

Homogenization of dispersal ability across bird species in response to landscape change

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Human land use is known to homogenize biotic communities, increasing similarity in their genetic, taxonomic and functional diversity. Explanations have focused almost exclusively on human-mediated extinction and range expansion. However, homogenization could also be produced by land use driving selection for similar traits across species. We propose a novel hypothesis to explain how human land use homogenizes dispersal ability across species. With habitat loss and increasing human land use intensities there should be larger increases in the costs of dispersal for dispersive than sedentary species, because dispersive species interact with non-habitat more frequently. In contrast, the benefits of dispersal should increase more for sedentary than dispersive species, because sedentary species are at greater risk from inbreeding depression, predation and competition associated with habitat loss. Therefore we predict that sedentary species become more dispersive in a human-altered landscape, and dispersive species more sedentary. We tested this prediction using wing pointedness to estimate the initial dispersal ability and change in dispersal ability for 21 North American passerines over the 20th century. More pointed wings are associated with stronger dispersal ability. Thus our prediction would be supported by a negative cross-species relationship between these two measurements. We found a strong, negative relationship, as predicted. This resulted in declines in the variability in wing pointedness among species over time. Although other things can cause wing shape to change, including changes in habitat availability, none of these explained the observed relationship. Our result provides the first evidence that human landscape alteration is homogenizing bird communities, driving selection for intermediate dispersal ability across species. It also implies that more dispersive species are more at-risk from human landscape use because, when rates of landscape alteration are faster than a species' ability to adapt to that change, the costs of dispersal increase more for dispersive than sedentary species.

A species' dispersal ability may evolve in response to human-caused landscape change, due to changes in the cost/benefit ratio of dispersal (Fahrig 2007). The main costs of dispersal are increased risk of mortality in the non-habitat ('matrix') parts of the landscape and energy expenditure during movement, which may in turn reduce reproductive success (Baker and Rao 2004, Johnson et al. 2009). The main benefits of dispersal are that it allows individuals to track available resources, and avoid inbreeding, competition, and predation (Bollinger et al. 1993, Tellería and Pérez-Tris 2003, Cronin et al. 2004, Moore et al. 2006). All else being equal, species dispersal ability should decline when landscape change increases the costs of dispersal more than its benefits, and dispersal ability should increase when landscape change increases the benefits of dispersal more than its costs.

A given landscape change may increase both the costs and benefits of dispersal. For example, habitat loss increases the costs of dispersal, because it increases the distances between habitat patches and decreases habitat patch sizes, leading to more frequent interaction of individuals with the matrix (Hill et al. 1996, Baker and Rao 2004, Johnson et al. 2009).

Habitat loss also increases the benefits of dispersal, because individuals need to move farther to locate habitat when habitat fragments are farther apart, and because risks of inbreeding and competition increase when habitat patches are smaller and more isolated (Matthysen et al. 1995, Ramsay et al. 1997, Saccheri et al. 1998). This suggests that how a species' dispersal ability changes in response to habitat loss depends on whether habitat loss increases the costs of dispersal more than its benefits.

We hypothesize that a species' initial dispersal ability affects how its dispersal ability changes in response to human-caused landscape change, because its initial dispersal ability determines whether landscape change increases the costs of dispersal more than its benefits. We expect larger increases in the costs of dispersal for dispersive than sedentary species when habitat is lost and human land-use intensity increases, because dispersive species interact with matrix more frequently than sedentary species. In contrast, if interaction with matrix is rare, individuals will rarely experience the costs of movement through matrix. This follows from Öckinger et al. (2009), who found that the negative

effects of habitat patch isolation increased with species dispersal ability. On the other hand, we expect larger increases in the benefits of dispersal for sedentary than dispersive species. This is because the negative effects of small habitat patches decrease with dispersal ability (Öckinger et al. 2009). Sedentary species should be more sensitive to declining patch areas than dispersive species, because they are at greater risk from inbreeding depression, competition, and predation when patch sizes decline, and they cannot supplement their limited local resources by movement among habitat fragments. In summary, habitat loss should increase the benefits of dispersal more than its costs for sedentary species, driving selection for greater dispersal ability in sedentary species, but habitat loss and increasing land use intensity should drive selection for lower dispersal ability in more dispersive species. Therefore we predict that sedentary species will become more dispersive in a human-altered landscape, while more dispersive species become less dispersive.

We tested this prediction using an existing data set (Desrochers 2010) to estimate the initial dispersal ability and change in dispersal ability for 21 North American passerine species over the 20th century. Additionally, evolution of dispersal ability in a given species should depend on how much habitat that species has lost (Bonte et al. 2006, 2010, Ahlroth et al. 2010, Desrochers 2010). To account for this in our analysis, we also tested for a relationship between the change in dispersal ability and change in species' habitat cover over the study period.

Methods

Our estimates of the initial dispersal ability and change in dispersal ability were derived from data in Desrochers (2010), who used the primary wing projection as an index of species dispersal ability:

$$\text{primary wing projection} = 100((w - a)/w)$$

where a = distance from the carpal joint of the wing to the distal end of the outermost secondary feather, and w = distance from the carpal joint of the wing to the wing tip. We note that this measure has also been referred to as the hand-wing index (Claramunt et al. 2012) and is equivalent to measuring Kipp's distance (Dawideit et al. 2009). The primary wing projection approximates the wing aspect ratio ($\text{wingspan}^2/\text{wing area}$), which cannot be directly measured for museum specimens because the wings cannot be unfolded to measure the wing area. The wing aspect ratio (and its correlates) measures wing pointedness: wings with large aspect ratios are long and narrow, while wings with small aspect ratios are short and broad. To reflect this relationship, and simplify terminology, we refer to 'wing pointedness' rather than 'primary wing projection' from here forward. More pointed wings are associated with greater dispersal ability (Dawideit et al. 2009), likely because they result in more energy-efficient sustained flight (Rayner 1988, Bowlin and Wikelski 2008). Previous studies suggest wing shape is heritable, and can evolve rapidly within species (Åkesson et al. 2007, Tarka et al. 2010, Brown and Brown 2013). For these reasons, wing pointedness has been accepted as an index of dispersal ability (Claramunt et al. 2012, White 2016), although we

acknowledge that this proxy cannot account for all factors that determine actual dispersal rates or distances.

Desrochers (2010) measured the wing pointedness of 851 adult (> 1 month post-fledging) museum specimens of 21 passerine species collected between 1900 and 2008 by the Cornell Univ. Museum of Vertebrates or the Canadian Museum of Nature (Table 1). Species inclusion was limited by numbers of specimens and time spent at museums: only species with > 10 specimens, collection dates spanning at least 50 years, and wings small enough to be measured by digital calipers were included. Species were also selected to represent two contrasting human impacts over the last century (extensive clearcuts in boreal forests and afforestation in New England), and habitat associations (mature forest to open habitats). The right wing was measured for each specimen, except when it was damaged or missing (3% of individuals).

Population-level estimates of initial wing pointedness and the change in wing pointedness over time were estimated from a linear regression model of wing pointedness against year of specimen collection for each species. Sex was included as a covariate in each model. We estimated the initial wing pointedness for a species as the model intercept (i.e. estimated primary projection in 1900) and the change in wing pointedness as the model slope (i.e. change in primary projection per 100 years). Note that for *Sitta canadensis* Desrochers (2010) analysed measurements for boreal and temperate populations separately; to avoid double-counting this species we used only the boreal data. Our conclusions did not depend on whether we used the boreal or temperate population.

Table 1. Summary of data from Desrochers (2010) used to estimate the initial wing pointedness and change in wing pointedness over time, for each of the 21 North American passerine species.

Species	Sample size (female/male)	Years sampled
<i>Ammodramus henslowii</i>	23 (5/18)	1903–1953
<i>Ammodramus savannarum</i>	27 (6/21)	1900–1971
<i>Certhia americana</i>	38 (10/28)	1900–2006
<i>Dendroica caerulescens</i>	47 (12/35)	1900–2006
<i>Dendroica castanea</i>	66 (28/38)	1900–1999
<i>Dendroica cerulea</i>	18 (6/12)	1905–1964
<i>Dendroica coronata</i>	54 (19/35)	1902–2008
<i>Dendroica magnolia</i>	40 (8/32)	1900–2008
<i>Dendroica pinus</i>	24 (5/19)	1900–2008
<i>Dendroica tigrina</i>	75 (20/55)	1900–1984
<i>Melospiza lincolnii</i>	19 (6/13)	1900–2008
<i>Oporornis philadelphia</i>	29 (9/20)	1900–2004
<i>Parus hudsonicus</i>	76 (51/25)	1905–1989
<i>Perisoreus canadensis</i>	48 (14/34)	1904–1983
<i>Piranga olivacea</i>	43 (6/37)	1900–2007
<i>Sitta canadensis</i> *	59 (7/52)	1915–1982
<i>Sitta carolinensis</i>	50 (21/29)	1900–2006
<i>Spizella pusilla</i>	29 (7/22)	1900–2005
<i>Sturnella magna</i>	24 (5/19)	1901–1975
<i>Wilsonia citrine</i>	28 (8/20)	1900–2005
<i>Wilsonia pusilla</i>	14 (4/10)	1905–2000

*For *S. canadensis* Desrochers (2010) analysed measurements for boreal and temperate populations separately; to avoid double-counting this species we used only the boreal data.

We recognize that comparisons between an initial sample of a population (e.g. wing pointedness values from a given bird species) and the change between that sample and subsequent sample(s) of the same population can be biased by a statistical phenomenon known as ‘regression to the mean’, which causes a spurious negative relationship between the initial sample and its change. However, previous simulations suggest that the negative bias is minimized when these parameters are estimated as the intercept and slope from regression models of measurements taken at more than two time points, as in our analyses (Chiolero et al. 2013). In addition, we evaluated the potential impact of regression to the mean on our results. We used simulations to estimate the proportion of the observed relationship between wing pointedness and the change in wing pointedness that could be attributed to regression to the mean. This analysis demonstrated that regression to the mean does not explain our empirical findings (see Supplementary material Appendix 1 for details of the simulation model).

We estimated the change in species-specific habitat cover over the study period, for each species, so that we could directly assess the relationship between the change in wing pointedness and species’ habitat cover. We derived the distribution of 11 land cover classes in North America from published land cover maps for 1900 and 1990 (Goldewijk 2007; Fig. 1). Continent-scale satellite imagery or aerial

photography was not available in the early 20th century. Thus land cover estimates depended on models that extrapolate past land cover distributions from more recent land cover data (the 1992–1993 DISCover land cover data set, 1-km resolution; Loveland et al. 2000), and estimates of natural vegetation patterns derived from a modified version of the BIOME climatic model (Goldewijk 2001). Changes in agricultural and pasture land covers depended on the assumption that these land covers increase with human population density. Despite its limitations (Goldewijk 2001), to our knowledge this is the best available estimate of historical land cover for North America, and it should provide reasonable (although coarse) estimates of habitat change at the scale of the species’ North American ranges.

To estimate the change in habitat cover, we first estimated the species range as the minimum convex polygon around all routes where the species was detected at least once during the time series (1966–2013) of the North American Breeding Bird Survey (BBS; Pardieck et al. 2014). The BBS provides a continent-wide, multi-year data set of species counts for breeding birds along more than 4100 roadside survey routes. Point counts are conducted at 50 stops spaced along each 39.4-km-long route once per year during the breeding season. At each point count, all birds seen or heard within a 0.4 km radius are recorded over a 3 min interval.

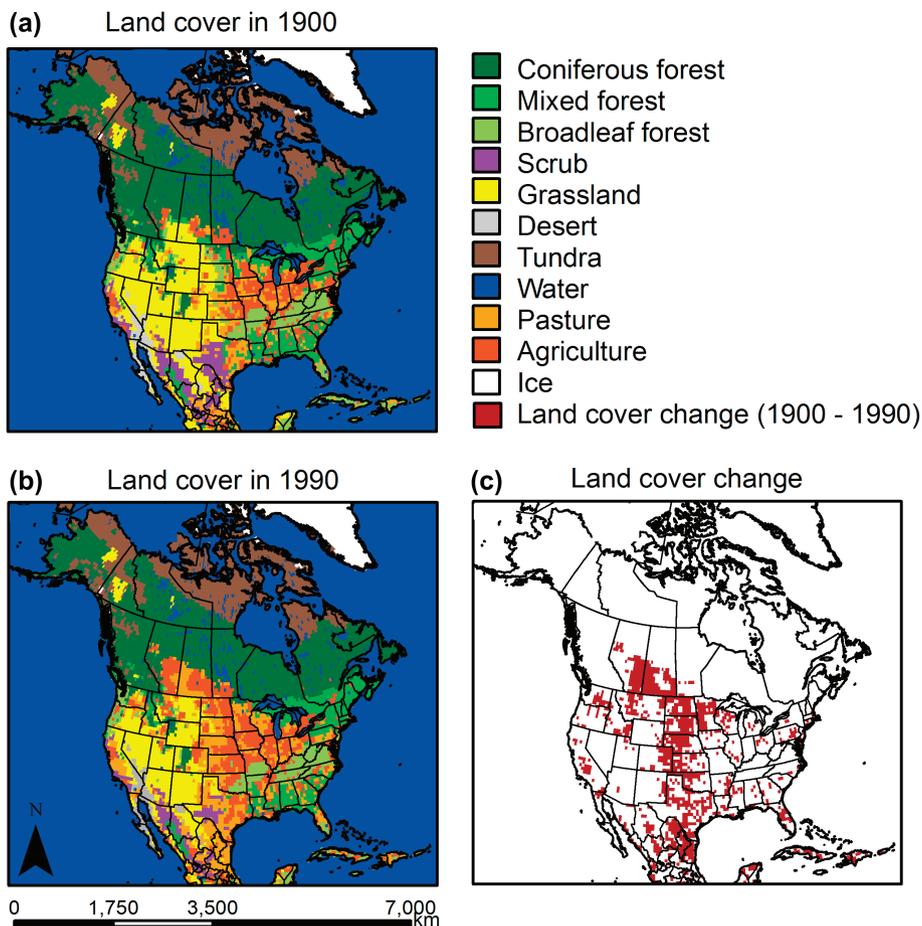


Figure 1. Estimates of (a) land cover in 1900, (b) land cover in 1990, and (c) land cover change between 1900 and 1990. Land cover was derived from Goldewijk (2007).

We then estimated the habitat associations of each species using the 1990 land cover map (Fig. 1b) and BBS data. We used habitat selection ratios (HSR_i) to identify which of 11 land cover classes was habitat for each species. HSR_i for a given species and land cover class i was measured as the proportion of the observations of that species in land cover class i , divided by the proportion of all sample sites within the species' range in land cover class i (Manly et al. 2002). A sample site consisted of the first 10 stops of a BBS route sampled in 1988–1992, summing the species counts across these years. We used only the first 10 stops, because bird detectability is greater for the initial stops, which are sampled earlier in the morning (Robbins 1981). We selected 1988–1992 to bracket the year of the land cover data (1990). Land cover classes with HSR_i values greater than one for a given species were classified as habitat for that species, because more individuals were observed in areas dominated by that land cover class than expected, given the availability of that land cover class within the species range and set of sample sites.

We estimated the change in habitat cover as the proportional habitat cover in 1990 minus the proportional habitat cover in 1900. Proportional habitat cover in each year (1990 and 1900) was measured for each species:

$$\text{proportional habitat cover} = A_{\text{habitat}}/A_{\text{range}}$$

where A_{range} = area (km^2) of the species' range (as estimated above), and A_{habitat} = area (km^2) of that species' habitat within that range. A_{habitat} was estimated using the 1990 and 1900 land cover maps (Fig. 1a–b), summing the areas (km^2) of the land cover classes classified as habitat for that species (i.e. with $HSR_i > 1$; Supplementary material Appendix 2).

We used multi-model inference based on the small-samples Akaike information criterion (AICc) to compare among four candidate models, modeling the change in wing pointedness as a function of the 1) initial wing pointedness + change in habitat cover, 2) initial wing pointedness, 3) change in habitat cover, and 4) the null (intercept-only) model. To account for non-independence of observations caused by phylogenetic relatedness, we used a generalized least squares model, where covariance between a given pair of species was based on a phylogenetic tree and a Brownian model of evolution (Martins and Hansen 1997). To account for uncertainty in the phylogenetic relationships among species, we used a random sample of 5000 possible phylogenetic trees for our species, chosen from the pseudo-posterior distribution of trees with a Hackett backbone (Jetz et al. 2012), and fitted our candidate models 5000 times, each time using a different phylogeny. To determine the support for a given model we used the median results from multi-model inference, i.e. the median AICc, ΔAICc , and model weight from the 5000 analyses. Our hypothesis would be supported by a negative cross-species relationship between initial wing pointedness and change in wing pointedness.

Data analyses were conducted in R (<www.r-project.org>), using the 'MuMIn' (Barton 2014) and 'nlme' (Pinheiro et al. 2014) packages.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.2522c>> (Martin et al. 2016).

Results

For 11 species, wings became more pointed over time, while for the remaining 10 species, wings became less pointed over time. Initial wing pointedness (i.e. primary wing projection) values ranged from 10.15, for *Ammodramus henslowii*, to 33.24, for *Dendroica cerulea*. Assuming that the habitat associations of species have remained constant, 76% (16/21) of our study species lost habitat over the last century. Changes ranged from a loss of 8.06% habitat cover, for *Sitta carolinensis*, to a gain of 14.44% habitat cover, for *Ammodramus savannarum*.

Sedentary species became more dispersive over time, while more dispersive species became less dispersive, as predicted. We found strong support for a negative cross-species relationship between initial wing pointedness and change in wing pointedness (Fig. 2a). The model relating the change in wing pointedness to initial wing pointedness had the strongest support of all models in our candidate model set, and the null model was not included in the most supported model set (i.e. the null model had $\Delta\text{AICc} = 7.28$; Table 2). Supplementary analyses suggest that this strong, negative relationship was not caused by regression to the mean: the observed negative correlation between the initial wing pointedness and change in wing pointedness ($r = -0.72$) was six times larger than the most likely (i.e. average) correlation expected from regression to the mean, and three times larger than the maximum correlation expected from regression to the mean (Supplementary material Appendix 1).

There was also moderate support for a relationship between the change in dispersal ability and the change in habitat cover, when we controlled for the species' initial dispersal ability. This model was the second most supported model in our candidate set (with $\Delta\text{AICc} = 2.75$; Table 2). The result suggests a tendency towards decreasing dispersal ability in the species that have been losing habitat, and increasing dispersal ability in the species that have been gaining habitat (Fig. 2b).

Discussion

Our results support the prediction that sedentary bird species have become more dispersive, while more dispersive species have become less dispersive over the past century. We infer that habitat loss and the increasing intensity of human land uses over the past century had different effects on dispersive and sedentary species, because these landscape changes decreased the cost/benefit ratio of dispersal for sedentary species and increased the cost/benefit ratio of dispersal for dispersive species. The higher costs of dispersal for more dispersive species are due to their more frequent interaction with matrix, and the higher benefits of dispersal for sedentary species are due to their greater risk from inbreeding depression, competition, and predation. Although previous studies have tested hypotheses to explain how landscape change influences selection for increased/decreased dispersal ability (Merckx et al. 2003, Ahlroth et al. 2010), to our knowledge this is the first to suggest that a species' evolutionary response to human-caused landscape change depends on its prior dispersal ability. Interestingly, Van Houtan et al. (2007)

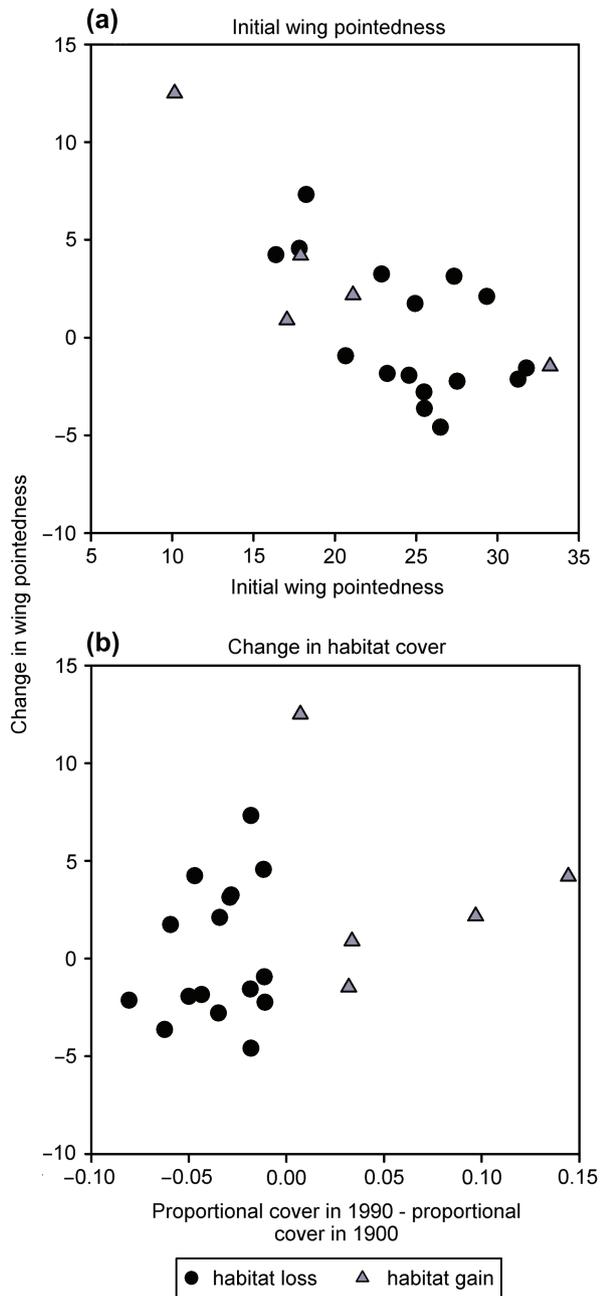


Figure 2. Change in wing pointedness versus (a) initial wing pointedness and (b) change in species-specific habitat cover. Each point represents one of 21 species. For each species we used a linear regression of wing pointedness against year of specimen collection to estimate the initial wing pointedness (i.e. wing pointedness in 1900) as the model intercept and change in wing pointedness (i.e. change in wing pointedness per 100 years) as the model slope. See Methods for calculation of wing pointedness values. We estimated the change in species-specific habitat cover as the proportional habitat cover in 1990 minus the proportional habitat cover in 1900.

found similar changes in the dispersal ability of tropical birds immediately following forest habitat loss; i.e. less dispersive tropical birds tended to move more frequently and farther following habitat loss, while more dispersive birds moved less frequently and shorter distances. Although Van Houtan et al. (2007) measured the immediate response to habitat loss rather than an evolutionary change, i.e. they compared

Table 2. Results of multi-model inference of the cross-species relationship between the change in wing pointedness and the initial wing pointedness and change in species-specific habitat cover. For each species we used a linear regression of wing pointedness against year of specimen collection to estimate the initial wing pointedness (i.e. wing pointedness in 1900) as the model intercept and change in wing pointedness (i.e. change in wing pointedness per 100 years) as the model slope. We estimated the change in habitat cover as the proportional habitat cover in 1990 minus the proportional habitat cover in 1900. Relationships were modeled by a generalized least squares model, with a covariance matrix to account for phylogenetic relationships among species. Presented are the degrees of freedom (DF), small samples Akaike information criterion (AICc), change in AICc (Δ AICc), and weight for all subsets of the global model. AICc, Δ AICc, and weights are the medians from the set of 5000 analyses conducted with different possible phylogenetic trees.

Model	DF	AICc	Δ AICc	Weight
Initial wing pointedness	3	127.97	0.00	0.77
Initial wing pointedness + change in habitat cover	4	130.70	2.75	0.20
Null	2	135.24	7.28	0.02
Change in habitat cover	3	137.94	9.97	0.01

only the three years before and after forest clear-cutting, their study supports our suggestion that prior dispersal ability influences the species response to a given landscape change, such as habitat loss.

Other things can cause changes in wing shape; however, none of these explain the negative cross-species relationship between the initial wing pointedness and the change in wing pointedness we observed. For example, our results suggest that habitat loss favors selection for decreased dispersal ability and habitat gain favors selection for increased dispersal ability. However, this did not cause the observed relationship between initial dispersal ability and the change in dispersal ability. Habitat change could only cause the observed relationship between the initial wing pointedness and change in wing pointedness if the most dispersive species were losing habitat and the least dispersive species were gaining habitat. We found no support for such a relationship (Supplementary material Appendix 3).

Our finding that habitat loss favors selection for decreased dispersal ability and habitat gain favors selection for increased dispersal ability is consistent with theory and most previous empirical findings (Travis and Dytham 1999, Bonte et al. 2006, 2010, Ahlroth et al. 2010). However, we note that Desrochers (2010) came to the opposite conclusion. This is likely because Desrochers (2010) classified habitat preferences and habitat change via expert opinion and literature review, rather than using empirical data sets, resulting in different estimates of habitat change for many species in the two studies. For example, while our classification of *Wilsonia citrina* habitat preferences agreed with Desrocher's classification as a temperate mature forest species (Supplementary material Appendix 2), our estimates of habitat change for this species did not. We estimated an 8% loss of habitat, while Desrocher suggested habitat gains for this species over the 20th century. Our estimate of habitat loss is consistent with empirical evidence of contemporary forest loss within the species' range: Sleeter et al. (2013) estimated a 4.4% decline in Eastern temperate forest cover from 1973–2000.

Although we found the expected positive relationship between the change in dispersal ability and the change in habitat cover, this relationship was weaker than expected. This may be, at least in part, because of low variability in the rates of land cover change among our study species. This may also reflect uncertainty in historical land cover estimates used to calculate the change in habitat cover. Finally, a weak relationship may occur, in part, because our estimates of habitat preference do not account for potential changes in species habitat preferences over time (Barnagaud 2011). We note that, although uncertainty in historical land cover estimates and habitat preferences may reduce the strength of the relationship between land cover change and the change in wing pointedness, we can think of no reason to expect either source of uncertainty to cause the observed relationship. This would only occur if habitat cover in 1900 was underestimated relative to 1990 for species with increasing wing pointedness, but overestimated in 1900 for species with decreasing wing pointedness. Such a bias seems highly unlikely.

Another potential explanation for a change in wing pointedness of a given species over time is a shift in the migration behavior of that species, because migratory individuals tend to have more pointed wings than non-migratory individuals (Marchetti et al. 1995, Lockwood et al. 1998). However, this could only cause the observed cross-species relationship between initial wing pointedness and change in wing pointedness if migratory species became less migratory, and non-migratory species became more migratory over the last century. We can think of no reason why habitat loss would drive such changes, and studies suggest a warming climate should generally favor a non-migratory strategy (Rivalan et al. 2007, Pulido and Berthold 2010). Furthermore, we tested and found no empirical support for a relationship between the change in wing pointedness and migration status for these species (Supplementary material Appendix 4).

Brown and Brown (2013) found evidence that bird wing shape changes in response to road mortality, favoring selection of shorter wings that allow for more vertical take-off. However, this cannot explain the negative relationship between initial wing pointedness and the change in wing pointedness. If road mortality was driving the observed changes in wing shape in our study, we should have seen general declines in wing pointedness across species because (a) less pointed wings allow for more vertical take-off (Swaddle and Lockwood 2003), and (b) the number of roads and traffic volume have increased in North America over the 20th century. Instead, we found approximately equal numbers of species showing increases and decreases in wing pointedness.

Wing shape is also associated with a species' foraging behavior (e.g. aerial versus ground foraging; White 2016), thus shifts in foraging behavior over time could also potentially explain a change in wing pointedness. If true, we would expect evidence of a relationship between the change in wing pointedness and foraging behavior of our species. We tested and found no empirical support for this relationship (Supplementary material Appendix 5).

There is some evidence that wing pointedness also depends on the characteristics of the foraging habitat; i.e. that species foraging in open habitats have more pointed wings than

those foraging in habitats with dense vegetation (Forstmeier and Keblor 2001, White 2016). However, this could only explain our observed relationship if there was a shift in the local conditions where specimens of a given species were collected over time, such that the vegetation density within the foraging grounds of initially open-habitat foraging species has increased over time, while vegetation density within the foraging grounds of initially dense-habitat foraging species has decreased. We have no reason to expect such changes; however, we acknowledge that this possibility could not be explicitly evaluated.

Finally, there was no evidence of between-species biases in our data set that could confound interpretation of the relationship between initial wing pointedness and its change over time. Although the number of specimens varied among species (14–76 specimens/species), as did the range of sampled years (50–108 years), neither was linearly related to estimates of wing pointedness or the change in wing pointedness (Table 1, Supplementary material Appendix 6). Similarly, there was no evidence that either wing pointedness parameter was affected by a change in the specimen frequency over time (Supplementary material Appendix 6). Finally, we recognize that it is possible that left-right asymmetry in wing pointedness may increase with habitat loss, as has been observed for other wing characteristics (e.g. wing and feather length; Anciães and Marini 2000, Helle et al. 2011). However, there is no evidence or theory to suggest that this asymmetry would be directional (e.g. right wings always more pointed than left wings) or that the direction of asymmetry varies among species. Therefore, our inference that habitat loss and the increasing intensity of human land uses over the past century had different effects on dispersive and sedentary species is the most likely explanation for our results.

Implications

An interesting implication of our result is that it suggests there has been a decline over time in the variation in dispersal ability among species. This is supported by a strong, negative correlation between the variance in wing pointedness among species and time ($r = -0.79$, $p = 0.002$; Fig. 3). One of the known consequences of human land use is that it homogenizes biotic communities, resulting in reduced genetic, taxonomic, and functional diversity (McKinney and Lockwood 1999). Much focus has been on how human-mediated extinction of some species and range expansion of others homogenizes biotic communities (Blair and Johnson 2008, Davey et al. 2012). Extinctions may also homogenize species traits. For example, in cases where the most dispersive (or sedentary) species are the ones that go extinct, there would be reduced variability in dispersal abilities among the remaining species. However, human land use can also homogenize communities by driving selection for similar traits across persisting species. For example, previous study suggests that habitat specialization of bird species is declining over time, homogenizing species habitat preferences (Barnagaud et al. 2011). Our study is the first to suggest a similar trend in species dispersal ability, with human land use driving selection of intermediate dispersal ability across species. Future study is needed to determine whether

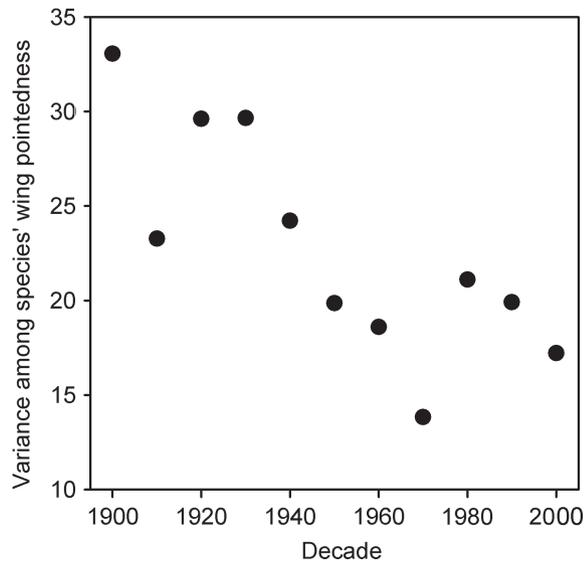


Figure 3. Variability among species in wing pointedness declines over time. The variance for each decade was calculated from the mean wing pointedness values of each species in that decade. The mean wing pointedness of each species was calculated from all individuals sampled in that decade.

our hypothesis is supported for other taxonomic groups and geographic regions.

Our inference that habitat loss and land use intensification increase the costs of dispersal more for dispersive than sedentary species also has implications for species conservation. If species are able to adapt to the landscape change then this may mitigate, to some degree, the role of dispersal ability in extinction risk. This may explain, at least in part, the weak cross-species relationship between dispersal ability and the North American population trend (Supplementary material Appendix 7). However, when the rate of landscape change is faster than the species' evolutionary response to that change, larger increases in the costs of dispersal for dispersive species should put them at greater risk than more sedentary species. This indirectly supports theoretical and empirical findings that extinction risk in human-altered landscapes is greatest for the most dispersive species (Gibbs 1998, Casagrandi and Gatto 1999, Fahrig 2001, Shahabuddin and Ponte 2005). Thus, our results suggest that, when habitat loss is rapid, the most dispersive species should be prioritized for conservation action.

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Supplementary material (available online as Appendix oik-03859 at <www.oikosjournal.org/appendix/oik-03859>). Appendix 1–7.