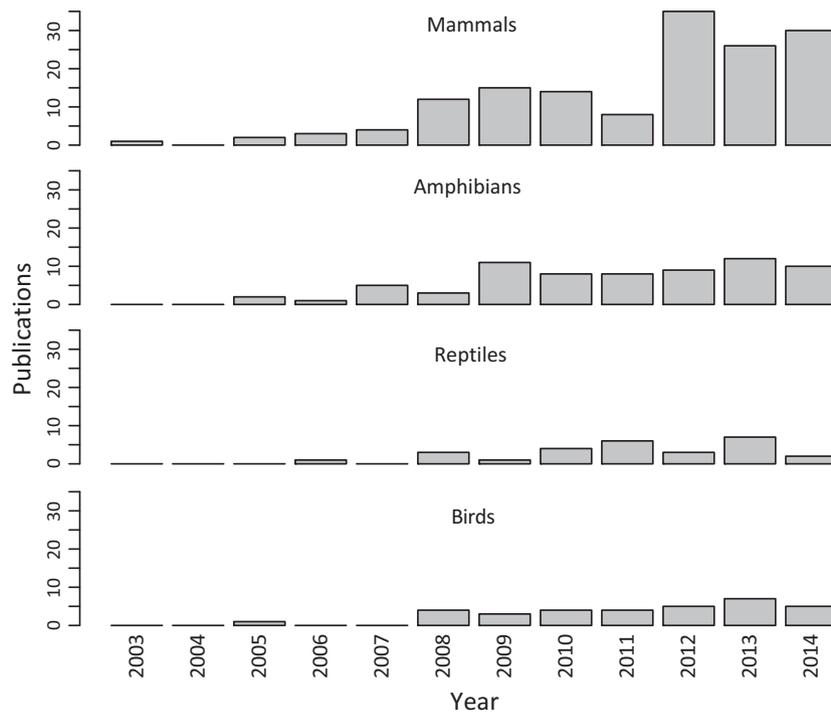
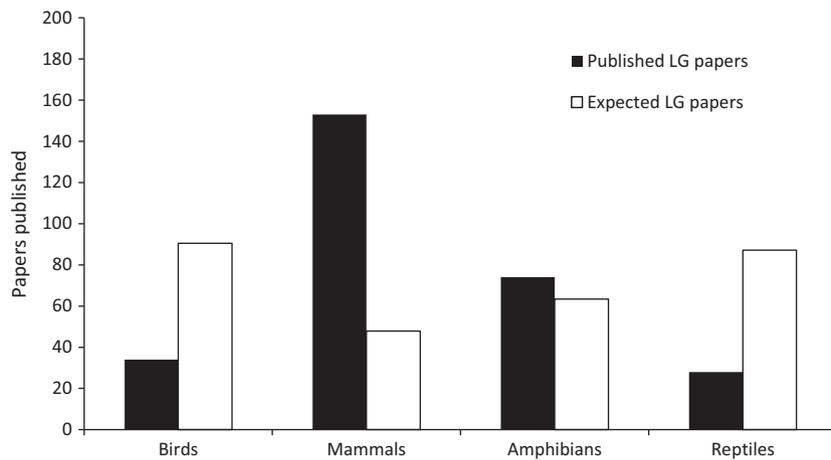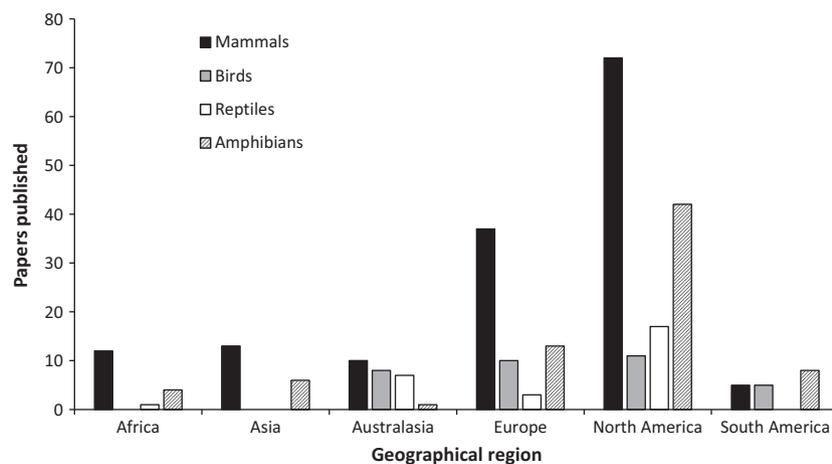**Fig. 1.** Number of landscape genetic papers published per year (2003–2014) for each tetrapod Class.

Fig. 2. Comparison between the numbers of published (2003 to 9 April 2015) landscape genetic (LG) papers for each tetrapod Class and the numbers expected if papers were published proportionally to numbers of known species from each Class (IUCN 2014).

and South America, all taxa were represented relatively equally, compared with other areas. In North America, Europe, Asia and Africa, landscape genetic research was dominated by mammals, with birds representing a relatively small proportion of papers published ($n = 21$ of 241 papers). Using the database of Newton (2003) there is evidence for geographical heterogeneity in

avian landscape genetic research effort relative to avian species diversity ($P < 0.001$, Fisher's exact test with 10^6 Monte Carlo simulations; Fig. 4). However, the geographical distribution of species diversity in birds is very similar to that of mammals (Jenkins *et al.* 2013). Therefore, the observed discrepancy between birds and mammals in the frequency of landscape genetic studies is not likely

Table 1. Comparison between published (2003 to 9 April 2015) landscape genetic (LG) papers per tetrapod taxon and numbers that would be expected if papers had been published proportionally to total numbers of known species per taxon (IUCN 2014). The percentage representation of each taxon within the total known tetrapod species, landscape genetic papers and population genetic (PG) papers are also depicted.

|	Published LG papers	Expected LG papers	Total known species	% of total known tetrapod species	% of total LG papers	% of total PG papers
Birds	34	91	10 425	31.3	11.8	25.2
Mammals	153	48	5513	16.6	52.9	52.1
Amphibians	74	63	7302	21.9	25.6	9.9
Reptiles	28	87	10 038	30.2	9.7	12.8
Total	289	289	33 278			

Fig. 3. Geographical distribution of landscape genetic papers published (2003 to 9 April 2015) for each tetrapod Class. Location for each paper is based on the location of its study population.

to be a result of geographical heterogeneity in landscape genetic research activity.

Significant taxonomic bias in landscape genetics towards mammals is consistent with observed publication bias across other fields of zoology (Shine & Bonnet 2000, Bonnet *et al.* 2002, Clark & May 2002, Seddon *et al.* 2005), generally considered to reflect perceived charisma and appeal of these endotherms. However, this bias towards endotherms is not wholly reflected in the landscape genetic literature, in which birds are under-represented and amphibians over-represented relative to the broader zoological literature. The distribution of landscape genetic literature between each of the tetrapod Classes was significantly different to that expected based on numbers of general zoological papers published per taxon ($\chi^2 = 161.91$, df = 3, $P < 0.001$; Fig. 5, Table 1). The greatest difference was for birds, which made up 11.8% of landscape genetic papers but 36.3%

of general zoological papers. In contrast, studies of amphibians constituted 25.6% of landscape genetic papers but only 8.7% of general zoological papers. Mammals, which are highly represented in zoological research generally (39.9%), are represented even more highly among landscape genetic papers (52.9%). Reptiles are even more under-represented in landscape genetics (9.7%) than they are in the general zoological literature (15.2%). Chi-square results for each taxon are reported in Table S4.

A focus on 'model taxa' that are particularly well suited to landscape genetics may explain the observed taxonomic bias, as similarly proposed by Stahlschmidt (2011) for the prevalence of avian studies in the literature on parental care. We believe there is negative taxonomic bias towards the study of birds in landscape genetics because they are perceived as being particularly vagile, which would be expected to result in less spatial genetic structuring (Hillman *et al.* 2014).
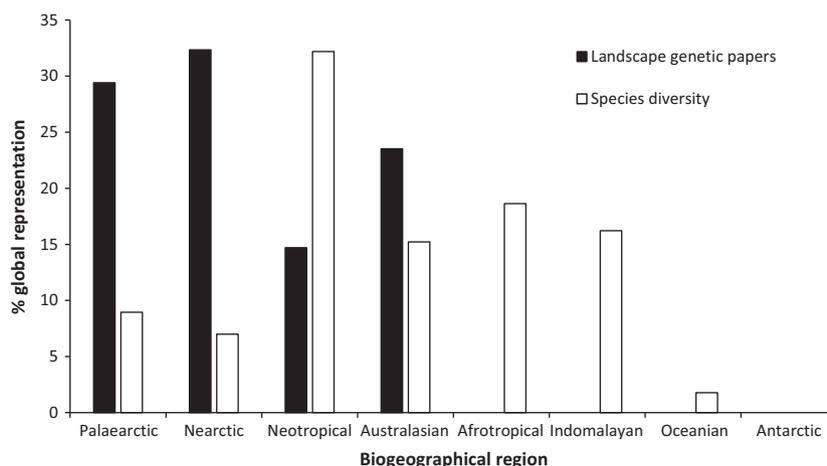
Fig. 4. Distribution of avian species diversity among biogeographical regions based on Newton (2003), and locations of published (2003 to 9 April 2015) avian landscape genetic studies.
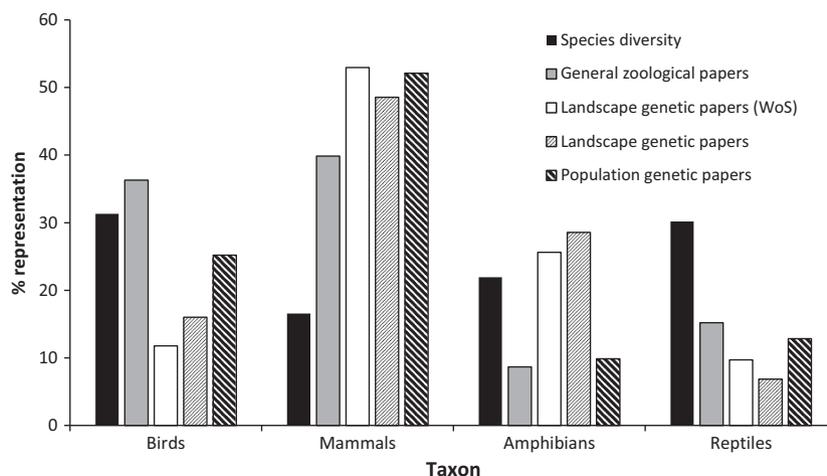

Fig. 5. Relative frequency of publications (2003 to 9 April 2015) across vertebrate classes: general zoological papers, population genetic papers and landscape genetic papers. These are based on Zoological Record searches, with the exception of landscape genetic papers found using Web of Science (WoS). The relative contribution of each taxon to species diversity is also depicted.

Furthermore, they may have the ability to fly over, and therefore be less constrained by, landscape features. Species with less spatial genetic structuring would naturally be less appealing models for the study of landscape genetics, and this may be the cause of the under-representation of birds in the avian landscape genetic literature.

The distribution of dispersal distances from avian landscape genetic and population genetic studies was strongly contrasting, with landscape genetic studies more frequent for less dispersive species and population genetic studies more frequent for more dispersive species ($P < 0.001$,

Fisher's exact test with 10^6 Monte Carlo simulations; Fig. 6). This contrast suggests a lower inclination to choose species with high dispersal ability for landscape genetics, perhaps due to the assumption that they will display minimal spatial genetic structuring across landscapes. This assumption could also influence choice of tetrapod Class for landscape genetic research if Classes were perceived to differ in dispersal distances, although for birds in comparison with mammals, this would be misguided (see below). The assumption that high dispersal species will display minimal spatial genetic structuring also appears incorrect for many
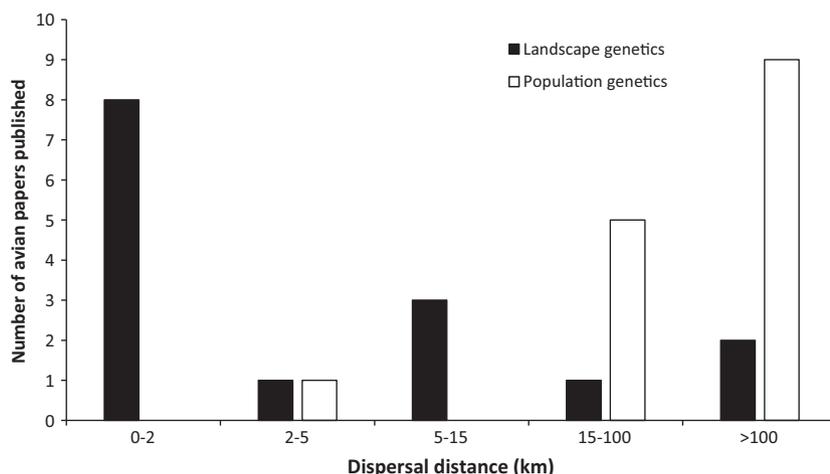
Fig. 6. Dispersal distances of bird species featured in published (2003 to 9 April 2015) landscape and population genetic studies. Only includes papers where the dispersal distance of the study species is specified in the text. The studies corresponding to each distance class are listed in Table S2.

bird species, as significant genetic structuring has been observed at spatial scales similar to, or shorter than, observed dispersal distances (e.g. Martínez-Cruz *et al.* 2007, Alcaide *et al.* 2009, Mira *et al.* 2013). Although most of these studies cite philopatry or habitat fragmentation as the cause of genetic isolation, effects of landscape on genetic structure were not specifically tested in any of them. Mammalian studies also revealed landscape-related genetic structuring in species of high dispersal ability (e.g. Neaves *et al.* 2009, Pease *et al.* 2009, Robinson *et al.* 2012). Although Amos *et al.* (2014) found support for their hypothesis that more mobile species are less likely to be subject to genetic isolation in a fragmented landscape, the Yellow-tufted Honeyeater *Lichenostomus melanops*, one of the more mobile study species among a suite of 10 birds in their study, exhibited genetic isolation with fragmentation.

The relative lack of published avian landscape genetic studies may reflect difficulty detecting genetic structure at the landscape scale, and investigations intended to be 'landscape genetics' may revert to being 'population genetics' publications that lack any quantitative assessment of landscape influence on genetic structuring. The increasing availability and power of genomic techniques provides the opportunity to delineate genetic structure to finer scales (Allendorf *et al.* 2010) more appropriate for landscape analyses. Although these techniques are superseding traditional molecular tools in studies of gene flow, their uptake has been limited for landscape genetic studies in birds (e.g. Manthey & Moyle 2015, Szulkin *et al.* 2016, Wenzel *et al.* 2016). This may again reflect the underlying assumption that spatial genetic structure will be difficult to detect in birds. However, in one of the published examples, populations from different habitats only 5.6 km apart were distinguishable, in contrast to a previous 10-locus microsatellite dataset (Szulkin *et al.* 2016). Similarly, genotype–environment associations have been observed at spatial scales comparable to natal dispersal distances (Garroway *et al.* 2013).

The avian landscape genetic literature, small as it is, demonstrates that landscape-related genetic structuring can occur in birds, and that flight does not automatically impart either high dispersal ability or landscape-independent dispersal behaviour (e.g. Lindsay *et al.* 2008, Unfried *et al.* 2013). Bird species that disperse short (<15 km) distances are relatively common (Paradis *et al.* 1998, Sutherland *et al.* 2000, Mabry *et al.* 2013), and forest birds have been shown to be highly reliant upon forest patches for their movement (Bélisle *et al.* 2001, Bélisle & Desrochers 2002, Desrochers *et al.* 2011, Villard & Haché 2012). Birds have a similar frequency distribution of natal dispersal distances across species to mammals (Sutherland *et al.* 2000, also see data from Mabry *et al.* 2013) and thus should not be considered a less suitable taxon for landscape genetic studies on the presumption of long-distance or unconstrained dispersal, and nor do they necessarily require study at larger spatial scales.

Logistical difficulties could have contributed to the under-representation of birds in landscape genetics. Landscape genetics may require large sample sizes from fine spatial scales to identify often weak correlations with landscape features (Balkenhol & Fortin 2016). Birds tend to move frequently and may nest in difficult-to-reach locations, which can impede sampling. Similarly, the requirement of researchers to be present during trapping (e.g. mist-netting) typically results in spatially clustered sampling, which can be undesirable for landscape genetics under some circumstances (Balkenhol & Fortin 2016). However, other fields also requiring the direct capture of animals do not exhibit the same under-representation as landscape genetics of birds. Our Zoological Records Plus search for population genetic studies of birds also returned over 2000 results (approximately 25% of all tetrapod population genetic papers), and bias against birds for population genetics appears less than for landscape genetics (Fig. 5). There are also numerous examples of mark-recapture and other banding studies of birds that require direct capture. Although landscape genetics may necessitate a relatively high sampling effort, the difficulty of capturing birds does not appear to have impeded avian research efforts in other fields. Furthermore, non-invasive sampling can also be conducted (e.g. Regnaut et al. 2006, Hogan et al. 2008). While the tractability of a given project is an important consideration for all researchers, the ease with which results may be obtained from a particular taxon should not indefinitely favour its use.

Seasonal migration is another factor that may complicate landscape genetic research in birds. Seasonal migration is more common in birds than in mammals, with an estimated 50 billion of the 200–400 billion individual birds on this planet migrating annually (Berthold 2001). Long-distance migrants may travel many thousands of kilometres annually between breeding sites and feeding grounds, and it has been suggested that they will disperse farther than non-migratory species (Paradis et al. 1998, Sutherland et al. 2000, Winkler et al. 2005). However, many migratory birds exhibit strong philopatry (Fowler 2005, Lecomte et al. 2009), or require specific habitats for breeding (Norris & Marra 2007), which may constrain dispersal and contribute to spatial genetic structure despite a clearly and frequently demonstrated ability to traverse long distances. It has also been suggested that non-migratory species may be more likely to disperse because they spend more of their life in close proximity to potentially different breeding sites, yet no difference in dispersal distance with migratory status has been observed (Tittler et al. 2009). Migratory birds are largely unstudied in landscape genetics, and studies focusing on breeding habitat preferences and local environmental conditions at breeding sites, rather than the composition of landscape intervening breeding sites, may better predict spatial genetic variation (e.g. Pease et al. 2009).

Birds frequently display strong preferences for specific breeding habitats (Cody 1985, Jones 2001, Davis & Stamps 2004). The distribution of such habitats should therefore be expected to influence species distribution and dispersal, which would then be reflected in spatial genetic variation. In this context, birds may actually disperse more readily across poor habitat (e.g. Coulon et al. 2010, Berkman et al. 2013) but may be less inclined to disperse long distances across good habitat, where the resources required for reproduction can be found easily. This could be tested by using traditional ecological techniques such as telemetry and mark-recapture (Shirk et al. 2010, Spear et al. 2010, Shafer et al. 2012, Pflüger & Balkenhol 2014) to determine whether individuals of a species move over particular habitat types, and whether poor quality habitat should be considered in landscape genetic analyses as conducive or limiting to dispersal.

SUGGESTIONS FOR THE FUTURE

Birds are present in almost every terrestrial habitat, and their ability to fly, together with their unique life history characteristics, means that their interactions with the landscape, and the factors that affect avian population genetic variation, are distinct from other taxa. Birds also frequently fill important ecological roles upon which other species uniquely depend, such as seed dispersal (Levey et al. 2005, Sethi & Howe 2009), pollination (Anderson et al. 2011) and control of herbivorous insects (Van Bael et al. 2003), which places great importance on understanding their dispersal. Habitat loss and fragmentation is continuing globally and is strongly related to declines in bird populations (Herkert 1994, Bregman et al. 2014), particularly in tropical regions (Bregman et al. 2014), yet most landscape genetic research occurs in the temperate regions of Europe and North

America. Understanding and predicting the effects of anthropogenic landscape change, including habitat fragmentation, on birds is crucial for us to understand how we can mitigate these impacts, and is urgently needed in the tropics. Furthermore, we strongly encourage future landscape genetic research to focus on how habitat fragmentation and loss might compound overall habitat decline by affecting bird species that play important roles in maintaining such habitats (e.g. Wenney & Levey 1998, Van Bael *et al.* 2003, Agostini *et al.* 2006). Landscape genetics cannot adequately investigate these roles through the study of non-avian species, with the possible exception of bats, studies of which are also relatively few in landscape genetics.

Landscape genetics is a young discipline, and the 13 years of its formal existence have been characterized by the constant development and refinement of analytical techniques, undergoing frequent changes in methods (Storfer *et al.* 2010). During such a formative period, focusing on perceived 'ideal model' taxa may be useful, producing clearer and more predictable results that more easily facilitate the testing and comparing of methods. However, eventually the knowledge gained from this period must be applied more widely, as continued taxonomic bias yields diminishing returns in the accumulation of scientific knowledge as compared with a more diverse, inclusive approach. Landscape genetics, if it is to reach its potential as an informative zoological discipline, must adopt this latter approach. We note that the publication frequency of avian landscape genetic papers does not appear to have increased following the period examined by our formal literature searches (i.e. after 2014), remaining relatively low compared with other taxa.

While comparatively small in number, landscape genetic studies conducted on birds have already made significant contributions to our understanding of landscape influences on genetic variation. Most commonly, this has involved understanding the influence of spatial habitat heterogeneity on genetic variation and, by proxy, population connectivity (e.g. Alda *et al.* 2011, 2013, Shanahan *et al.* 2011). This has included documentation of the time-lags associated with the impacts of anthropogenic habitat fragmentation on genetic variation (Coulon *et al.* 2008, Pavlacky *et al.* 2009, Unfried *et al.* 2013). Sex-biased dispersal is common among bird species (Mabry *et al.* 2013), and investigations have also identified landscape features differentially influencing population genetic structuring among sexes (Pierson *et al.* 2010, Amos *et al.* 2014). There have also been studies highlighting the importance of local vs. intervening habitat to our understanding of spatial genetic variation (Porlier *et al.* 2012). However, specific recommendations for the future of avian landscape genetic research can be made based on our assessment of past studies.

Our understanding of landscape influence on population genetic variation in birds will be improved by the greater use of higher-resolution genomic approaches, providing more detailed spatial patterns of genetic variation that can be tested against landscape variables (Allendorf *et al.* 2010). This has already been demonstrated in birds (Szulkin *et al.* 2016). However, a wealth of existing avian datasets exhibiting spatial genetic variation can also be subjected to formal, quantitative, landscape genetic analysis. This presumes that such analyses have not been conducted before, and we encourage studies that fail to detect landscape influence on genetic patterns to be documented as formal papers with 'negative' results (e.g. Kozakiewicz *et al.* 2017). Likewise, explicit statements within papers that have been reframed as more traditional 'population genetic' studies are required to avoid biasing our understanding of landscape influence on genetic variation within birds through the 'file-drawer' problem (Rosenthal 1979). The spatial scales and intensities of sampling can be improved using non-invasive techniques, matched with careful planning of sampling activities (Balkenhol & Fortin 2016). The abundance and ease with which behavioural observations can be made for birds should also be employed when deciding which landscape variables to assess, and how they are predicted to influence dispersal (facilitating or inhibiting), not necessarily from the common perspective of 'ease of movement' but also from the perspective of 'habitat selection'. Finally, the focus of research activities should not be directed to certain taxa based on presumptions of 'likelihood of success' in terms of statistical significance, but rather in terms of filling existing knowledge gaps instead of smoothing the surface of those that are already well-filled.

REFERENCES

Agostini, K., Sazima, M. & Sazima, I. 2006. Bird pollination of explosive flowers while foraging for nectar and caterpillars. *Biotropica* **38**: 674–678.

Alcaide, M., Serrano, D., Negro, J.J., Tella, J.L., Laaksonen, T., Müller, C., Gal, A. & Korpimäki, E. 2009. Population fragmentation leads to isolation by distance but not genetic impoverishment in the philopatric Lesser Kestrel: a comparison with the widespread and sympatric Eurasian Kestrel. *Heredity* **102**: 190–198.

Alda, F., Sastre, P., De La Cruz-Cardiel, P.J. & Doadrio, I. 2011. Population genetics of the endangered Cantabrian capercaillie in northern Spain. *Anim. Cons.* **14**: 249–260.

Alda, F., García, J., García, J.T. & Suárez-Seoane, S. 2013. Local genetic structure on breeding grounds of a long-distance migrant passerine: the Bluethroat (*Luscinia svecica*) in Spain. *J. Hered.* **104**: 36–46.

Allendorf, F.W., Hohenlohe, P.A. & Luikart, G. 2010. Genomics and the future of conservation genetics. *Nat. Rev. Genet.* **11**: 697–709.

Amos, J.N., Bennett, A.F., MacNally, R., Newell, G., Pavlova, A., Radford, J.Q., Thomson, J.R., White, M. & Sunnucks, P. 2012. Predicting landscape-genetic consequences of habitat loss, fragmentation and mobility for multiple species of woodland birds. *PLoS ONE* **7**: e30888.

Amos, N., Harrisson, K.A., Radford, J.Q., White, M., Newell, G., Mac Nally, R., Sunnucks, P. & Pavlova, A. 2014. Species- and sex-specific connectivity effects of habitat fragmentation in a suite of woodland birds. *Ecology* **95**: 1556–1568.

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S. & Terry, J. 2011. Cascading effects of bird functional extinction reduce pollination and plant density. *Science* **331**: 1068–1071.

Balkenhol, N. & Fortin, M.J. 2016. Chapter 4: Basics of study design: sampling landscape heterogeneity and genetic variation for landscape genetic studies. In Balkenhol, N., Cushman, S.A., Storfer, A.T. & Waits, L.P. (eds) *Landscape Genetics: Concepts, Methods, Applications*: 58–76. Chichester: John Wiley & Sons, Ltd.

Balkenhol, N., Waits, L.P. & Dezzani, R.J. 2009. Statistical approaches in landscape genetics: an evaluation of methods for linking landscape and genetic data. *Ecography* **32**: 818–830.

Bélisle, M. & Desrochers, A. 2002. Gap-crossing decisions by forest birds: an empirical basis for parameterizing spatially-explicit, individual-based models. *Landsc. Ecol.* **17**: 219–231.

Bélisle, M., Desrochers, A. & Fortin, M.-J. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* **82**: 1893–1904.

Berkman, L.K., Nielsen, C.K., Roy, C.L. & Heist, E.J. 2013. Resistance is futile: effects of landscape features on gene flow of the Northern Bobwhite. *Cons. Genet.* **14**: 323–332.

Berthold, P. 2001. *Bird Migration: A General Survey*. New York: Oxford University Press Inc.

Bolliger, J., Lander, T. & Balkenhol, N. 2014. Landscape genetics since 2003: status, challenges and future directions. *Landsc. Ecol.* **29**: 361–366.

Bonnet, X., Shine, R. & Lourdais, O. 2002. Taxonomic chauvinism. *Trends Ecol. Evol.* **17**: 1–3.

Bregman, T.P., Sekercioglu, C.H. & Tobias, J.A. 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biol. Cons.* **169**: 372–383.

Bruggeman, D.J., Wiegand, T. & Fernandez, N. 2010. The relative effects of habitat loss and fragmentation on population genetic variation in the Red-cockaded Woodpecker (*Picoides borealis*). *Mol. Ecol.* **19**: 3679–3691.

Clark, J.A. & May, R.M. 2002. Taxonomic bias in conservation research. *Science* **297**: 191–192.

Cody, M.L. (ed) 1985. *Habitat Selection in Birds*. London: Academic Press Inc..

Coulon, A., Fitzpatrick, J.W., Bowman, R., Stith, B.M., Makarewich, C.A., Stenzler, L.M. & Lovette, I.J. 2008. Congruent population structure inferred from dispersal behaviour and intensive genetic surveys of the threatened Florida Scrub-jay (*Aphelocoma coerulescens*). *Mol. Ecol.* **17**: 1685–1701.

Coulon, A., Fitzpatrick, J.W., Bowman, R. & Lovette, I.J. 2010. Effects of habitat fragmentation on effective dispersal of Florida Scrub-jays. *Cons. Biol.* **24**: 1080–1088.

Cushman, S.A. & Landguth, E.L. 2010. Spurious correlations and inference in landscape genetics. *Mol. Ecol.* **19**: 3592–3602.

Davis, J.M. & Stamps, J.A. 2004. The effect of natal experience on habitat preferences. *Trends Ecol. Evol.* **19**: 411–416.

Desrochers, A., Bélisle, M., Morand-Ferron, J. & Bourque, J. 2011. Integrating GIS and homing experiments to study avian movement costs. *Landsc. Ecol.* **26**: 47–58.

Fowler, A.C. 2005. Fine-scale spatial structuring in cackling Canada geese related to reproductive performance and breeding philopatry. *Anim. Behav.* **69**: 973–981.

Garroway, C.J., Radersma, R., Sepil, I., Santure, A.W., Cauwer, I., Slate, J. & Sheldon, B.C. 2013. Fine-scale genetic structure in a wild bird population: the role of limited dispersal and environmentally based selection as causal factors. *Evolution* **67**: 3488–3500.

Hanski, I. 1998. Metapopulation dynamics. *Nature* **396**: 41–49.

Herkert, J.R. 1994. The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecol. Appl.* **4**: 461–471.

Hillman, S.S., Drewes, R.C., Hedrick, M.S. & Hancock, T.V. 2014. Physiological vagility and its relationship to dispersal and neutral genetic heterogeneity in vertebrates. *J. Exp. Biol.* **217**: 3356–3364.

Hogan, F.E., Cooke, R., Burridge, C.P. & Norman, J.A. 2008. Optimizing the use of shed feathers for genetic analysis. *Mol. Ecol. Res.* **8**: 561–567.

IUCN 2014. The IUCN Red List of Threatened Species. Version 2014.3. http://www.iucnredlist.org/ (downloaded 9 April 2015).

Jenkins, C.N., Pimm, S.L. & Joppa, L.N. 2013. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl Acad. Sci. USA* **110**: E2602–E2610.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. *Auk* **118**: 557–562.

Kozakiewicz, C.P., Carver, S., Austin, J.J., Shephard, J.M. & Burridge, C.P. 2017. Intrinsic factors drive spatial genetic variation in a highly vagile species, the Wedge-tailed Eagle (*Aquila audax*), in Tasmania. *J. Avian Biol.*. https://doi.org/10.1111/jav.01326.

Lecomte, N., Gauthier, G., Giroux, J.-F., Milot, E. & Bernatchez, L. 2009. Tug of war between continental gene flow and rearing site philopatry in a migratory bird: the sex-

biased dispersal paradigm reconsidered. *Mol. Ecol.* **18**: 593–602.

Levey, D.J., Bolker, B.M., Tewksbury, J.J., Sargent, S. & Haddad, N.M. 2005. Effects of landscape corridors on seed dispersal by birds. *Science* **309**: 146–148.

Lindsay, D.L., Barr, K.R., Lance, R.F., Tweddale, S.A., Hayden, T.J. & Leberg, P.L. 2008. Habitat fragmentation and genetic diversity of an endangered, migratory songbird, the Golden-cheeked Warbler (*Dendroica chrysoparia*). *Mol. Ecol.* **17**: 2122–2133.

Mabry, K.E., Shelley, E.L., Davis, K.E., Blumstein, D.T. & Van Vuren, D.H. 2013. Social mating system and sex-biased dispersal in mammals and birds: a phylogenetic analysis. *PLoS ONE* **8**: e57980.

Manel, S., Schwartz, M.K., Luikart, G. & Taberlet, P. 2003. Landscape genetics: combining landscape ecology and population genetics. *Trends Ecol. Evol.* **18**: 189–197.

Manthey, J.D. & Moyle, R.G. 2015. Isolation by environment in White-breasted Nuthatches (*Sitta carolinensis*) of the Madrean Archipelago sky islands: a landscape genomics approach. *Mol. Ecol.* **24**: 3628–3638.

Martínez-Cruz, B., Godoy, J.A. & Negro, J.J. 2007. Population fragmentation leads to spatial and temporal genetic structure in the endangered Spanish Imperial Eagle. *Mol. Ecol.* **16**: 477–486.

Mira, S., Arnaud-Haond, S., Palma, L., Cancela, M.L., Beja, P. & Fuchs, J. 2013. Large-scale population genetic structure in Bonelli's Eagle *Aquila fasciata*. *Ibis* **155**: 485–498.

Neaves, L.E., Zenger, K.R., Prince, R.I., Eldridge, M.D. & Cooper, D.W. 2009. Landscape discontinuities influence gene flow and genetic structure in a large, vagile Australian mammal, *Macropus fuliginosus*. *Mol. Ecol.* **18**: 3363–3378.

Newton, I. 2003. *The Speciation and Biogeography of Birds*. San Diego: Academic Press Inc.

Norris, D.R. & Marra, P. 2007. Seasonal interactions, habitat quality, and population dynamics in migratory birds. *Condor* **109**: 535–547.

Paradis, E., Baillie, S.R., Sutherland, W.J. & Gregory, R.D. 1998. Patterns of natal and breeding dispersal in birds. *J. Anim. Ecol.* **67**: 518–536.

Pavlacky, D.C., Jr, Goldizen, A.W., Prentis, P.J., Nicholls, J.A. & Lowe, A.J. 2009. A landscape genetics approach for quantifying the relative influence of historic and contemporary habitat heterogeneity on the genetic connectivity of a rainforest bird. *Mol. Ecol.* **18**: 2945–2960.

Pawar, S. 2003. Taxonomic chauvinism and the methodologically challenged. *Bioscience* **53**: 861–864.

Pease, K.M., Freedman, A.H., Pollinger, J.P., McCormack, J.E., Buermann, W., Rodzen, J., Banks, J., Meredith, E., Bleich, V.C., Schaefer, R.J., Jones, K. & Wayne, R.K. 2009. Landscape genetics of California mule deer (*Odocoileus hemionus*): the roles of ecological and historical factors in generating differentiation. *Mol. Ecol.* **18**: 1848–1862.

Pflüger, F.J. & Balkenhol, N. 2014. A plea for simultaneously considering matrix quality and local environmental conditions when analysing landscape impacts on dispersal. *Mol. Ecol.* **23**: 2146–2156.

Pierson, J.C., Allendorf, F.W., Saab, V., Drapeau, P. & Schwartz, M.K. 2010. Do male and female Black-backed Woodpeckers respond differently to gaps in habitat? *Evol. App.* **3**: 263–278.

Porlier, M., Garant, D., Perret, P. & Charmantier, A. 2012. Habitat-linked population genetic differentiation in the Blue Tit *Cyanistes caeruleus*. *J. Hered.* **103**: 781–791.

Pysek, P., Richardson, D.M., Pergl, J., Jarosik, V., Sixtova, Z. & Weber, E. 2008. Geographical and taxonomic biases in invasion ecology. *Trends Ecol. Evol.* **23**: 237–244.

Regnaut, S., Lucas, F.S. & Fumagalli, L. 2006. DNA degradation in avian faecal samples and feasibility of non-invasive genetic studies of threatened capercaillie populations. *Cons. Genet.* **7**: 449–453.

Robinson, S.J., Samuel, M.D., Lopez, D.L. & Shelton, P. 2012. The walk is never random: subtle landscape effects shape gene flow in a continuous white-tailed deer population in the Midwestern United States. *Mol. Ecol.* **21**: 4190–4205.

Rosenthal, R. 1979. The file drawer problem and tolerance for null results. *Psychol. Bull.* **86**: 638.

Schwartz, M.K. & Mills, L.S. 2005. Gene flow after inbreeding leads to higher survival in deer mice. *Biol. Cons.* **123**: 413–420.

Seddon, P.J., Soorae, P.S. & Launay, F. 2005. Taxonomic bias in reintroduction projects. *Anim. Cons.* **8**: 51–58.

Sethi, P. & Howe, H.F. 2009. Recruitment of Hornbill-dispersed trees in hunted and logged forests of the Indian Eastern Himalaya. *Cons. Biol.* **23**: 710–718.

Shafer, A.B., Northrup, J.M., White, K.S., Boyce, M.S., Côté, S.D. & Coltman, D.W. 2012. Habitat selection predicts genetic relatedness in an alpine ungulate. *Ecology* **93**: 1317–1329.

Shanahan, D.F., Possingham, H.P. & Riginos, C. 2011. Models based on individual level movement predict spatial patterns of genetic relatedness for two Australian forest birds. *Landsc. Ecol.* **26**: 137–148.

Shine, R. & Bonnet, X. 2000. Snakes: a new 'model organism' in ecological research? *Trends Ecol. Evol.* **15**: 221–222.

Shirk, A.J., Wallin, D.O., Cushman, S.A., Rice, C.G. & Warheit, K.I. 2010. Inferring landscape effects on gene flow: a new model selection framework. *Mol. Ecol.* **19**: 3603–3619.

Spear, S.F., Balkenhol, N., Fortin, M.-J., McRae, B.H. & Scribner, K. 2010. Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. *Mol. Ecol.* **19**: 3576–3591.

Stahlschmidt, Z.R. 2011. Taxonomic chauvinism revisited: insight from parental care research. *PLoS ONE* **6**: e24192.

Storfer, A., Murphy, M.A., Evans, J.S., Goldberg, C.S., Robinson, S., Spear, S.F., Dezzani, R., Delmelle, E., Vierling, L. & Waits, L.P. 2007. Putting the 'landscape' in landscape genetics. *Heredity* **98**: 128–142.

Storfer, A., Murphy, M.A., Spear, S.F., Holderegger, R. & Waits, L.P. 2010. Landscape genetics: where are we now? *Mol. Ecol.* **19**: 3496–3514.

Sutherland, G.D., Harestad, A.S., Price, K. & Lertzman, K.P. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Cons. Ecol.* **4**: 16.

Szulkin, M., Gagnaire, P.A., Bierne, N. & Charmantier, A. 2016. Population genomic footprints of fine-scale differentiation between habitats in Mediterranean Blue Tits. *Mol. Ecol.* **25**: 542–558.

Tittler, R., Villard, M.-A. & Fahrig, L. 2009. How far do songbirds disperse? *Ecography* **32**: 1051–1061.

Unfried, T.M., Hauser, L. & Marzluff, J.M. 2013. Effects of urbanization on Song Sparrow (*Melospiza melodia*) population connectivity. *Cons. Genet.* **14**: 41–53.

Van Bael, S.A., Brawn, J.D. & Robinson, S.K. 2003. Birds defend trees from herbivores in a Neotropical forest canopy. *Proc. Natl Acad. Sci. USA* **100**: 8304–8307.

Villard, M.-A. & Haché, S. 2012. Conifer plantations consistently act as barriers to movement in a deciduous forest songbird: a translocation experiment. *Biol. Cons.* **155**: 33–37.

Wang, I.J. 2010. Recognizing the temporal distinctions between landscape genetics and phylogeography. *Mol. Ecol.* **19**: 2605–2608.

Wang, I.J. 2011. Choosing appropriate genetic markers and analytical methods for testing landscape genetic hypotheses. *Mol. Ecol.* **20**: 2480–2482.

Wenney, D.G. & Levey, D.J. 1998. Directed seed dispersal by bellbirds in a tropical cloud forest. *Proc. Natl Acad. Sci. USA* **95**: 6204–6207.

Wenzel, M.A., Douglas, A., James, M.C., Redpath, S.M. & Piertney, S.B. 2016. The role of parasite-driven selection in shaping landscape genomic structure in Red Grouse (*Lagopus lagopus scotica*). *Mol. Ecol.* **25**: 324–341.

Winkler, D.W., Wrege, P.H., Allen, P.E., Kast, T.L., Senesac, P., Wasson, M.F. & Sullivan, P.J. 2005. The natal dispersal of Tree Swallows in a continuous mainland environment. *J. Anim. Ecol.* **74**: 1080–1090.

Zeller, K.A., McGarigal, K. & Whiteley, A.R. 2012. Estimating landscape resistance to movement: a review. *Landsc. Ecol.* **27**: 777–797.

APPENDIX 1

Citation indexes for *Web of Science Core Collection (1945–present)* used for literature search

- Science Citation Index Expanded (1945 to present)
- Social Sciences Citation Index (1956 to present)
- Arts & Humanities Citation Index (1975 to present)
- Conference Proceedings Citation Index-Science (1990 to present)
- Conference Proceedings Citation Index- Social Science & Humanities (1990 to present)
- Emerging Sources Citation Index (2015 to present)
- Current Chemical Reactions (1985 to present) *(Includes Institut National de la Propriete Industrielle structure data back to 1840)*
- Index Chemicus (1993 to present)

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Articles used for the analysis of terrestrial vertebrate landscape genetic literature ($n = 289$).

Table S2. Landscape genetic and population genetic papers reporting dispersal distance of study species ($n = 30$).

Table S3. Zoological Record Plus search results for avian population genetic articles ($n = 2147$).

Table S4. Results from chi-square tests comparing numbers of landscape genetic (LG) papers published for each tetrapod Class with numbers expected based on known species diversity, and with numbers expected based on each taxon's representation in the general zoological literature.