

# Climate-driven variation in dispersal ability predicts responses to forest fragmentation in birds

Received: 29 July 2022

Accepted: 18 April 2023

Published online: 29 May 2023

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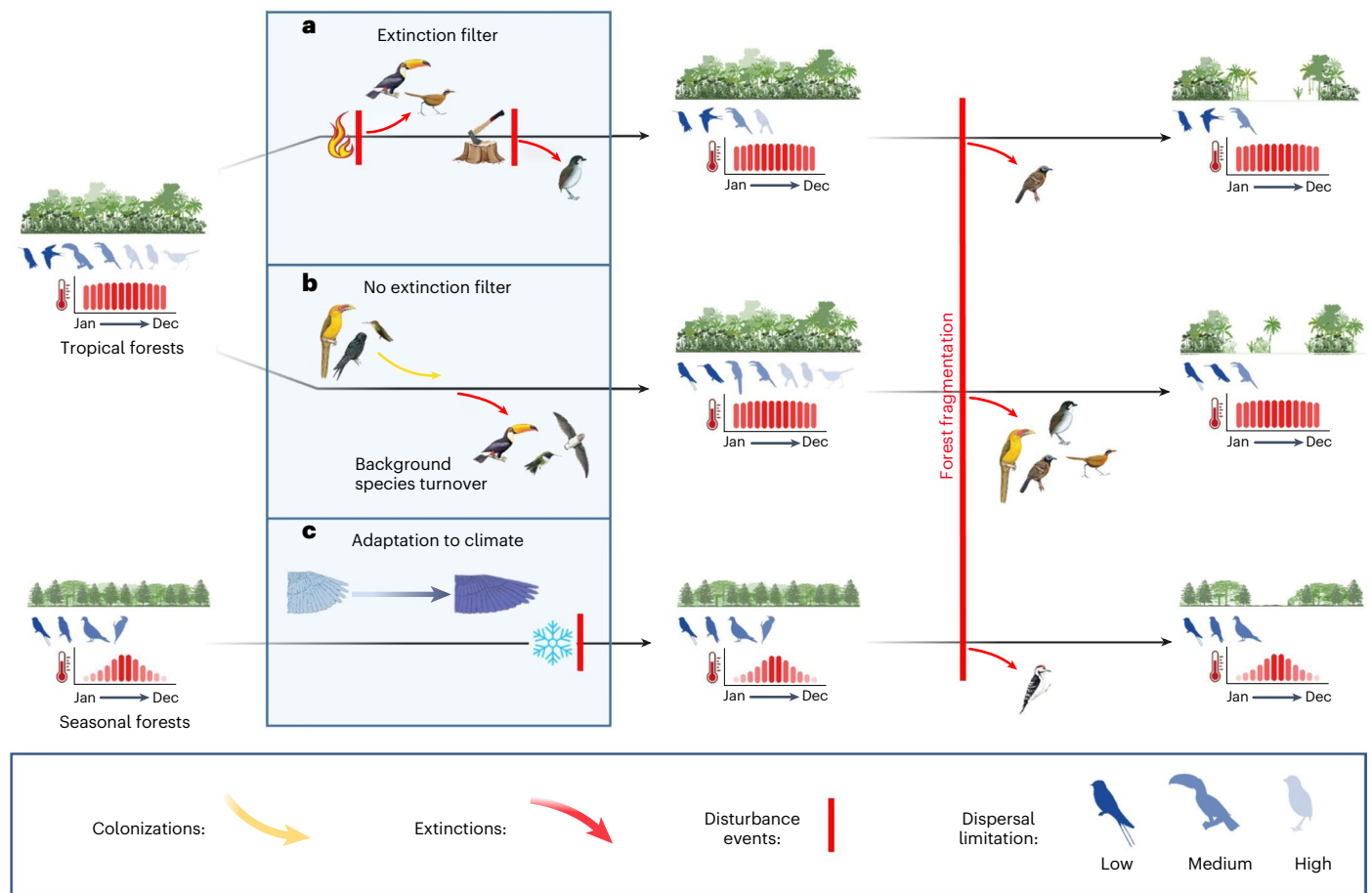
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Species sensitivity to forest fragmentation varies latitudinally, peaking in the tropics. A prominent explanation for this pattern is that historical landscape disturbance at higher latitudes has removed fragmentation-sensitive species or promoted the evolution of more resilient survivors. However, it is unclear whether this so-called extinction filter is the dominant driver of geographic variation in fragmentation sensitivity, particularly because climatic factors may also cause latitudinal gradients in dispersal ability, a key trait mediating sensitivity to habitat fragmentation. Here we combine field survey data with a morphological proxy for avian dispersal ability (hand-wing index) to assess responses to forest fragmentation in 1,034 bird species worldwide. We find that fragmentation sensitivity is strongly predicted by dispersal limitation and that other factors—latitude, body mass and historical disturbance events—have relatively limited explanatory power after accounting for species differences in dispersal. We also show that variation in dispersal ability is only weakly predicted by historical disturbance and more strongly associated with intra-annual temperature fluctuations (seasonality). Our results suggest that climatic factors play a dominant role in driving global variation in the impacts of forest fragmentation, emphasizing the need for more nuanced environmental policies that take into account local context and associated species traits.

Habitat fragmentation is a major driver of biodiversity decline<sup>1–3</sup>. At a global scale, the impacts are often most apparent in forest species, many of which are poorly adapted to land-use change caused by anthropogenic disturbance, including urbanization, logging and agricultural expansion<sup>4</sup>. Forest fragmentation threatens many species by creating barriers to connectivity among fragmented populations<sup>5–7</sup>, in conjunction with ‘edge effects’ and habitat loss, resulting in reduced availability

of habitat and other resources<sup>8</sup>. The strength of these impacts varies widely, both across species and geographically, with a prominent latitudinal gradient in sensitivity to forest fragmentation reported in some taxonomic groups<sup>9,10</sup>. Despite numerous studies focusing on the effects of forest fragmentation at local and landscape scales, the mechanisms driving these global patterns in fragmentation sensitivity remain unclear<sup>11</sup>.

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**Fig. 1 | Hypotheses predicting the distribution of fragmentation-sensitive species.** The top pathway (a) illustrates how ‘extinction filters’ linked to historical disturbances (for example, fire and anthropogenic forest loss) can be non-random, removing species traits associated with sensitivity to disturbance and retaining more resilient survivors. Tropical bird communities that have largely avoided severe historical disturbance theoretically contain more species with disturbance-sensitive traits (such as poor dispersal and ecological specialization), accentuating the impacts of forest fragmentation (b). Background turnover of species, shown in (b) but present in all pathways,

is random with respect to disturbance-sensitive traits. A different mechanism involves the evolution of flight adaptations to cope with seasonal fluctuations in temperature and resources (including vegetation, insects, flowers and fruits). In birds, the predominant adaptation to seasonality involves increased mobility (from local dispersal to long-distance migration), so highly seasonal communities lack dispersal-limited species, potentially increasing their resilience to forest fragmentation (c) in comparison with climatically stable regions (b). Relative species richness is shown by the number of bird silhouettes in the community.

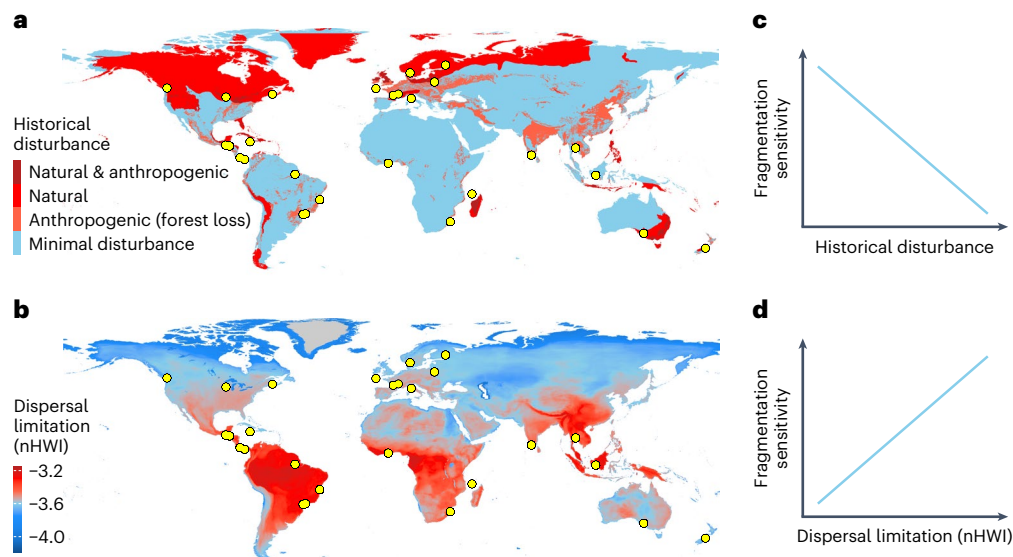
One proposed mechanism based on the concept of ‘extinction filters’ is that geographical variation in fragmentation sensitivity is driven by differential patterns of extinction whereby fragmentation-sensitive species have already been lost from landscapes that have historically incurred higher levels of environmental disturbance<sup>12</sup>. This concept is sometimes expanded beyond the effects of extinction to include the impacts of historical disturbance on surviving species, which are more likely to have evolved adaptations to persist in fragmented landscapes<sup>9</sup>. Thus, through both extinction and evolution, species surviving periods of intense disturbance are predicted to have one or more traits—including stronger dispersal ability, wider ecological niches, smaller area requirements and ‘faster’ life-history strategies—making them more resilient to current levels of habitat fragmentation (Fig. 1a). Accordingly, if landscapes exposed to the strongest or most frequent historical disturbances are clustered towards higher latitudes (Fig. 2a), extinction filters may explain the latitudinal gradient in fragmentation sensitivity (Fig. 2c).

Although previous analyses have shown that extinction filters contribute to global patterns in fragmentation sensitivity<sup>9</sup>, additional mechanisms are almost certainly involved, perhaps playing a dominant role. Even in the absence of historical disturbance or extinction, natural selection is expected to generate latitudinal gradients in niche-related

or life-history traits, many of which are adaptations to intra-annual climatic fluctuation (seasonality)<sup>13</sup> (Fig. 1c). In particular, fragmentation sensitivity may be accentuated by dispersal limitation<sup>2</sup>, which appears to be most prevalent in tropical biota<sup>14</sup> (Fig. 2b).

Recent global analyses focusing on birds (the study taxa with the most comprehensive data available) reveal that climatic seasonality predicts variation in dispersal ability, even when accounting for latitude<sup>15</sup>. At higher latitudes and in highly seasonal tropical environments such as savannahs and dry forests, many species have mobile lifestyles, characterized by seasonal territoriality, flocking in the non-breeding season, spatial resource tracking and migratory behaviour<sup>16,17</sup>. Conversely, in many tropical forest birds, stable climatic conditions and the consequent year-round availability of food resources give rise to sedentary lifestyles, characterized by ecological specialization, year-round territoriality and reduced natal dispersal distance<sup>18–21</sup>. The concept is not limited to birds as reduced dispersal distance is also evident in many other tropical forest animals<sup>22</sup> and plants<sup>23</sup> for similar reasons.

Variation in dispersal limitation is linked to fragmentation sensitivity in birds because less dispersive species have reduced gap-crossing ability<sup>24–26</sup>, increasing rates of extinction in habitat patches and reducing the likelihood of recolonization after extinction events<sup>18,27</sup>. Equally,



**Fig. 2 | Global patterns of landscape disturbance and dispersal limitation.** **a**, The presence of natural or anthropogenic historical disturbances recorded in each grid cell. Natural disturbance pressures (bright red) include major fires, storms and glaciation; these events have typically persisted for longer periods of time and may cause complete removal of forest biota. Anthropogenic forest loss (pale red) represents more recent disturbance that often alters composition of local assemblages without complete eradication. **b**, Variation in nHWI averaged across species occurring in each grid cell, ranging from low (blue) to

high (red) dispersal limitation. Dispersal limitation data are calculated from measurements of 10,562 bird species, logarithmically scaled for visualization ( $\log(1/\text{HWI})$ ). Yellow dots show study landscapes (21 from BIOFRAG; 10 from additional sampling). Grid cells in **a** and **b** are 2.5 arc minutes. **c, d**, Hypothetical relationships: extinction filters predict that fragmentation sensitivity is negatively associated with historical disturbance (**c**), while dispersal-related mechanisms predict that fragmentation sensitivity is positively associated with dispersal limitation (**d**).

if lineages evolving at high latitudes are inherently more dispersive as a result of ecological adaptation to widely fluctuating intra-annual climatic regimes, their sensitivity to forest fragmentation may be reduced (Fig. 1). The reported latitudinal gradient in dispersal limitation<sup>14,15</sup> may therefore cause the parallel gradient in species sensitivity to forest fragmentation<sup>9,10,26</sup> (Fig. 2d), potentially even explaining the apparent relationship between fragmentation sensitivity and historical disturbance (Fig. 2).

To provide a more nuanced analysis of the relative roles of different mechanisms, we estimate fragmentation sensitivity of bird species reported by field surveys in 22 countries (Fig. 2). We quantify the effect of fragmentation on these populations on the basis of their aversion to forest edges, accounting for continuous gradients in tree cover<sup>28</sup>. We then use Bayesian phylogenetic mixed-effect models to assess whether fragmentation sensitivity is best predicted by historical disturbance or hand-wing index (HWI)—a metric of wing shape that predicts dispersal distance<sup>21</sup> and gap-crossing ability in forest birds<sup>29,30</sup>. We use negative (inverse) hand-wing index score (nHWI) to represent dispersal limitation, because this helps to clarify the mechanistic link with fragmentation sensitivity (see Methods).

Historical disturbance and dispersal limitation are not mutually exclusive hypotheses. Rather, dispersal limitation is one of several potential underlying mechanisms for the effects of historical disturbance (Fig. 1). A history of disturbance may lead to the decline and extinction of dispersal-limited species and could also drive selection for increased dispersal ability in surviving lineages<sup>31,32</sup>. Nonetheless, if fragmentation sensitivity is more strongly associated with dispersal than disturbance, this would imply a primary role for other factors. We examine this possibility further by testing whether historical disturbance or climatic seasonality influence fragmentation sensitivity directly or via downstream effects on dispersal (HWI). Taken together, these analyses offer new insights into the relative roles of extinction filters and ecological adaptation, with implications for the design of effective conservation strategies in fragmented ecosystems.

## Results

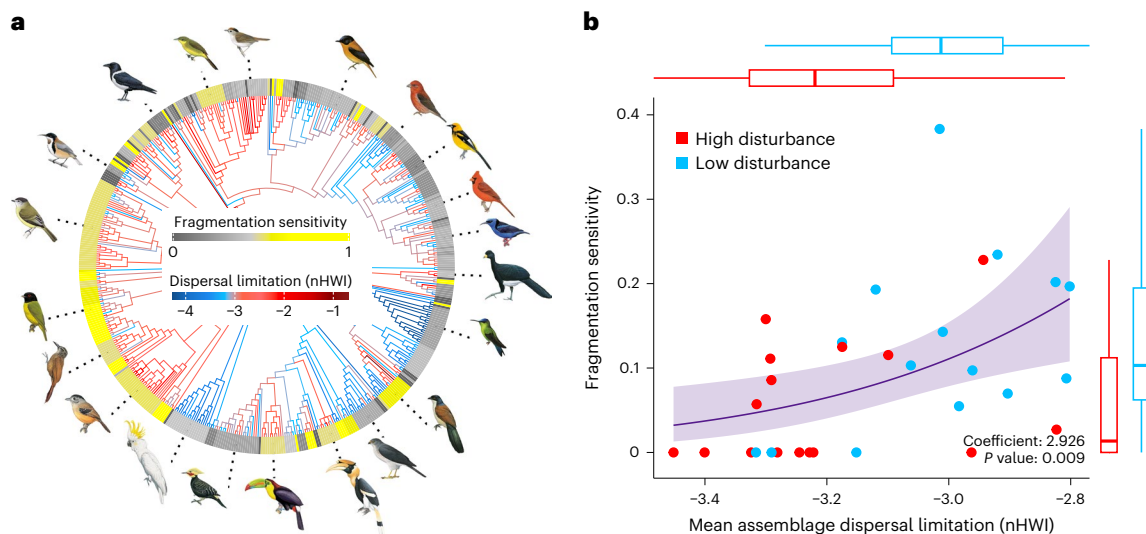
We compiled data from 31 study landscapes spanning from 0.8 to 62.6 degrees latitude (Fig. 2) and sampling sites with high historical disturbance ( $n = 16$ ) and low historical disturbance ( $n = 15$ ; see Methods and Supplementary Data 1). Intensive field surveys recorded 1,564 populations of 1,034 bird species, of which 276 are treated by BirdLife International<sup>33</sup> as ‘Forest-specialists’ and 874 as ‘Forest-associated’ (that is, the same 276 species combined with a further 598 species with medium forest dependency). The remaining 160 species are not associated with forest (Supplementary Data 1). To focus our analyses on relevant populations, we only assigned fragmentation sensitivity to Forest-specialists (Restricted analyses) and Forest-associated species (Expanded analyses; see Methods). Analyses were conducted at three different levels: landscapes, populations and species, depending on the hypothesis being tested (see Methods).

### Historical disturbance and dispersal limitation

We estimated latitude and historical disturbance for each study landscape ( $n = 31$ ) using a previously described approach<sup>9</sup> and then inferred dispersal limitation (nHWI) for all study species ( $n = 1,034$ ) using global data on wing morphology<sup>15,34</sup> (see Methods). In line with predictions (Fig. 2a), we found a correlation between the latitude of study landscapes and the level of historical disturbance, increasing towards the poles ( $W$ -statistic: 183,  $P = 0.013$ ) (Extended Data Fig. 1). Similarly, we found the expected opposite gradient in dispersal limitation (Fig. 2b), with mean assemblage nHWI ( $n = 31$ ) decreasing with latitude ( $\beta: -0.007, P < 0.001$ ) (Extended Data Fig. 2), consistent with global patterns of avian dispersal ability<sup>15</sup>.

### Patterns of fragmentation sensitivity

Based on patterns of abundance with respect to distance from forest edge, most (225/382; 58.9%) ‘Forest-specialist’ populations and many (583/1,302; 44.8%) ‘Forest-associated’ populations were classified as ‘Forest-core’ (that is, BIOFRAG software assigned them a ‘Forest’ habitat preference and a ‘Core’ affinity, suggesting edge-intolerance; see



**Fig. 3 | Fragmentation sensitivity increases with dispersal limitation in bird assemblages.** **a**, Variation in fragmentation sensitivity and dispersal ability plotted on a consensus phylogenetic tree. Each branch represents a genus ( $n = 441$ ), with data at tips averaged across families ( $n = 115$ ) for visualization. Branch colours indicate dispersal limitation (least dispersive species in red); tip colours show the proportion of fragmentation-sensitive species in each family (expanded analysis; most sensitive in yellow). **b**, Data points (coloured by level of historical disturbance) are means for 31 study landscapes. For each assemblage, fragmentation sensitivity is assigned to forest-core species

Methods). We restricted classification as fragmentation sensitive to these two groups in our Restricted and Expanded analyses, respectively. In our Restricted analysis, we found that 14.4% ( $n = 225$ ) of all study populations ( $n = 1,564$ ) were fragmentation sensitive, increasing to 37.3% ( $n = 583$ ) in our Expanded analysis (see Methods). Despite being more prevalent in some clades (for example, suboscine passerines) than others (Fig. 3a), fragmentation sensitivity was widespread across our sample and its phylogenetic signal ranged from low (Expanded sample,  $d = 0.83$ ) to moderate (Restricted sample,  $d = 0.57$ ).

The proportion of fragmentation-sensitive bird populations in each assemblage ( $n = 31$ ) decreased with absolute latitude (Extended Data Fig. 3a,b), supporting predictions (Fig. 2) based on the results of previous studies<sup>9,10</sup>. In our Restricted analyses, the mean proportion of fragmentation-sensitive species in low-disturbance landscapes (12%) was approximately double that found in high-disturbance landscapes (5%), with similar results in Expanded analyses (37% versus 18%, respectively) (Fig. 3b), as well as previous analyses based on a subset of the same data<sup>9</sup>. At the landscape level, we found a strong positive correlation between mean dispersal limitation (nHWI) and the proportion of fragmentation-sensitive species in each assemblage. This result was similar in both the Restricted ( $\hat{\beta} = 2.926$ ,  $P = 0.009$ ; Fig. 3a) and Expanded analyses ( $\hat{\beta} = 2.790$ ,  $P = 0.004$ ; Extended Data Fig. 4).

### Drivers of fragmentation sensitivity

The Bayesian posterior distributions from our analysis of 1,564 study populations indicate that species sensitivity to forest fragmentation was best explained by dispersal limitation (nHWI) in both our Restricted and Expanded analyses (Fig. 4). Indeed, once our models included nHWI, all other covariates explained little additional variation in the likelihood of a species being classified as fragmentation sensitive. In each case, the posterior distributions of these covariates became centred close to 0, suggesting that their relationship with fragmentation sensitivity is accounted for by dispersal limitation (Fig. 4 and Extended Data Table 1).

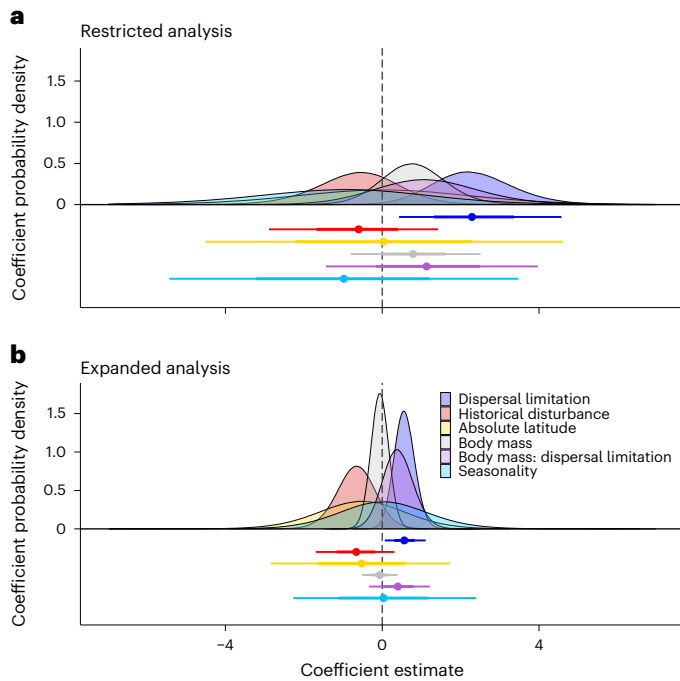
with high forest dependency (Restricted analysis), and mean dispersal limitation is the nHWI averaged across all species; nHWI is logarithmically scaled ( $\log(1/\text{HWI})$ ) for visualization. Statistics are from a generalized linear model with quasi-binomial errors; purple line shows model fit ( $R^2 = 0.180$ ); shaded region shows 95% confidence intervals. Boxplots in **b** show the same distributions with median value, interquartile range and whiskers to extreme values (outliers are data points  $>1.5 \times$  quartiles). Results for the expanded sample are shown in Extended Data Fig. 4.

We included body size in our models because larger-bodied species have greater space requirements and may be forced to cross gaps between habitat patches more often, either to access different parts of their territory or to obtain sufficient food<sup>24,35</sup>. In our Restricted analysis, we found a weak (non-significant) positive effect of body mass on fragmentation sensitivity (Fig. 4a), with a stronger effect size for the interaction term between body mass and dispersal limitation (nHWI). However, credible intervals include 0 and the effect is reduced in our Expanded analyses (Fig. 4b).

Our classification of disturbed landscapes spans different time-scales, including both ongoing or deep-time natural disturbances (fires, storms and glaciation) as well as more recent anthropogenic disturbance (forest loss). To assess whether these temporal scales have different implications for fragmentation sensitivity, we re-classified disturbance as either anthropogenic (forest loss) or natural (fires, storms and glaciation), then re-ran our models (see Supplementary Information). In both cases, the main results were unchanged, with posterior distributions similar to those produced from our main model (Extended Data Figs. 5 and 6, and Supplementary Tables 1 and 2).

### Historical versus climatic mechanisms

Our analyses suggest that dispersal limitation (nHWI) plays a dominant role in shaping patterns of fragmentation sensitivity, but what drives variation in dispersal ability? Given that a combination of both historical and climatic factors is potentially involved (Fig. 1), we explored the relative roles of disturbance history, latitude and seasonality in generating patterns of dispersal limitation (Supplementary Table 3). Using local-scale metrics calculated at the landscape level for each of these covariates, we found a negative association between disturbance history and nHWI (Fig. 5a). However, when we added landscape latitude to the model, the strongest correlation with nHWI switched from disturbance history to latitude (Fig. 5b), suggesting that other latitudinal factors may predominate. Indeed, when we included seasonality as a third covariate, we found seasonality to



**Fig. 4 | Dispersal limitation (nHWI) explains variation in fragmentation sensitivity.** Results of Bayesian phylogenetic mixed-effect models predicting fragmentation sensitivity for all 1,564 bird populations ( $n = 1,034$  species). Populations were classified as fragmentation sensitive if they were identified as 'Forest-core' by BIOFRAG. Restricted analysis assigned fragmentation sensitivity only to 'Forest specialists' (a); Expanded analysis assigned fragmentation sensitivity to both 'Forest specialist' and 'Forest associated' species (b); see Methods). Bayesian posterior distribution is shown above the line; effect-size estimates with credible intervals (CI) are below the line (thick error bars, 68%; thin error bars, 95%). High effect sizes indicate a positive association with fragmentation sensitivity; low effect sizes indicate a negative association. Historical disturbance is a binary variable (1/0) calculated using all disturbance layers (forest loss, glaciation, storms and fires).

be the only significant driver of dispersal limitation, whereas disturbance history and latitude explained little additional variation (Fig. 5c). When we re-ran these analyses using disturbance, latitude and climate data averaged across species breeding ranges, results were similar (Extended Data Fig. 7 and Supplementary Table 4). Despite the correlation between historical disturbance, latitude and climate variables, collinearity between these predictors was checked via variance inflation factors (VIFs) and found to be acceptable ( $<6$ ) in all models.

The proportion of variance in dispersal limitation (nHWI) explained by each model was modest, although the full trivariate model explained substantially more variance ( $R^2 = 0.056$ ) than either the univariate ( $R^2 = 0.009$ ) or bivariate models ( $R^2 = 0.041$ ). Furthermore, of the total variance explained by the full model, we found that seasonality explained the majority (59.35%), whereas historical disturbance (5.93%) and latitude (34.71%) have comparatively limited explanatory power (Fig. 5d–f). Results were similar regardless of whether we averaged species-level data at the local landscape level or across the breeding range of each species (see Methods and Extended Data Fig. 7). The switch in both statistical significance and explanatory power towards seasonality in the full model suggests that the effects of disturbance and latitude in simpler models are mostly explained by co-occurring effects of seasonality. This conclusion was further supported by a phylogenetic structural equation model, which identified seasonality, not historical disturbance, as the fundamental driver of variation in dispersal limitation (see Supplementary Fig. 1).

## Discussion

We have shown that dispersal limitation estimated from wing morphology (nHWI) and, to a lesser extent, the interaction between nHWI and body mass, are key predictors of fragmentation sensitivity in birds. Although these global gradients in dispersal limitation may be shaped by historical factors, particularly latitudinal variation in natural or anthropogenic disturbance<sup>9,36,37</sup>, our results reveal that the main driver of this pattern is a strong environmental mechanism associated with intra-annual climatic variation (seasonality)<sup>15</sup>.

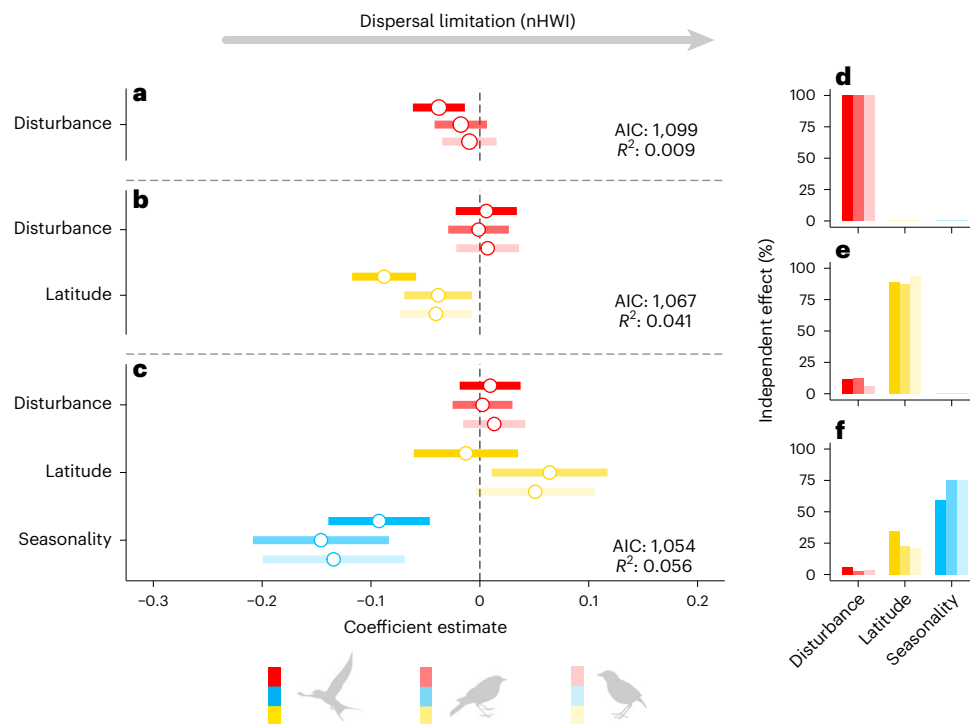
It could be argued that seasonality is simply another form of disturbance and that our findings highlight an additional example of extinction filters shaping the distribution of fragmentation-sensitive species. However, this conceptualization seems inappropriate because seasonality is not explicitly historical; it is an ongoing process by which species adaptations arise gradually through natural selection and rarely by extinction<sup>13,38</sup>. In this context, dispersal limitation offers a more general mechanism that helps to explain the link previously identified between historical disturbance and fragmentation sensitivity<sup>9</sup>, and also provides a framework for understanding how climate shapes the responses of biodiversity to land-use change<sup>39</sup>. Ultimately, the role of dispersal limitation highlights a mechanism by which population decline or extinction can be driven by fragmentation per se, as opposed to area effects<sup>40</sup>.

## Dispersal as a unifying mechanism

A strong latitudinal gradient in sensitivity to forest fragmentation was reported in a global analysis<sup>9</sup>, in line with previous studies suggesting that tropical forest species are on average less equipped to cope with forest fragmentation for a range of physiological reasons, including low dispersal, aversion to light, and adaptation to the cooler and more stable temperatures of tropical forest interiors<sup>10,41,42</sup>. The reduced proportion of fragmentation-sensitive species in high-disturbance sites was thought to reflect an extinction filter, whereby fragmentation sensitive species were already lost from assemblages. Our analyses reveal the same patterns, with a progressive decrease in the proportion of fragmentation-sensitive species from low to high latitudes (Extended Data Fig. 4) and a similar decrease in the proportion of fragmentation-sensitive species from low-disturbance to high-disturbance sites (Fig. 3a). However, once variation in morphological dispersal constraints is accounted for, both patterns become non-significant, suggesting that the effects of dispersal override those of landscape history.

Similarly, the widespread finding that dietary groups differ in their sensitivity to fragmentation (for example, refs. 43–45) might not be related to diet and food abundance per se but rather the fact that dispersal limitation (nHWI) varies significantly within and between trophic niches (Extended Data Fig. 8). Specialist invertivores, for example, tend to be more dispersal-limited than other dietary groups, including nectarivores, granivores and omnivores, which typically have more mobile lifestyles<sup>15</sup>. Moreover, sensitivity to fragmentation appears to vary widely within specialized trophic niches, including invertivores<sup>45,46</sup> and frugivores<sup>47,48</sup>. This within-guild variation can be explained by differences in dispersal ability among members of the same trophic group. For example, terrestrial and understory insectivores are generally less dispersive and more sensitive to habitat fragmentation than canopy or aerial insectivores<sup>14,42</sup>, suggesting that flight efficiency and gap-crossing ability outweigh diet as the key factor determining responses to fragmentation in tropical forests<sup>29,30</sup>.

The effect of dispersal limitation on fragmentation sensitivity makes sense in light of evidence from observational<sup>24,49</sup> and experimental studies<sup>29,30</sup> indicating that forest bird species with reduced dispersal capacity are much less inclined to cross gaps of inhospitable habitat. For a substantial proportion of tropical forest species, constrained gap-crossing ability reduces population connectivity in forested landscapes<sup>24</sup> and constrains recolonization of isolated habitat



**Fig. 5 | Predictors of dispersal limitation in birds.** Results shown are outputs of phylogenetic generalized least-squares models predicting dispersal limitation (nHWI) across all bird species sampled, including long-distance migrants (swallow image, dark bars;  $n = 1,034$ ), only resident species and short distance/partial migrants (thrush image, medium bars;  $n = 921$ ) or only resident species (pitta image, pale bars;  $n = 858$ ). Panels present three sets of models with increasing complexity: a univariate model with single predictor (**a,d**), and multivariate models with two (**b,e**) and three (**c,f**) predictors. Each predictor is calculated at the species level by averaging across landscapes where each species

is present. Disturbance (red) is the local binary disturbance score, latitude (yellow) is the absolute latitude of the landscape centroids and seasonality (blue) is the standard deviation of mean monthly temperature values. **a–c**, Effect-size estimates with 95% confidence intervals; a negative effect indicates reduced dispersal limitation (that is, increased dispersal ability).  $R^2$  and Akaike information criterion (AIC) values are calculated for full sample models only. **d–f**, Proportion of independent variation explained by each model covariate, calculated using hierarchical partitioning.

fragments after local extinction events<sup>18</sup>. This impact is compounded by an increased hostility of matrix (non-forest) habitats to forest specialists, which are often constrained by specialized ecological traits unsuited to typical matrix conditions<sup>27,50–52</sup>. In effect, hostile matrix gaps present a greater barrier to movements of forest specialists, theoretically increasing the cost of dispersal limitation<sup>53–55</sup>. We see evidence of this higher cost in the larger effect sizes of dispersal limitation (nHWI) in our Restricted versus Expanded analyses.

Previous studies have suggested that dispersal limitation accentuates the negative impacts of tropical forest loss<sup>36</sup> and fragmentation<sup>2</sup>, or highlighted associations between fragmentation sensitivity and other traits related to dispersal, including sedentary or non-migratory lifestyles<sup>10,57,58</sup>. Our results go further in showing that dispersal limitation is a pervasive underlying mechanism potentially mediating or driving the effects of historical disturbance<sup>9</sup>, habitat preference<sup>56</sup> and diet<sup>45</sup> on fragmentation sensitivity. Thus, while it is often assumed that the impacts of fragmentation per se on biodiversity are mediated primarily by edge effects<sup>3,40</sup>, our findings highlight the importance of gap effects, with variation in the ability to cross habitat gaps being a key determinant of which species win or lose in fragmented environments<sup>24–26</sup>.

### Caveats and clarifications

Our results appear to conflict with long-term studies at one locality in Amazonian Brazil which found no significant relationship between forest fragmentation sensitivity and dispersal limitation in birds<sup>59,60</sup>. However, this previous finding may be explained by methodological issues because dispersal ability was only scored indirectly through expert opinion and the study landscape was not consistently fragmented. At times, substantial regrowth was allowed to develop between

fragments<sup>61</sup>, no doubt increasing the movement of species with poor dispersal ability through the disturbed landscape<sup>62</sup>. Our analyses based on a more objective metric, estimated over a larger sample of species and landscapes, show that dispersal limitation is a powerful predictor of latitudinal gradients in fragmentation sensitivity. Thus, we find no support for the hypothesis that highly sedentary tropical species are under reduced pressure to cross habitat gaps, hence alleviating the impacts of fragmentation<sup>59,60</sup>. While inverse relationships between dispersal limitation and fragmentation sensitivity may occur temporarily, or in partially fragmented landscapes with large patch-size, the opposite pattern predominates at global scales.

We only find weak and inconclusive support for the effect of body size in our full models, in line with several previous studies of vertebrates<sup>63–65</sup>. However, the interaction term between body size and dispersal limitation receives stronger support in both models, presumably because larger-bodied species typically require larger areas of habitat to meet their resource requirements and sustain a viable population of individuals<sup>66,67</sup>. These larger home ranges are more easily fragmented, increasing the need to move between habitat patches<sup>35</sup>. In both these cases, the spatial context means that larger-bodied species only thrive in fragmented landscapes if they can easily move across matrix gaps. Thus, species with both large body size and poor dispersal suffer a ‘double jeopardy’ and are particularly sensitive to habitat fragmentation<sup>24</sup>.

A final point to consider is the BIOFRAG sampling design, which focuses on edge tolerance rather than occurrence in isolated fragments<sup>28</sup>. It is not immediately obvious why dispersal limitation should influence edge tolerance any more than other traits associated with edge aversion, including year-round territoriality, restriction to ground or understorey habitats, light sensitivity, thermal intolerance and a

slow-paced life-history strategy<sup>41,42,68,69</sup>. One possibility is that dispersal limitation may indicate edge sensitivity through correlation with these other traits, although they are all strongly related to latitude and seasonality<sup>14,27</sup>, which have much weaker effect than dispersal limitation in our models. In addition, we excluded BIOFRAG sites where continuous forest was over-sampled and restricted our additional sampling to highly fragmented landscapes containing many isolated forest patches with correspondingly high ratio of edge to core (see Supplementary Information). Therefore, our measure of fragmentation sensitivity strongly reflects the extent to which species persist in isolated habitat patches compared to continuous areas of forest. The difficulty of crossing hostile matrix gaps is almost certainly the dominant impact of dispersal limitation in such landscapes<sup>18</sup>.

### Dispersal limitation: cause or consequence?

If major historical disturbance events led to fragmented forest landscapes that disfavoured species with poor dispersal, then extinction filters, as conceptualized in ref. 9, may directly shape the patterns we detect in wing morphology. However, we only found inconclusive evidence for this relationship in univariate models (Fig. 5 and Extended Data Fig. 7). The weakness of these simplified models is that disturbance appears to be correlated with seasonality (Extended Data Fig. 9), so a univariate analysis may pick up a signal from seasonality rather than disturbance per se. We addressed this problem using multivariate and structural equation models, both of which reveal that dispersal traits are best explained not by historical disturbance but by temperature variability.

Our findings align with the view that high-dispersal traits of high-latitude species are adaptations to seasonality, that is, part of a behavioural strategy or programme, typically involving either migration or movement between sites, to allow survival during periods of the year when there is little or no production of food in the breeding area (see ref. 17). For example, many avian insectivores breeding in boreal forests are migratory or highly dispersive and therefore capable of surviving in fragmented landscapes or recolonizing habitat patches after local extinction events<sup>27,70</sup>. Seasonality is by far the strongest predictor of latitudinal variation in avian wing morphology, with dispersal adaptations peaking in the most seasonal landscapes<sup>15</sup>. This fits a more general pattern of increased dispersal ability and decreased fragmentation sensitivity at higher latitudes where climatic variability results in strong selection for niche flexibility<sup>14,23</sup>.

Our analyses suggest that climatic effects predominate in shaping global patterns of dispersal limitation and hence fragmentation sensitivity in birds. However, this does not exclude a role for other drivers. All models presented here detect large variation in the effect of species-level covariates on the likelihood of a species being classified as fragmentation sensitive. We found some, albeit weak, support for an effect of landscape-level predictors, including historical disturbance. Several other candidate traits were not included in our models. Thus, although the latitudinal gradient of fragmentation sensitivity in birds appears to be primarily driven by natural selection for increased dispersal ability at higher, more seasonal latitudes, a variety of other behavioural, ecological and historical factors may contribute to variation across species in sensitivity to forest fragmentation.

Further studies are needed to understand the combined roles of climate, disturbance regimes and dispersal limitation in shaping the response of biodiversity to environmental change. Current attempts to disentangle the influence of seasonality from historical disturbance are limited by data quality. In particular, treatment of disturbance as a coarse binary variable increases uncertainty in our analyses. Further resolution of the issue requires higher-quality disturbance data, which may be available in the near future for some regions (for example, maps of fire history are under construction for North America). Ultimately, the combination of habitat fragmentation and climate change may be the most severe threat hanging over species with poor dispersal

ability, since these tend to decline in fragmented landscapes and then disappear altogether when they cannot track climates<sup>71,72</sup>.

## Conclusions

Ecological traits can provide highly resolved information about a species' fundamental niche<sup>73–75</sup>, so it makes sense that variation in traits such as dispersal limitation may drive responses to habitat fragmentation. Given that dispersal limitation also peaks at the equator<sup>14,15</sup>, we conclude that dispersal traits offer a compelling explanation for widely reported spatial gradients in fragmentation sensitivity<sup>9,10,76</sup>. Our results also highlight how avian wing morphology provides a simple metric to identify communities and species most sensitive to fragmentation, with potential uses in land-use management and the design of protected area networks.

These findings have important implications, both for understanding the mechanisms causing fragmentation effects, and formulating appropriate management interventions. Our results are consistent with previous studies suggesting that forest fragmentation will have more severe effects on tropical species<sup>9,10</sup>, and provide strong evidence that this pattern reflects inherent differences among species in their ability to cope with edge effects and to disperse across deforested terrain. A major management implication is that maintaining structural connectivity between forest fragments, such as corridors and 'stepping stones' of natural habitat, is a priority worldwide and particularly urgent in the tropics. Taken together, our results highlight the need for flexible and dynamic conservation strategies tailored to local contexts, including climatic conditions and associated species adaptations.

## Methods

To estimate fragmentation sensitivity of species populations, we used BIOFRAG software<sup>28</sup> to analyse a refined and updated version of the BIOFRAG dataset<sup>77</sup>. BIOFRAG provides a direct estimate of the effects of landscape-level fragmentation on each population of each species<sup>9,28</sup> (see Supplementary Information). Populations of the same species may be identified as fragmentation sensitive in some landscapes and insensitive in others. We define fragmentation-sensitive populations as those avoiding forest edges in fragmented landscapes and occurring mainly in the forest core. We follow methods explained in greater depth elsewhere<sup>9,28,77</sup>, summarizing the key points in the following sections, with details of updates and modifications.

### Study landscapes and surveys

We compiled bird assemblage data from published surveys of fragmented forest landscapes, coupled with fragmentation data extracted from GIS vegetation layers. The core sample was downloaded from the BIOFRAG database containing species abundance from 32 abundance surveys and tree-cover maps of associated study landscapes from the year 2000 (refs. 9,77). We excluded 11 studies from our analysis because of potential pseudoreplication (see Supplementary Information). To expand our sample, we gathered further post-1998 bird survey data from (or cited within) forest fragmentation studies via a literature search of the Web of Science core collection, using the default 'Topic' search for literature published after 2010, with terms: Birds OR Bird OR Avian AND Forest OR Wood\* OR Rainforest AND Sample OR Survey OR Census AND Fragment\* AND Plot\* OR Site\* AND Abundance.

After adding 10 new studies to the original BIOFRAG dataset, the final sample contained 31 survey datasets sampled between 1998 and 2013 across six continents (Africa, 3; South America, 5; North America, 10; Europe, 7; Asia, 3; Oceania, 3) (Fig. 2 and Supplementary Data 1). We calculated the absolute latitude of each study landscape as the centroid latitude of all the sampling points within each survey using the geosphere package in R<sup>78</sup>. In all cases, surveys targeted both forest and non-forest matrix with varying levels of tree-cover heterogeneity and multiple (average, 153) sampling locations. We omitted surveys reporting only presence-absence and limited our sampling to surveys reporting abundance or relative abundance of bird species at each

sampling location. We converted raw abundance estimates to relative abundance to allow comparison across the full sample of landscapes. Although we limited sampling to landscapes in which the original forest cover had become fragmented by a non-forest matrix, this included a range of forest types embedded in various matrix types (Supplementary Data 1).

We included mist-netting, point-count and line-transect surveys in our sample and accounted for differences in survey method among studies using a mixed-effects modelling approach. We excluded studies using multiple survey methods inconsistently across the study landscape. Accurate geolocation of avian populations is key to identifying the affinity of species to forest edges. However, geolocation is challenging in field surveys, particularly in dense forest where detectability of birds is often low and 95% of birds are identified through auditory signals<sup>79–81</sup>. To maximize accuracy of geolocation, we excluded point-count radii greater than 100 m and transects larger than  $100 \times 100$  m. Our sample contains four mist-net surveys, all located in Brazilian tropical forests. Although sampling bird communities using mist-nets leads to inaccuracies in abundance estimates based on capture rate<sup>82</sup>, they have the advantage that identification and geolocation of mist-netted bird species are generally accurate.

### Forest fragmentation and edge effects

To estimate responses of bird species to fragmentation, we began by combining bird survey data with information on habitat. We downloaded tree-cover maps and non-habitat masks for the year 2000 at 30 m resolution<sup>82,83</sup> using the following methods replicated from previous studies<sup>9,28</sup>. We set the value of each pixel in the tree-cover maps to the percentage tree cover within each  $30 \times 30$  m pixel (hereafter termed ‘point cover’). The non-habitat masks estimated forest cover as a binary value (forest and non-forest), which we used to identify forest edge boundaries with improved precision. To create map layers for each study landscape, we then extracted and cropped the tree-cover and non-habitat mask layers to a minimum convex polygon with a 5 km buffer around the sampling points using Google Earth Engine<sup>84</sup>. To minimize distortion of the distance and direction between sample points, we projected maps and sample points into azimuthal equidistant projection (AEQD), giving coordinates in metres with origin equal to the sample points centroid<sup>9</sup>.

Following previously proposed methods<sup>28</sup>, we quantified the level of edge influence (EI) within a specified radius from sample points. We used BIOFRAG software to calculate 30 m resolution EI maps using the tree-cover maps downloaded from Google Earth Engine. We then specified the ‘depth of edge influence’ (DEI), as the size of the radius around each pixel. We then calculated the level of tree-cover heterogeneity as a function of the mean and standard deviation of point-cover values within the DEI radius. DEI was set to 1 km as default, with adjustments where necessary according to the scale of particular datasets (see Supplementary Information).

Forest edges within the DEI radius strongly influence the EI value, meaning that EI is representative of both the amount of forest edge surrounding each pixel and the local tree-cover variation, accounting for edge shape and patch size. We also implemented a Gaussian filter to smooth the point-cover values within the DEI radius, with a stronger smoothing effect on values farther away from the focal pixel. Implementing this filter ensures that variation in tree cover closer to the focal pixel has a larger impact on the EI value, in line with the assumption that the strength of edge effects is related to their proximity to the sampling location<sup>28</sup>.

EI for each grid cell  $i$  can be expressed as

$$EI_i = \max(\sigma C, |\bar{C} - C_i|) \times \text{sign}(\bar{C} - C_i)$$

where  $\bar{C}$  is the landscape average of tree cover per pixel,  $C_i$  is the percent tree cover at each pixel and  $\sigma C$  is the standard deviation of habitat cover at the landscape scale.

### Habitat preference and edge affinity

We used EI and point-cover maps for each study landscape to classify each species into three categories of habitat preference (Forest/Matrix/Generalist) and three categories of edge affinity (Core/Edge/noPref), resulting in nine different combinations (Supplementary Table 5). Classification was based on relative abundances of species across a range of point-cover and EI values through a Naïve Bayes Classifier-based approach (see Supplementary Information). We restricted our sample to populations with a ‘Forest’ habitat preference and then assigned populations to a binary response variable (fragmentation sensitive or fragmentation insensitive) based predominantly on their edge affinity classification.

A potential source of inaccuracy in classifications of habitat preference and edge affinity arises because tree cover may change between the time of survey and the year 2000 when our tree-cover maps were created. Tree-cover change may mean that values extracted from the EI and tree-cover maps do not represent the point-cover and surrounding tree-cover heterogeneity at the time of the survey. However, when we ran a sensitivity analysis to assess the influence of post-survey tree-cover change, we found that these changes have only minor effects on our results and do not alter the conclusions from our main analyses (see Supplementary Fig. 2).

### Assigning fragmentation sensitivity to bird populations

Previous studies assumed that populations classified as ‘Forest-core’ by the BIOFRAG algorithm are fragmentation sensitive, on the grounds that avoidance of forest edge habitats indicates sensitivity to edge effects<sup>9,28</sup>. However, this approach can be sensitive to inaccurate geolocation of species observation points, reducing confidence in estimates of edge affinity, potentially resulting in open-country bird species being classified as Forest-core species.

To reduce the number of misclassified populations, we limited assignment of fragmentation sensitivity to 225 populations of 165 species classified by BirdLife International<sup>33</sup> as having a high forest dependency (‘Forest specialist’), in addition to qualifying as Forest-core. We also relaxed the threshold by including less-specialized species, leading to classification of 583 populations of 418 species with either high or medium forest dependency (‘Forest associated’), in addition to Forest-core status. Further details of how species were assigned to high and medium forest dependency are provided in ref. 85. Analyses based on these two definitions of fragmentation sensitivity are referred to as ‘Restricted’ and ‘Expanded’ analyses, respectively. Restricting the assignment of fragmentation sensitivity to either Forest-specialist or Forest-associated species meant that 60 populations of 53 species were identified as insensitive to forest fragmentation despite being classified as ‘Forest-core’ species (Supplementary Table 6). These species are highly unlikely to be sensitive to forest fragmentation because most are abundant in non-forest habitats, favouring open areas, gardens or forest edges (for example, *Elaenia chiriquensis*, *Molothrus ater*, *Serinus serinus*, *Thraupis sayaca*).

We examined latitudinal patterns of fragmentation sensitivity by extracting the centroid latitude of species geographical ranges from published data<sup>34</sup>. To assess whether fragmentation sensitivity was non-randomly distributed across the global bird phylogeny<sup>86</sup>, we created a majority rule consensus tree from 100 random phylogenies downloaded from BirdTree ([www.birdtree.org](http://www.birdtree.org)) using the Hackett backbone. We then quantified phylogenetic signal in fragmentation sensitivity as the sum of changes in estimated nodal values for binary traits ( $d$ )<sup>87</sup>. Values of  $d$  close to 0 indicate that fragmentation sensitivity is phylogenetically conserved; values close to 1 suggest a random distribution across the phylogenetic tree. In our dataset, families with a high proportion of fragmentation-sensitive species tend to be sedentary and largely restricted to the tropics, such as Trogonidae (Restricted: 70% sensitive; Expanded: 93% sensitive), Furnariidae (Restricted: 53% sensitive; Expanded: 61%



sensitive,) and Pycnonotidae (Restricted: 47% sensitive; Expanded: 47% sensitive).

### Historical disturbance

We estimated historical disturbance for each study landscape using previously described methods<sup>9</sup>. The likely impact of different types of historical disturbance was quantified using four sets of maps: glaciated areas at the last glacial maximum<sup>88</sup>, high-intensity forest crown fires<sup>89</sup>, tropical storms<sup>90</sup> and long-term anthropogenic forest loss (see Supplementary Information). Using the AEQD projection, we overlaid these map layers onto a minimum convex polygon with a 5 km buffer around each sample point. To align with ref. 9, we converted historical disturbance to a binary variable (High/Low), with landscapes scored as High disturbance if any disturbance layer was detected across the majority (>50%) of the landscape (see Supplementary Information).

Treating disturbance as a binary variable is simplistic but makes sense because all forms of disturbance may have severe impacts on biodiversity regardless of whether they act independently or in combination with other factors. A potential weakness is that this approach groups together forms of disturbance operating over very different timescales. Natural disturbances act over deep time, whereas anthropogenic disturbances operate on a shorter timescale and often at smaller spatial scale. To account for this temporal distinction, we created three binary disturbance variables: 'natural' (fires, glaciation, storms), 'anthropogenic' (recent forest loss) and 'any' (all the above), then modelled their effect on fragmentation sensitivity separately.

### Dispersal limitation

To estimate variation in dispersal ability across species, we compiled HWI for all 1,034 study species using global datasets<sup>15,34</sup>. HWI is a measure of wing shape, and specifically wing elongation, correlated with wing aspect ratio<sup>91,92</sup>. HWI is therefore linked to flight efficiency, with high values of HWI strongly indicative of dispersive, migratory or aerial lifestyles<sup>15,21</sup>. HWI predicts dispersal distance in birds<sup>21,93</sup>, thus providing a morphological metric widely used as a proxy for dispersal ability in macroecological studies<sup>15,94–97</sup>. Variation in HWI across our study sample ( $n = 1,034$  species) is large (range = 1.9–71.8; mean = 22.7; s.d. = 12.2) and broadly representative of all birds ( $n = 9,993$ ; mean = 25.7; s.d. = 15.06; see Supplementary Fig. 3a).

The relationship between HWI and dispersal ability is positive<sup>21,93</sup>, whereas its relationship with dispersal limitation is negative (high HWI reflects low dispersal limitation). To reflect this inversion and to ease the interpretation of analyses, we took the negative of the species mean trait value (nHWI) as a proxy of dispersal limitation (that is, high nHWI reflects high dispersal limitation). We found that dispersal traits are distributed fairly evenly throughout the phylogenetic tree of our sample (Fig. 2b), suggesting that variation in nHWI is not especially biased by particular taxonomic groups. To conduct analyses at the assemblage level, we summarized the average level of dispersal limitation (nHWI) in each study landscape ( $n = 31$ ) by taking the mean dispersal limitation score for all species present at that site.

### Body size

Small species with high HWI (for example, swallows) are often far more dispersive than large species with low HWI (for example, kiwis), highlighting why HWI provides a more accurate prediction of avian dispersal ability than more traditional metrics, such as body mass. Although initial analyses reported an association between body size and dispersal distance in birds<sup>98,99</sup>, body size does not predict avian dispersal ability at global scales<sup>15</sup>. Nonetheless, body size is an important correlate of fragmentation sensitivity<sup>50</sup> and dispersal<sup>100</sup> in animals, as well as an important morphological predictor of threat status and fragmentation sensitivity<sup>50,101</sup>. We therefore accounted for variation in body size by including species mean body mass as a covariate in our models and assessed interactions between body mass and dispersal. Such

interactions could be predicted if the effects of dispersal limitation are accentuated in species with larger body size owing to their inherent characteristics, including low population density, slow reproductive output and susceptibility to hunting<sup>68,101–103</sup>. Body mass estimates were extracted from recently updated global datasets<sup>34</sup>.

### Defining scales

We performed analyses using data calculated across three different scales. Landscape-level analyses (Fig. 3b) used geographical or climatic data extracted from the landscape or species-specific data averaged across all species within the landscape assemblage (such as community mean dispersal limitation). Population-level analyses (Fig. 4) used data specific for each population and therefore captured intra-specific variation (for example, fragmentation sensitivity varying across different localities). Species-level analyses (Supplementary Fig. 1) used data averaged across all populations of the same species (for example, fragmentation sensitivity), generated at species level (for example, mean body mass)<sup>34</sup> or extracted from GIS layers and averaged across all cells of the species distributional range (for example, range-wide seasonality).

### Seasonality

To tease apart the effects of dispersal limitation (nHWI) from other correlated traits associated with seasonal climates, we included seasonality in our models. For landscape-level analyses, we quantified seasonality at the centroid of survey points for each study landscape ( $n = 31$ ). Using these centroids, we extracted local intra-annual temperature variation from WorldClim.org<sup>104</sup> at 2.5 min resolution (~5 km<sup>2</sup>), with raster cell values equal to the standard deviation in local mean monthly temperatures across the year. For species-level analyses, we also extracted this metric of seasonality across the distribution of each species by calculating an average from all raster cells overlapping the species' breeding range (see Supplementary Information).

### Statistical analyses

We performed a generalized linear model to assess whether community mean dispersal limitation (nHWI) is related to the overall fragmentation sensitivity of bird assemblages at the landscape level. To avoid overdispersion in our residuals, we calculated the proportion of fragmentation-sensitive species in each of our 31 study landscapes and modelled whether this proportion was dependent on community mean dispersal limitation (nHWI) using a quasi-binomial error structure.

To assess the effect of predictor variables on species sensitivity to habitat fragmentation at the species level, we performed multivariate Bayesian phylogenetic mixed-effects models on each of our fragmentation sensitivity methods (for model design and rationale, see Supplementary Table 7). In both Expanded and Restricted analyses, we modelled the effects of historical disturbance, absolute latitude, seasonality, dispersal limitation and body mass (as well as an interaction term between body mass and dispersal limitation) on the likelihood of being classified as fragmentation sensitive. Seasonality and body mass were logarithmically scaled before analysis. We included study and species as random effects to account for repeated sampling of particular species across multiple studies, as well as the non-independence of species sampled within the same study landscape (Extended Data Table 1). To allow accurate effect-size comparisons between continuous variables and our binary disturbance variable, we standardized all continuous variables by 2 standard deviations<sup>105</sup>. Collinearity between predictor variables was checked via VIFs and found to be acceptable (<10).

To perform sensitivity analyses, we re-ran the same set of models with minor adaptations (see Supplementary Information). First, we replaced the binary historical disturbance variable with subsets restricted to anthropogenic and natural disturbances. To account for possible conflation between dispersive traits and migratory behaviour, we removed long-distance migrants from our sample and re-ran

our Restricted analysis (Supplementary Fig. 4). Finally, to ensure that results were not driven by extreme values of nHWI, we repeated our analyses with Apodiformes removed from the dataset (see Supplementary Information).

Models were constructed using the brms package in R<sup>106</sup>, with Markov chain iterations and priors kept consistent across all models. We selected 10,000 total iterations with a 2,000-iteration warmup-phase. We used the no u-turn sampler (NUTS) to reduce autocorrelation between successive iterations and as such, no thinning was required. We assigned weakly informative priors normal (0,10) to the slope parameters and the intercept as previously recommended<sup>107</sup>. Each of our models ran four Markov chains in parallel, which were assessed for convergence. We used 100 random trees from the global bird phylogeny<sup>86</sup> as described above and ran all of our models separately across this sample of trees. This resulted in 400 chains per model, which were then combined to produce our final posterior distribution accounting for phylogenetic uncertainty<sup>108</sup>. We report estimated effect sizes ( $\beta$ ) as the means of the posterior distributions, along with 95% credible intervals (Extended Data Table 1). The effects of each of our variables on fragmentation sensitivity were inferred through assessment of posterior distributions.

### Inferring causal mechanisms

To identify drivers of fragmentation sensitivity, we constructed structural equation models using the phylopath package in R<sup>109</sup>. The results of structural equation models provide insight into the relative importance of different drivers but should be treated with caution given the hierarchical complexity of our data structure (see Supplementary Information and Fig. 1). Therefore, in addition, we modelled the effects of historical disturbance, latitude and seasonality on nHWI (Supplementary Tables 3 and 4) to test the role of these factors in explaining variation in dispersal limitation across study species ( $n = 1,034$ ). Given that extinction filters may act at a local scale through removing and then preventing recolonization by maladapted species in the landscape<sup>12</sup>, we calculated historical disturbance, latitude and seasonality using landscape-level data. For each species, we used GIS layers to extract the historical disturbance score (binary variable: High = 1, Low = 0), local temperature variation<sup>104</sup> and absolute latitude of the landscape centroid for all landscapes where the species was present. We then averaged these scores to obtain species-level values on the basis of variables extracted from the relevant study landscapes.

We then ran three phylogenetic generalized least-squares models using 100 random phylogenies (see above) for (1) all study species, (2) residents, short distance migrants and partial migrants (only excluding long-distance migrants) and (3) residents only. Data and definitions for these migratory classes are provided in ref. 110. In each case (1–3), we first assessed the relationship between historical disturbance and nHWI as a univariate model. Second, we added latitude as an additional covariate and third, we added seasonality as a third covariate. Multicollinearity between the three covariates was addressed by assessment of VIFs and found to be acceptable (VIF < 6). For each model, we established the relative proportion of independent variance explained by each driver using hierarchical partitioning implemented with the R package hier.part<sup>111</sup>. Evolutionary drivers such as habitat disturbance and climate may act on species traits at regional rather than local scales, so we re-ran these analyses with disturbance, seasonality and latitude estimated across the distribution of each study species (see Supplementary Information).

### Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

### Data availability

All data are available at [https://github.com/tomlweeks1994/Dispersal\\_mediates\\_fragmentation\\_sensitivity](https://github.com/tomlweeks1994/Dispersal_mediates_fragmentation_sensitivity).

### Code availability

The code to conduct analyses and replicate figures is available at [https://github.com/tomlweeks1994/Dispersal\\_mediates\\_fragmentation\\_sensitivity](https://github.com/tomlweeks1994/Dispersal_mediates_fragmentation_sensitivity).

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## Acknowledgements

We thank the BIOFRAG project for supplying data and numerous data contributors, including V. Arroyo-Rodriguez, D. Cleary, H. Jactel, J. Karubian, J. Lasky, S. Melles, J. C. Morante Filho, V. Proenca, S. Raman, P. Round and J. Terraube. Trait data collection was supported by Natural Environment Research Council grant NE/I028068/1 and UKRI Global Challenges Research Fund grant ES/P011306/1 (J.A.T.). Analysis was funded by the Natural Environment Research Council studentship through the Science and Solutions for a Changing Planet Doctoral Training Programme NE/S007415/1 (T.L.W.). Illustrations were reproduced with permission from the Cornell Lab of Ornithology. For the purpose of open access, T.L.W. has applied a Creative Commons Attribution (CC BY) license to any Author Accepted Manuscript version arising.

## Author contributions

T.L.W. and J.A.T. conceived and developed the study, with input from M.G.B., M.P. and C.W.; data from particular sites were contributed by M.B., C.B.-L., L.B., J.B., A.C., C.M.K., U.G.K., C.J.M., P.I.O., B.T.P., H.P.P. and E.M.W.; T.L.W. integrated datasets and ran all analyses with support from C.W. and M.G.B.; and T.L.W. wrote the first version of the manuscript and designed all figures with input from J.A.T. All authors contributed to subsequent drafts and gave final permission for publication.

## Competing interests

The authors declare no competing interests.

## Additional information

**Extended data** is available for this paper at <https://doi.org/10.1038/s41559-023-02077-x>.

**Supplementary information** The online version contains supplementary material available at <https://doi.org/10.1038/s41559-023-02077-x>.

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**Peer review information** *Nature Ecology & Evolution* thanks Benjamin Zuckerberg, Don Driscoll and Jacob Socolar for their contribution to the peer review of this work.

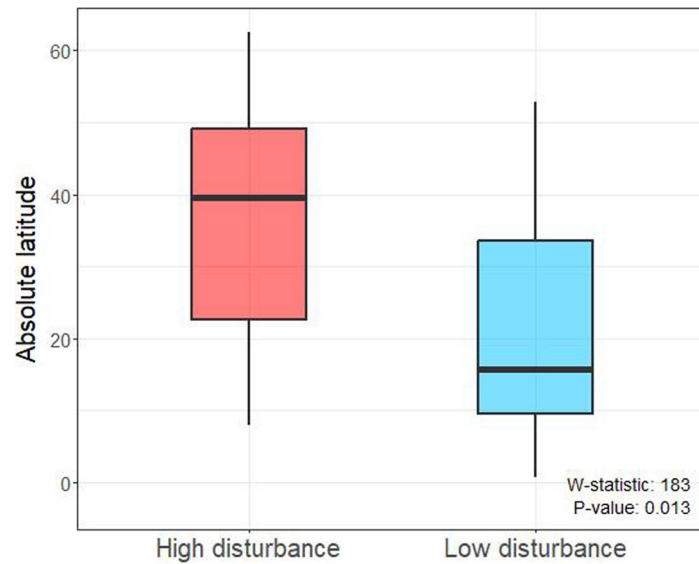
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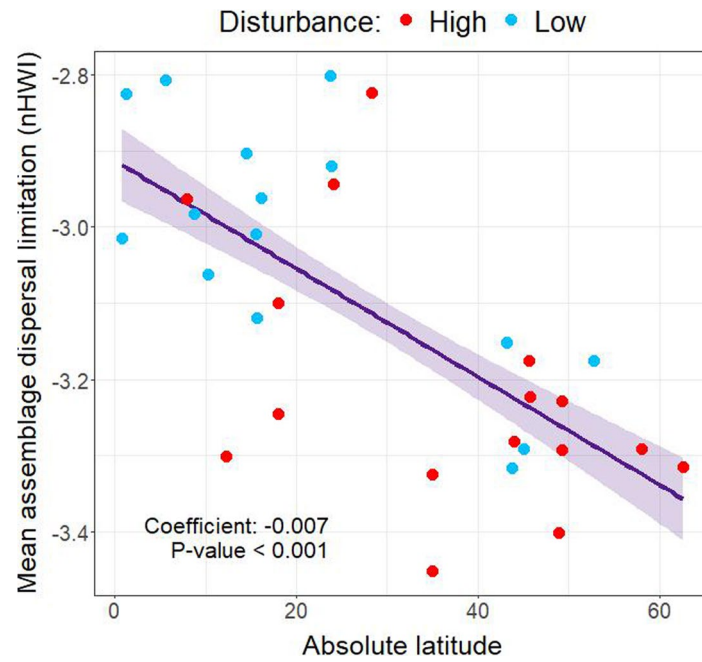
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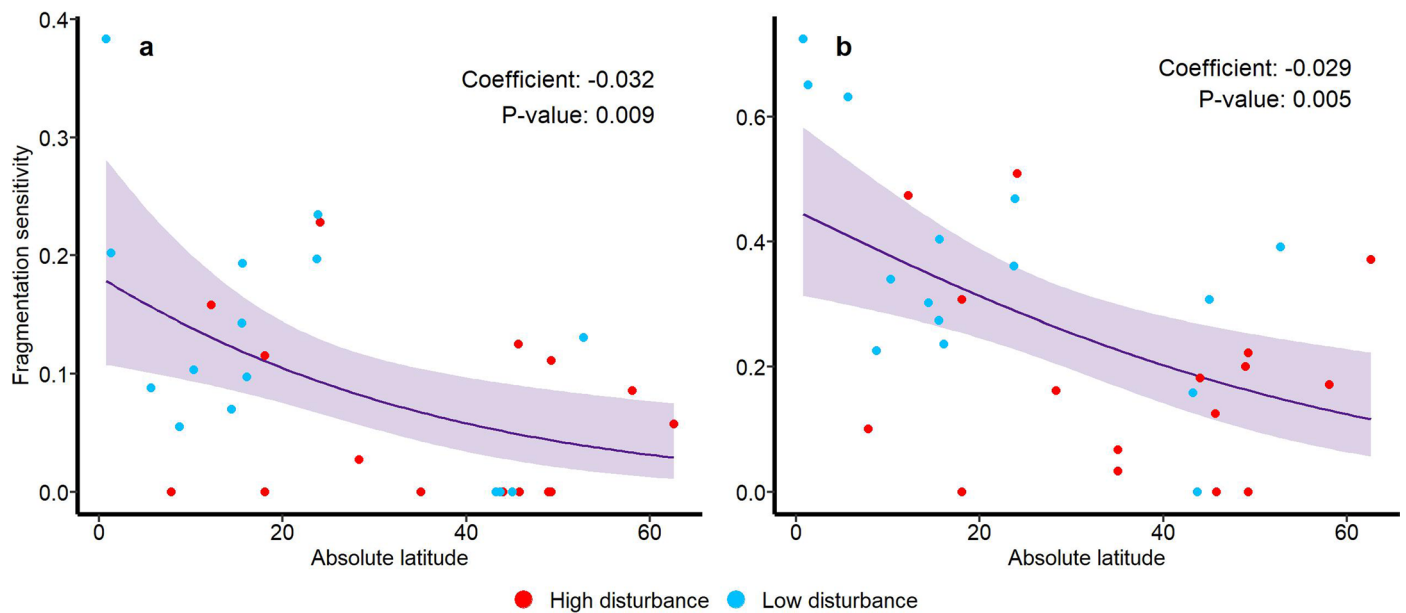
**Extended Data Fig. 1 | Correlation between disturbance and latitude.** Study landscapes exposed to high levels of historical disturbance ( $n = 16$  landscapes; red) tend to be found at higher latitudes than landscapes exposed to lower levels of historical disturbance ( $n = 15$  landscapes; blue). Disturbance level is estimated from global maps of major historical disturbance (for example fire, glaciation).

Absolute latitude is the centroid latitude of all sampling points in each study landscape. Boxplots show the median, interquartile range and whiskers extending to extreme values. Statistics show results of two-sided Wilcoxon rank sum test indicating that disturbance and latitude are correlated (without accounting for spatial auto-correlation).



**Extended Data Fig. 2 | The latitudinal gradient in average dispersal limitation of bird assemblages.** Data points (coloured by level of historical disturbance) show the community mean values for avian assemblages sampled at 31 study landscapes mapped in Fig. 1. The overall gradient is not explained by landscape disturbance history. Absolute latitude is the centroid latitude of all sampling

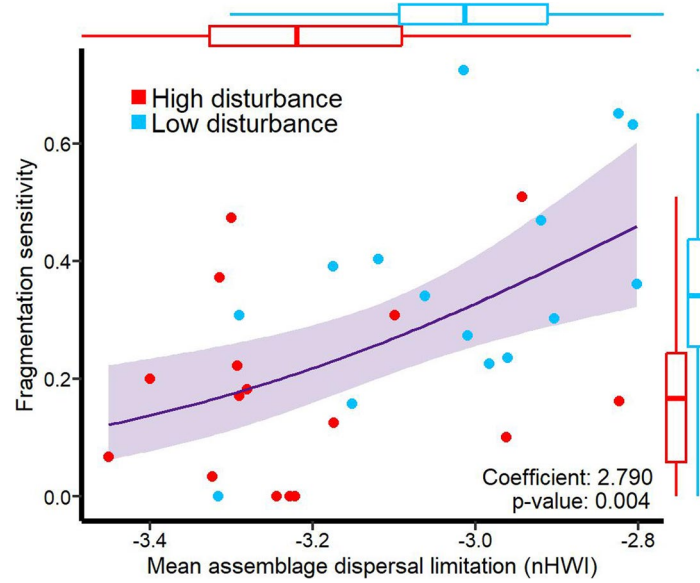
points in each study landscape. Mean dispersal limitation is the negative (that is inverse) hand-wing index (nHWI) averaged across all species in the assemblage; nHWI is logarithmically scaled ( $\log(1/\text{HWI})$ ) for visualization. Statistics are from a linear model with Gaussian errors; purple line shows model fit ( $R^2 = 0.44$ ); shaded region shows the standard error of the regression coefficient.



**Extended Data Fig. 3 | Correlation between fragmentation sensitivity and latitude in birds.** Data points (coloured by level of historical disturbance) are community mean values for avian assemblages at 31 study landscapes mapped in Fig. 1. For each assemblage, fragmentation sensitivity is assigned to (a) Forest-specialist species with 'Forest-core' habitat preference (Restricted analysis), and (b) Forest-associated species with 'Forest-core' habitat preference (Expanded

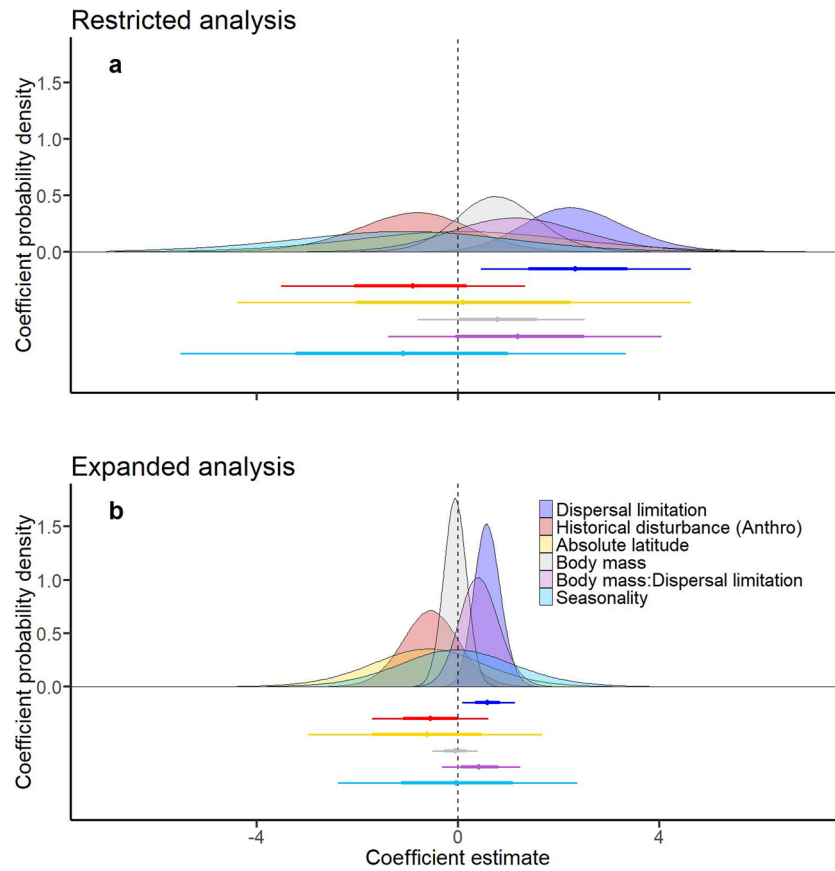
analysis). Absolute latitude is the absolute centroid latitude of all sampling points in each study landscape. Statistics are from generalized linear models with quasi-binomial errors; purple line shows model fit (Restricted analysis:  $R^2 = 0.2559$ , Expanded analysis:  $R^2 = 0.3208$ ); shaded region shows the 95% confidence intervals.





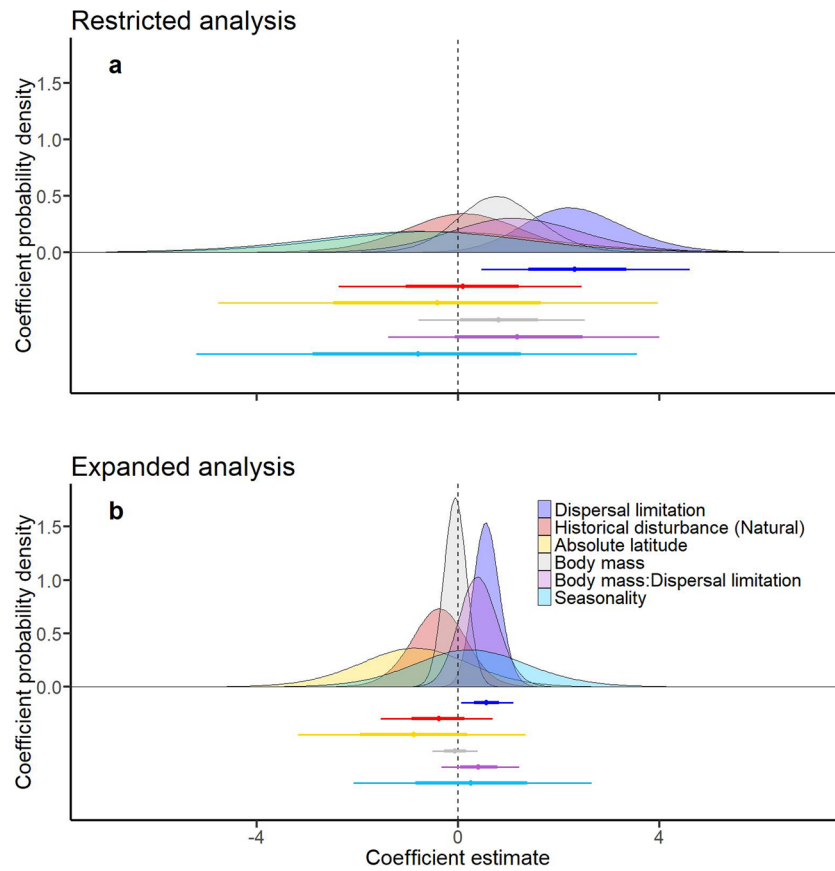
**Extended Data Fig. 4 | Correlation between fragmentation sensitivity and dispersal limitation in birds.** Data points (coloured by level of historical disturbance) are community mean values for avian assemblages at 31 study landscapes mapped in Fig. 1. For each assemblage, fragmentation sensitivity is assigned to species with ‘Forest-core’ habitat preference and either a high or medium forest dependency (Expanded analysis). Mean dispersal limitation is

the negative (that is inverse) hand-wing index (nHWI) averaged across all species in the assemblage; nHWI is logarithmically scaled ( $\log(1/\text{HWI})$ ) for visualization. Statistics are from a generalized linear model with quasi-binomial errors; purple line shows model fit ( $R^2 = 0.270$ ); shaded region shows 95% confidence intervals. Adjacent boxplots show the same distribution with median value, interquartile range, and whiskers to extreme values (outliers are data points  $>1.5\times$  quartiles).



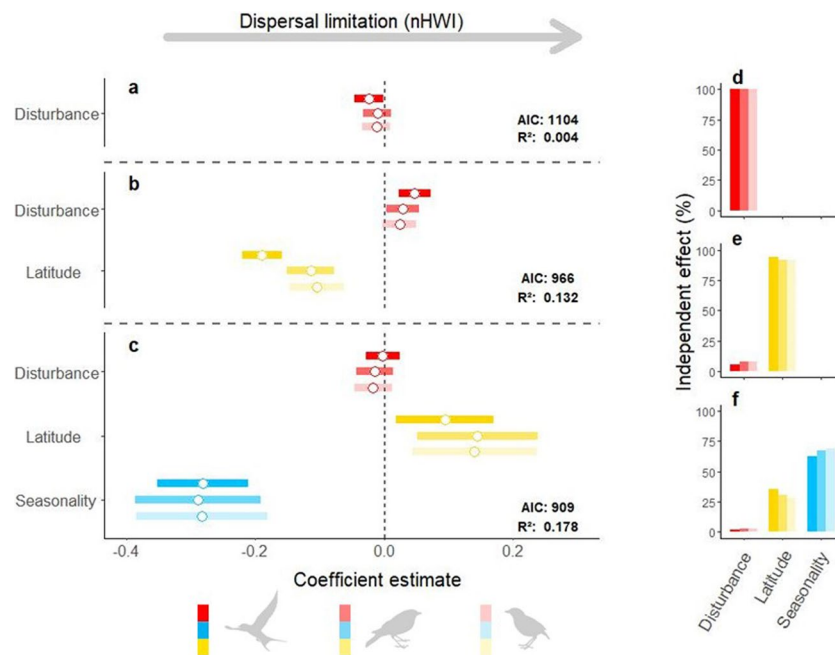
**Extended Data Fig. 5 | Drivers of fragmentation sensitivity with Anthropogenic disturbances.** Results of Bayesian phylogenetic mixed effect models predicting fragmentation sensitivity for 1564 bird populations ( $n = 1034$  species). Populations were classified as fragmentation sensitive if they were identified as 'Forest-core' by BIOFRAG. Restricted analysis assigned fragmentation sensitivity only to 'Forest specialists' (**a**); Expanded analysis assigned fragmentation sensitivity to both 'Forest specialist' and 'Forest

associated' species (**b**; see Methods). Bayesian posterior distribution is shown above the line; effect size estimates with credible intervals (CI) below the line (68%: thick errorbars; 95%: thin errorbars). High effect sizes indicate a positive association with fragmentation sensitivity; low effect sizes indicate a negative association. Finch and hawk silhouettes indicate that both models were run on a complete sample. Historical disturbance is a binary variable (1/0) calculated using anthropogenic disturbance (forest loss) only.



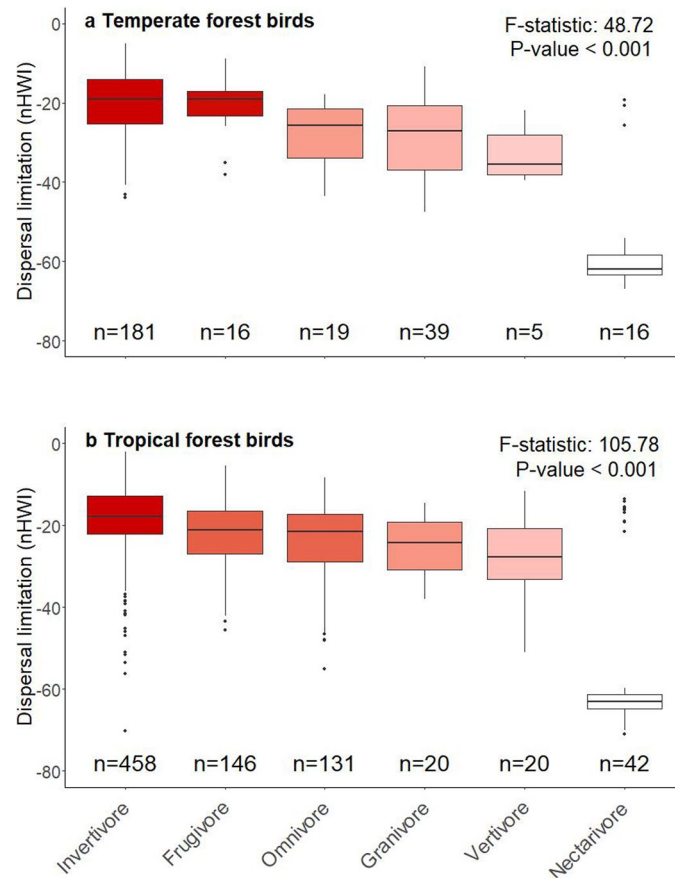
**Extended Data Fig. 6 | Drivers of fragmentation sensitivity with natural disturbances.** Results of Bayesian phylogenetic mixed effect models predicting fragmentation sensitivity for 1564 bird populations ( $n = 1034$  species). Populations were classified as fragmentation sensitive if they were identified as 'Forest-core' by BIOFRAG. Restricted analysis assigned fragmentation sensitivity only to 'Forest specialists' (**a**); Expanded analysis assigned fragmentation sensitivity to both 'Forest specialist' and 'Forest associated' species (**b**); see

Methods). Bayesian posterior distribution is shown above the line; effect size estimates with credible intervals (CI) below the line (68%: thick errorbars; 95%: thin errorbars). High effect sizes indicate a positive association with fragmentation sensitivity; low effect sizes indicate a negative association. Finch and hawk silhouettes indicate that both models were run on a complete sample. Historical disturbance is a binary variable (1/0) calculated using natural disturbance (for example fires, storms & glaciation) layers only.



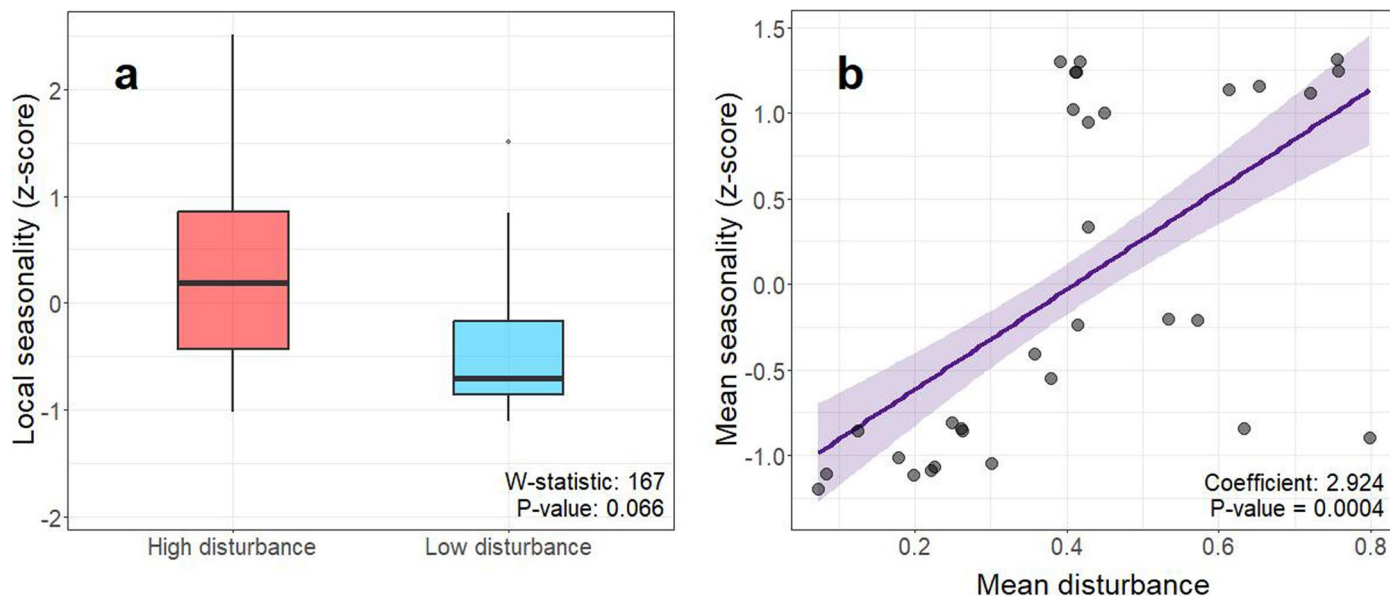
**Extended Data Fig. 7 | Predictors of dispersal limitation in birds.** Results shown are outputs of phylogenetic least squares model predicting dispersal limitation (nHWI) across all bird species sampled, including long-distance migrants (swallow image, dark bars;  $n = 1034$ ); only resident species and short distance/partial migrants (thrush image, medium bars;  $n = 921$ ); or resident species only (pitta image, pale bars;  $n = 858$ ). Panels present three sets of models with increasing complexity: a univariate model with single predictor (**a,d**), and multivariate models with two (**b,e**) and three (**c,f**) predictors. Each predictor is calculated at the species level by averaging across landscapes where each species is present. Disturbance (red) is calculated as the proportion of species

breeding range which overlaps areas of high natural (e.g. storms, glaciers, fires) or anthropogenic (e.g. forest loss) disturbance. Absolute latitude (yellow) is calculated as the centroid latitude of the species breeding range. Seasonality (blue) is calculated as the standard deviation of mean monthly temperature values throughout the year, averaged across all grid cells in the breeding range. **a–c**, Effect size estimates are given with 95% confidence intervals; a negative effect indicates reduced dispersal limitation (that is increased dispersal ability).  $R^2$  and AIC values are calculated for full sample models only. **d–f**, Proportion of independent variation explained by each model covariate, calculated using hierarchical partitioning.



**Extended Data Fig. 8 | Relationship between dispersal limitation (nHWI) and diet.** Data shown for (a) 276 bird species sampled across 18 temperate study landscapes, and (b) 817 bird species sampled across 13 tropical study landscapes. Dietary classes with <5 species were removed from the analysis. Diet

classifications are from Tobias and Pigot<sup>110</sup>. *F*-statistic and *P*-value are calculated with a two-way ANOVA. Boxplots show median, interquartile range, and whiskers to extreme values (outliers are data points >1.5x quartiles).



**Extended Data Fig. 9 | Correlation between seasonality and disturbance.** At the local landscape level (**a**), seasonality is calculated as the standard deviation of mean monthly temperature values throughout the year at the landscape centroid ( $n = 31$ ). High disturbance means 50% of the study landscape area overlaps areas of high natural (for example storms, glaciers, fires) or Anthropogenic (for example forest loss). Boxplots show median, interquartile range, and whiskers to extreme values (outliers are data points  $>1.5x$  quartiles). Statistics are from a two-sided Wilcoxon test. At the species level (**b**), community mean values

( $n = 31$ ), are calculated using species' distributional seasonality and disturbance scores. Disturbance is calculated as the proportion of the species breeding range which overlaps areas of high natural (for example storms, glaciers, fires) or anthropogenic (for example forest loss) disturbance. Seasonality is calculated as the standard deviation of mean monthly temperature values throughout the year, averaged across all grid cells in the species' breeding range. Statistics are from a linear regression with Gaussian errors; purple line shows model fit; shaded area is 95% confidence intervals.

**Extended Data Table 1 | Predictors of fragmentation sensitivity using all disturbance layers**

Fixed effects	Sample	Coefficient estimate	Lower 95% CI	Upper 95% CI
Dispersal limitation (nHWI)	Restricted	2.34	0.43	4.58
	Expanded	0.57	0.07	1.11
Historical disturbance (any)	Restricted	-0.64	-2.89	1.43
	Expanded	-0.67	-1.70	0.31
Absolute latitude	Restricted	0.04	-4.61	4.74
	Expanded	-0.53	-2.85	1.72
Body mass	Restricted	0.80	-0.80	2.51
	Expanded	-0.06	-0.51	0.39
Body mass * Dispersal limitation (nHWI)	Restricted	1.17	-1.43	3.98
	Expanded	0.41	-0.34	1.21
Seasonality	Restricted	-1.04	-5.78	3.49
	Expanded	0.04	-2.27	2.39
<b>Summary statistics</b>				
Conditional $R^2$	Restricted	0.654		
	Expanded	0.301		

Results shown are outputs of a Bayesian phylogenetic mixed effects model using all bird populations in our dataset ( $n = 1564$ , of  $n = 1034$  species). For our Restricted analysis, fragmentation sensitivity is assigned to forest-specialist birds with a forest-core habitat preference. In our Expanded analysis, the assignment of fragmentation sensitivity is extended to all forest-associated birds with forest-core habitat preference. See Methods for descriptions and Fig. 4a & b for visualisation. Results shown are coefficient estimates with 95% credible intervals.

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All studies must disclose on these points even when the disclosure is negative.

Study description

Our study assesses the drivers of sensitivity to habitat fragmentation in birds. Hierarchical mixed-effects models are used to address i) whether sensitivity to habitat fragmentation is driven by the following variables: dispersal limitation, seasonality, latitude, disturbance history, body size and its interaction with dispersal limitation. This analysis includes Landscape\_ID and Species\_ID as random effects. We also control for phylogeny using a variance-covariance matrix constructed using the Jetz phylogeny. N = 1564 species populations. ii) Whether dispersal limitation is driven by: Temperature Seasonality, Disturbance History or Absolute Latitude. N = 1034 species. Phylogeny is controlled using a pglms and a consensus tree built from the Jetz phylogeny.

Research sample

Analyses are performed at three levels. The population-level: 1564 bird populations. Species-level: 1034 bird species. Landscape-level: 31 study landscapes. Analyses are performed upon all data we had available. Data consisted of 31 avian surveys across different study landscapes. In total this consisted of 1564 separate bird populations covering a total 1034 species.

Sampling strategy

Sample sizes are from all available data. This provides us a sufficient sample to undertake a global study. 31 surveys are across a global distribution

Data collection

Data from 31 avian surveys were included in our analysis. 21 of these are stored in the BIOFRAG database. A further 10 surveys were found via key-word search using Web of Science conducted by Thomas Weeks. Survey method and name of original surveyors are as follows: 1) Ben Phalan - Point Count survey. 2) Charlie Marsh - Point count survey. 3-5) Cristina Banks Leite - Mist-net surveys. 6) Eric Wood - Point Count survey. 7) Alexis Cerezo - Point Count survey. 8) Urs Kormann - Point Count survey. 9) Jos Barlow - Mist Net survey. 10) Mat Betts - Point Count survey. 11) Victor Arroyo-Rodriguez - Point Count survey. 12 & 13) Hugh Possingham - Point Count Surveys. 14-15) Stephanie Melles - Point Count surveys. 16) Jose Carlos Morante Filho - Point Count surveys. 17) Pieter I Olivier - Point Count surveys. 18 & 19) Cristina Kennedy - Point Count survey. 20 & 21) Luc Barabaro - Point Count surveys. 22) Daniel Cleary - Line Transect survey. 23) Shankar Ramen - Point Count survey. 24) Phillip Round - Line Transect survey. 25) Julien Terraube - Line Transect survey. 26-29) Herve Jactel - Point Count survey. 30) Vania Proenca - Point Count survey. 31) Jesse Lasky - Point Count survey.

Timing and spatial scale

All surveys were conducted between 1998 and 2013. A range of survey methods are used point-count radii were kept below 100m and Transects kept below 100m x 100m. Surveys are distributed globally. Surveys covered varying sized areas: range between 250m<sup>2</sup> to 11500m<sup>2</sup>.

Data exclusions

We excluded data which resulted in biases in our habitat preference calculations based on a pre-established threshold. This occurred if there was not sufficient sampling points across fragmented and continuous areas of forest. We also excluded datasets which were deemed to induce pseudo-replication such as a time-series of multiple surveys from the same landscape in Australia.

Reproducibility

All attempts to repeat the experiment were successful

Randomization

All analysis used full samples with random-effects used to deal with non-independence induced by sampling across different studies

Blinding

Blinding was not relevant to our study as did not use human participants

Did the study involve field work?  Yes  No

## Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

### Materials & experimental systems

- | n/a                                 | Involvement in the study                               |
|-------------------------------------|--|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Antibodies                    |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Eukaryotic cell lines         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Palaeontology and archaeology |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Animals and other organisms   |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Clinical data                 |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Dual use research of concern  |

### Methods

- | n/a                                 | Involvement in the study                        |
|-------------------------------------|---|
| <input checked="" type="checkbox"/> | <input type="checkbox"/> ChIP-seq               |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> Flow cytometry         |
| <input checked="" type="checkbox"/> | <input type="checkbox"/> MRI-based neuroimaging |