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Soft Range Limits Shape Sensitivity to Forest Cover More Strongly Than Hard Range Limits

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ABSTRACT

Aim: Land-use change is a major threat to biodiversity, yet there remains considerable unexplained variation in how it affects different populations of the same species. Here, we examine how sensitivity to forest cover changes depending on proximity to different limits of a species' range. By comparing responses as species approach their coastal ('hard') and inland ('soft') range limits, we aim to provide insight into the relative influence of mass effects, as compared to abiotic and biotic environmental suitability in shaping population sensitivity.

Location: Global.
Time Period: 1996–2019.
Major Taxa Studied: Birds.
Methods: We combined data from several large databases to obtain a dataset of 2543 bird species surveyed across 116 studies, spanning six continents. Using expert-verified range maps, we calculated the position of populations relative to their species' nearest inland ('soft') and coastal ('hard') range limits and categorised the inland limits as equatorward- or poleward- facing. We investigated how distance to range limits and forest cover, derived from a 30 m-resolution global dataset, affect the probability of species' incidence.
Results: We found that bird populations are more sensitive to forest cover when located closer to their species' inland ('soft') range limits, whereas this was not the case at coastal ('hard') range limits. The heightened sensitivity to forest cover at soft range limits was similar regardless of whether the range limit faced equatorward or poleward.
Main Conclusions: These results highlight how populations close to the soft limits of their species' ranges are at higher risk of extirpation resulting from loss of forest cover. This suggests that environmental conditions (e.g., climate), which become more challenging away from the core of the species' range, drive variability in sensitivity to forest cover.

1 | Introduction

Effective biodiversity conservation requires accurately predicting the impacts of land-use change on extinction risks. Much work has been done to understand the interspecific variation in species' responses to land-use change and to categorize species based on their habitat affiliations (e.g., Bregman et al. 2014; Henle et al. 2004; IUCN 2024; Keinath et al. 2017; Lees and Peres 2008). Although this work has offered important insights into factors affecting responses of different species to land-use change and has informed current large-scale predictions of biodiversity responses, these models typically assume that all populations within a species will react uniformly (IPBES 2020). Yet, emerging evidence suggests that there is also important intraspecific variation in responses to land-use change, which has, until now, been largely overlooked. Specifically, populations of the same species can exhibit varying degrees of sensitivity to land-use change depending on their location (Anjos et al. 2010; Banks-Leite et al. 2022; Bellotto-Trigo et al. 2023; Hasui et al. 2024; Torrenta et al. 2022; Tourani et al. 2023; Valente et al. 2023; Williams and Newbold 2021). This has potentially important implications for current species-based approaches to conservation as the most effective conservation strategy for a single species can vary spatially. However, despite this critical importance, the causes of inter-population variation in sensitivity to land-use change remain unclear. Some of the inter-population variation in sensitivity to forest cover could be attributed to the position of a population within the species' geographic range, though the underlying drivers of range-wide variation in responses to forest cover remain a matter of debate (Banks-Leite et al. 2022). Resolving this requires consideration of the factors that limit the species' geographic range itself.

Potential explanations for the increased sensitivity to forest cover at range limits include mass effects or abiotic and biotic niche limitation. Mass effects refer to the dynamics whereby populations are maintained by dispersal of individuals from surrounding source populations (Leibold et al. 2004). Dispersal is likely to be more constrained at range limits because there are fewer surrounding source populations (Sexton et al. 2009; Shmida and Wilson 1985). Abiotic and biotic niche limitation could involve reduced climatic suitability, or stronger biotic competition, closer to the range limit (Banks-Leite et al. 2022; Williams and Newbold 2021). Both mass effects and abiotic/biotic niche limitation could contribute to populations at their species' range limits being smaller and potentially more sensitive to changes in forest cover (Sexton et al. 2009). The relative importance of mass effects and abiotic/biotic niche limitation is likely to vary at different types of range limits (Banks-Leite et al. 2022).

The geographic range of a species is often considered to be a representation of its niche in geographic space (Hargreaves et al. 2014), such that proximity to the limits of the range corresponds to lower environmental suitability (Gross and Price 2000; Lee-Yaw et al. 2016). Range limits that coincide with gradual deteriorations in abiotic or biotic niche conditions and where abundance and demographic rates decline gradually towards the limit are usually referred to as 'soft' range limits (Gilbert et al. 2024; Watts et al. 2024). In addition to soft range limits, some species' geographic ranges can also be delimited by physical barriers to dispersal, such as coastlines, that present abrupt truncations to the range. These are referred to as 'hard' range limits as the conditions deteriorate abruptly at the range limit so that high abundances and suitable conditions are expected even up to the range limit (Banks-Leite et al. 2022; Kirkpatrick and Barton 1997; Watts et al. 2024).

Mass effects are likely to be equally important at both hard and soft range limits, or potentially even more important at hard limits. By comparison, abiotic and biotic niche limitation (hereafter referred to as "niche limitation") is likely to be more important at soft range limits (Banks-Leite et al. 2022). Comparing how sensitivity to forest cover varies as species approach their soft versus hard range limits could therefore provide insights into the relative importance of niche limitation versus mass effects in driving inter-population variation in sensitivity to forest cover (Banks-Leite et al. 2022). It could also help resolve disparities across studies investigating how distance to range limit affects sensitivity to forest cover. Studies that found heightened sensitivity to forest cover at range limits considered only the inland limit of the species' range (Bellotto-Trigo et al. 2023; Orme et al. 2019), while studies that did not consistently find this relationship did not isolate the inland limit from the coastal limit of the range (Betts et al. 2019; Hasui et al. 2024). A direct quantitative comparison between how proximity to soft (inland) versus hard (coastal) range limits affects sensitivity to forest cover has not yet been undertaken, despite its importance for informing our understanding of how populations respond to deforestation.

In addition to differences between soft and hard boundaries, determinants of range limits are also expected to differ depending on the orientation of the range limit (Gross and Price 2000). There is a long-standing hypothesis, first proposed by Darwin (1859), that poleward-facing range limits are set predominantly by abiotic forces, while biotic interactions are relatively more important at equatorward-facing range limits (Louthan et al. 2015). This could be attributed to environments at lower latitudes being more productive and species-rich (Dobzhansky 1950; Paquette and Hargreaves 2021). Differences in the factors that determine poleward and equatorward range limits could influence how sensitivity to forest cover changes depending on proximity to these limits. Range limits driven by biotic factors might be more likely to have sharp declines in habitat suitability that resemble hard limits, if the range becomes abruptly truncated where it intersects with that of a neighbouring species whose niche it cannot exploit (Price and Kirkpatrick 2009; Benning and Moeller 2019). Gradual reductions in climatic suitability, which are expected to be relatively more important at poleward range limits (Paquette and Hargreaves 2021), have been shown to drive increased sensitivity to land-use change (Williams and Newbold 2021), suggesting that sensitivity to forest cover might be stronger at poleward limits.

Assessing inter-population variation at macroecological scales requires both broad geographic data and detailed regional sampling to capture populations at different positions within their species' range. Therefore, we compiled data from studies testing species responses to land-use change across three different databases (Hasui et al. 2018; Hudson et al. 2017; Pfeifer et al. 2014). Our global dataset consists of incidence (presence-absence) data from 2543 bird species sampled at 7634 sites, spanning six continents. Using expert-verified maps of species geographic ranges (BirdLife 2022) and high-resolution forest cover data (Hansen et al. 2013), we analysed how forest cover and distance to range limits affect bird incidence. We investigated how this relationship varies at different types of range limits, testing two main hypotheses: (1) The effect of distance to range limit on sensitivity to forest cover is stronger at soft limits compared to hard limits due to more prominent abiotic and biotic niche constraints at soft limits (Banks-Leite et al. 2022). (2) The effect of distance to range limit on sensitivity to forest cover is stronger at poleward range limits compared to equatorward range limits because equatorward limits are likely to be predominantly set by biotic factors and therefore may behave more like hard limits.

2 | Methods

2.1 | Bird Community Data

We compiled a global dataset consisting of studies of bird presence-absence (hereafter incidence) in response to changes in land-use across six continents. Birds are a widely relied-upon taxa for macroecological studies because their taxonomy and distributions are relatively well characterized (Burfield et al. 2017) and they are well sampled compared to other taxa (Callaghan et al. 2023). Furthermore, birds encompass a wide variety of range sizes (Gaston 2003) and are integral components of functioning ecosystems (Malhi et al. 2022). We compiled bird incidence data across landscapes of varying forest cover proportions. We use the term *site* to refer to a georeferenced location at which the sampling of a bird community took place. These sites are grouped into *studies*, where sites within the same study were sampled using the same method by the same investigator over the same time period (Table S1).

The studies in our dataset come from three different databases (Hasui et al. 2018; Hudson et al. 2017; Pfeifer et al. 2014). We chose these databases because the studies within them were designed to understand the effect of land-use change on ecological communities. First, the PREDICTS Project database collates data from published studies of ecological assemblages across varying human-modified landuses (Hudson et al. 2017). We excluded studies in non-forest ecoregions, defined according to the RESOLVE 2017 dataset—a globally consistent map of terrestrial ecoregions based on biogeographic and ecological characteristics (Dinerstein et al. 2017; Olson et al. 2001). Second, the BIOFRAG database collates primary datasets from studies of ecological assemblages within fragmented forests (Pfeifer et al. 2014). To maximize the size of the overall dataset, we included studies reporting bird species abundance or incidence but converted the abundance data to incidence to ensure we had a consistent response variable for our analyses. Third, the Atlantic Birds database compiles data on bird species' relative abundances (i.e., the number of individuals of a species recorded per unit of sampling time) across the Brazilian Atlantic Forest (Hasui et al. 2018). We converted this to incidence for each study; if a species was found at one site within a study, but not at another site within that same study, then we recorded that species as absent at the latter site. We also included four additional studies of bird communities in the Atlantic Forest sourced from relevant literature (Orme et al. 2019).

To examine responses to forest cover, we used the global tree cover dataset (Hansen et al. 2013; see section below) which provides maps of tree cover in the year 2000. To ensure that bird incidence could have been influenced by the forest cover in 2000, we filtered our incidence dataset to include only studies that were conducted after the year 2000, or where the timespan of the study included the year 2000.

We aligned the species taxonomy to the Birdlife International checklist v.8.1 (HBW and BirdLife International 2024) using crosswalk tables from AVONET (Tobias et al. 2022) and OpenTree (McTavish et al. 2024). Presence records located more than 200 km outside a species' known range were assumed to result from taxonomic misidentifications or inaccuracies in range mapping. If such an out-of-range observation occurred in only one study, the species was excluded from that study. However, if it occurred in multiple studies, the species was excluded from the entire analysis. We excluded species that do not use forests and only included species for which forest was listed as one of their habitat affiliations, according to the IUCN habitat classification (IUCN 2024).

In total, our dataset included incidence data from 2543 species at 7634 sites, collected from 116 studies conducted between 1996 and 2019 across six continents (Figure 1; Table S1). Each study comprised 2–754 sites (mean = 66). The studies included in this analysis employed a range of methods to document bird incidence: of the

116 studies, 72 employed point counts, 16 used mist nets, 17 employed line transects, two used visual encounter surveys, one used systematic searching and eight used various methods. We used random intercepts in our statistical models to account for variation in sampling methods and sampling efforts across studies. By combining studies from three different databases, we ensured that the majority of species were sampled at different positions within their ranges. Out of the 2543 species in our analyses, 56% (1424 species) were sampled in more than one study.

2.2 | Forest Cover

We calculated forest cover from the global tree cover dataset by Hansen et al. (2013), which provides the percentage of tree cover for each 30×30 m pixel in the year 2000. We converted this into a binary map distinguishing between forest and non-forest areas. Pixels with a tree cover percentage exceeding 70% were classified as forest, while those below 70% were considered non-forest. A study comparing forest cover estimates derived from different tree cover thresholds in the Hansen et al. (2013) dataset with ground truth data in Myanmar suggested that a 50% threshold achieved the highest accuracy in ecological zones other than tropical rainforests, whereas an 80% threshold was optimal for tropical rainforests (Lwin et al. 2019). Similarly, another study suggested an 80% threshold for assessing forest cover within the Amazon basin (Gasparini et al. 2019). Given that our dataset encompasses a variety of forest types, we opted for a 70% threshold. We calculated the percentage of forest pixels within a 600 m buffer surrounding each site (see Tables S6 and S7 for a sensitivity analysis). This buffer size reflects the sampling design of many of the original studies in the dataset (Banks-Leite et al. 2014; Boscolo and Metzger 2009) and was shown to be optimal for assessing bird responses to forest cover (Hatfield et al. 2018; Martínez-Penados et al. 2024; Morante-Filho et al. 2016).

2.3 | Distance to Range Limits

To examine how distance to geographic range limits affects sensitivity to forest cover, we obtained expert-verified maps of species' geographic ranges from BirdLife (BirdLife 2022). These maps are widely used for delimiting species' ranges. They are created using expert knowledge and habitat preference data to draw polygons around likely occurrence locations (Hawkins et al. 2008; Herkt et al. 2017; Marsh et al. 2022). We retained polygons classified with the origin category as 'native' or 'reintroduced' and presence category as 'extant' and 'possibly extant' to capture more of the potential distributions of species. This is following previous studies of how range characteristics affect extinction risks (e.g., Cardillo et al. 2008; Orme et al. 2019; Purvis et al. 2000). We transformed these range maps to equal-area raster files in the Behrmann projection at 4×4 km resolution. To categorize range limit pixels into soft (inland) and hard (coastal) limits, we used the full-resolution GSHHG coastline maps (Wessel and Smith 1996). Following Orme et al. (2019), we applied a 10 km buffer around the coastline because the BirdLife range maps showed small variations in the alignment of coastal limits. Range limit pixels that intersected with the buffered coastline were considered hard limits.

For each combination of site and species, we measured the distance between the site where the species was surveyed and the nearest soft limit pixel of the species' range. For species whose ranges intersected with the coastline, we also measured the distance between the site and the nearest hard limit pixel of that species' range. For observations < 200 km outside their species' range, we use negative values to indicate the distance to the range limit ($n = 5265$, 6% of total presence observations). Occasional movements of individuals outside their ranges are commonly attributed to vagrancy, which can be associated with stochastic environmental changes and the dynamic nature of species' ranges (Gaston 2003; Lees and Gilroy 2022).

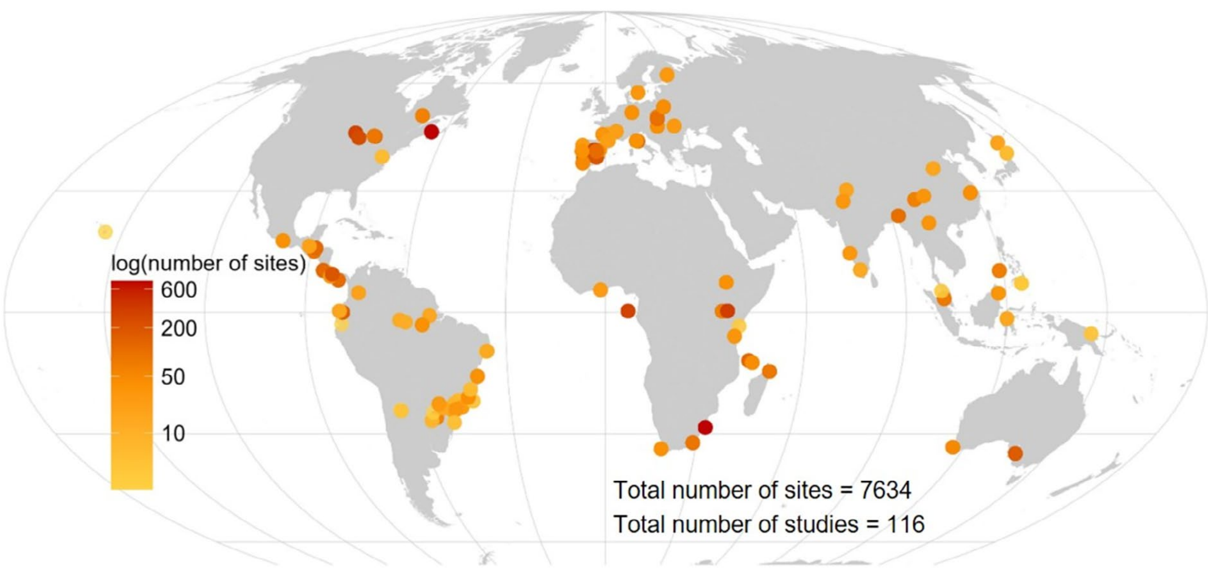

FIGURE 1 | Spatial distribution of sites. Each point represents the location of one study and points are coloured according to the number of sites in the study on a logarithmic scale.

To classify limits as equatorward- or poleward- facing, we compared the latitude of each site and its nearest soft range limit pixel for each species. As we were expressly interested in the roles of abiotic and biotic range limitation, we did not consider hard limits in this analysis, and measured distances only to the nearest soft range limit. Out of 508,259 site-by-species combinations, 34% ($n = 171{,}187$) were closest to a poleward-facing range limit and 50% ($n = 255{,}928$) were closest to an equatorward-facing limit. The difference in latitude was not detectable at 4 km resolution for the remaining 16% ($n = 81{,}144$) of site-by-species combinations, so these were excluded from the analysis of equatorward versus poleward range limits. Due to the complex shapes of some species' ranges, it was possible for a site to be closest to a poleward-facing range limit while being in the equatorward half of the species' range, and vice versa. We therefore also analysed whether sensitivity to forest cover varies depending on whether populations are located in the equatorward or poleward halves of their species range (Figure S2; Table S4).

2.4 | Statistical Analysis

To investigate how bird incidence is affected by distance to range limit and forest cover, we employed binomial generalised linear mixed models (GLMMs) with logit link functions using the R package *glmmTMB* (Brooks et al. 2025). The models included forest cover proportion and square-root transformed distance to range limit as interacting predictors of incidence (Orme et al. 2019). We confirmed that there was no correlation between these two predictors (Appendix 8). A significant interaction between the effects of distance to range limit and forest cover on incidence would show that distance to range limit affects sensitivity to forest cover because it would mean that the effect of forest cover on incidence changes depending on distance to the range limit (Orme et al. 2019). To test whether including an interaction improved the model fit, we compared the AIC scores of this model to those of simpler models (Table S8). The models also included a nested random intercept for study and for sampled site within study (1 | study/site), which accounted for variations in sampling methods and detection probabilities across studies. The models also included a random intercept and slope for each species (distance to range limit * forest cover | species) to allow for species-specific variation in incidence with the main effects and variation in baseline incidence among species (Orme et al. 2019). We tested for phylogenetic correlation in the species-level random effects using PGLS (Appendix 9). The assumptions underlying the statistical models were checked using the *DHARMa* package (Hartig and Lohse 2024) (Figures S4–S6).

To test whether sensitivity to deforestation is more strongly influenced by distance to soft range limits than hard limits, we analysed 230,837 site-by-species combinations which were located closer to hard limits than soft limits (Figure S1). This subset of data excluded species whose ranges did not intersect the coast, as well as cases where the species was surveyed closer to its soft limit than to the coast as distance to the coast is not meaningful in these cases. We focused on sites nearer to the coast than a soft limit because, under the mass effects hypothesis, only these sites would be expected to show an influence of coastal distance on species incidence and sensitivity to forest cover. We fitted a binomial GLMM to this subset of data using distance to the soft limit, forest cover and their interaction as predictors of incidence. We also fitted a similar model that used distance to the hard limit instead of distance to the soft limit. The hard limit model included species with no soft limits, such as island endemics with exclusively coastal range limits, whereas these species were excluded from the soft limit model as they did not have soft limits. By comparing the effect sizes and statistical significance of coefficients between the two models, we assessed whether distance to the soft limit was a stronger moderator of responses to forest cover than distance to the hard limit.

To compare equatorward- and poleward-facing soft range limits, we considered all combinations of site and species for which it was possible to measure distance to the soft range limit. This excluded species with no soft limits to their ranges. We fitted a single model with a three-way interaction term; in addition to forest cover and distance to the nearest soft range limit as interacting predictors, the model included a binary term describing whether the nearest soft range limit faced equatorward or poleward. All analyses were conducted in R version 4.4.1 (R Core Team 2024).

3 | Results

3.1 | Range Limit Hardness

For the subset of data consisting of sites closer to the hard limit than a soft limit, the probability of bird incidence was higher further from both hard and soft range limits (Hard: 0.08, $SE = 0.02$, $p < 0.001$.; Soft: 0.05, $SE = 0.01$, $p < 0.001$). Forest cover also had a positive effect on incidence in both models (Hard: 0.9, $SE = 0.2$, $p < 0.001$.; Soft: 1.9, $SE = 0.2$, $p < 0.001$). However, the interaction between distance to range limit and forest cover was only significant at soft limits (Hard: 0.006, $SE = 0.02$, $p = 0.8$.; Soft: -0.07, $SE = 0.01$, $p < 0.001$). This indicates that distance to soft range limits moderates the effect of forest cover on incidence. Close to soft range limits, forest cover has a positive effect on incidence. This effect gets weaker and even switches to a negative effect of increasing forest cover on incidence further from soft limits. By contrast, forest cover has a positive effect regardless of distance to hard range limits (Figure 2, Table S2).

3.2 | Range Limit Direction

Probability of incidence was higher further from both equatorward- and poleward- facing range limits (Equatorward: 0.07, $SE = 0.01$, $p < 0.001$.; Poleward: 0.06, $SE = 0.009$, $p < 0.001$). Probability of incidence also increased with forest cover (Equatorward: 1.6, $SE = 0.2$, $p < 0.001$.; Poleward: 1.7, $SE = 0.2$, $p < 0.001$) and there was a negative interaction between distance to range limit and forest cover at both types of range limit (Equatorward: -0.05, $SE = 0.01$, $p < 0.001$.; Poleward: -0.04, $SE = 0.01$, $p < 0.01$) (Figure 3, Table S3). Therefore, distance to both equatorward- and poleward- facing range limits moderated sensitivity to forest cover and there was no significant difference between equatorward and poleward limits in their effect on sensitivity. The effect of distance to range limit on sensitivity to forest cover was also similar regardless of whether populations

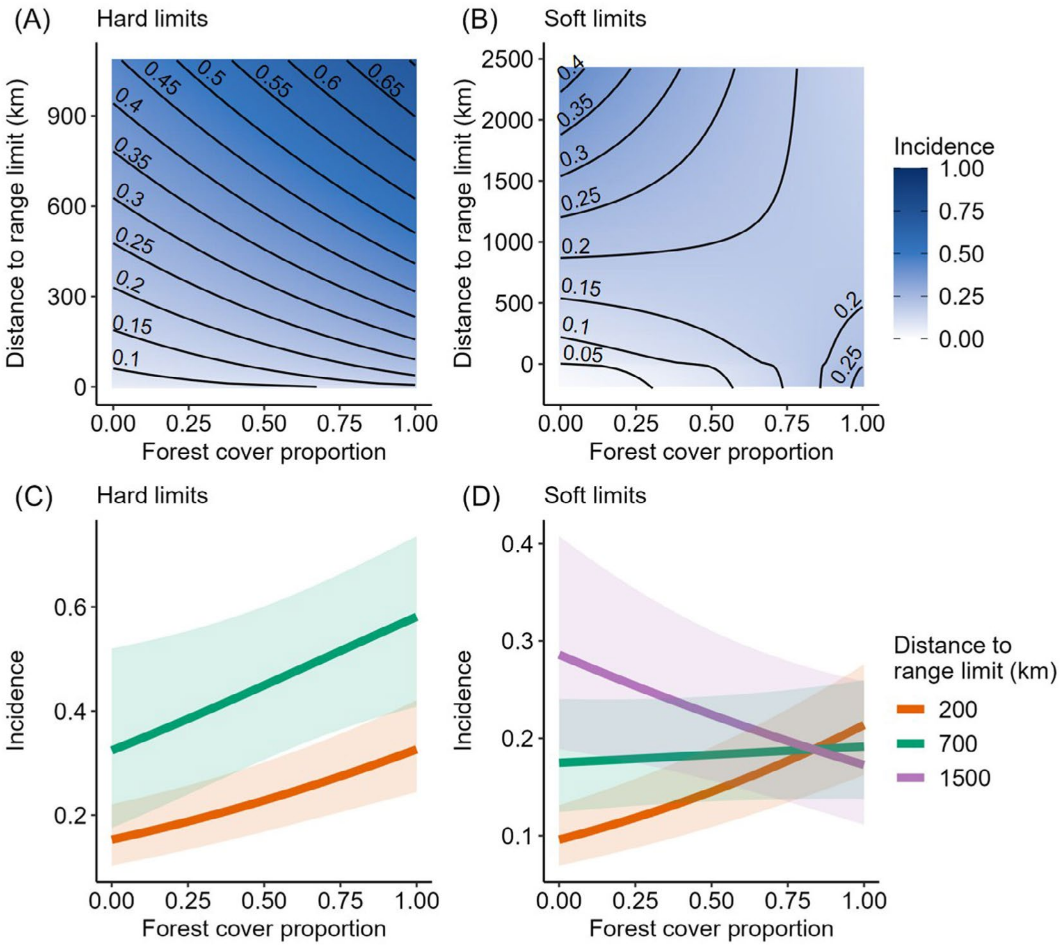

FIGURE 2 | Distance to soft range limits, but not hard range limits, modulates the relationship between species incidence and forest cover. Panels (A) and (B) are heatmaps showing how the average predicted probability of species incidence (represented by the contour lines and colour hue) varies with forest cover proportion (*x*-axis) and distance to range limit (*y*-axis). Panels (C) and (D) highlight the effects of forest cover on incidence at selected distances to range limit.

were located in the equatorward or poleward half of the species' range (Figure S2; Table S4). The model with distance to soft range limit, forest cover and their interaction as predictors of incidence had a lower AIC value than simpler models (Table S8), indicating that incorporating an interaction between forest cover and distance to soft range limit improves model fit. The model fit was not significantly improved by incorporating an additional term describing whether the range limit faced poleward or equatorward (Table S8).

4 | Discussion

In this study, we examined how proximity to different types of range limits influences bird populations' sensitivity to forest cover. We found that populations near soft (inland) limits of their species' range were significantly more sensitive to the amount of forest cover in the landscape, whereas populations further from these soft limits were less sensitive to changes in forest cover, and could even be positively affected by forest loss. This pattern was not found at hard (coastal) limits. The heightened sensitivity near soft range limits was similar regardless of whether the range limit faced poleward or equatorward. These findings highlight that population responses to forest cover are not uniform and depend strongly on their position within the species' range.

There was a significant interaction effect of distance to range limit and forest cover on incidence at soft limits but not hard limits (Figure 2, Table S2). Sensitivity to forest cover was heightened near soft limits, where abiotic and biotic niche conditions gradually become less suitable. In contrast, populations near hard (coastal) limits did not show this pattern, suggesting that niche limitation, rather than mass effects, is the dominant mechanism shaping population responses to forest cover. This finding provides strong empirical support for the hypothesis that soft range limits reflect declining niche suitability, making populations more vulnerable to environmental change. Future research should aim to uncover the specific abiotic and biotic mechanisms driving niche limitation at soft range limits as these are likely to be key in understanding and predicting species' responses to land-use change.

Differentiating between hard and soft range limits can help reconcile disparate findings on how proximity to the range limit affects sensitivity to forest cover. Studies that isolated soft limits from hard limits found heightened sensitivity to forest cover near the range limit (Bellotto-Trigo et al. 2023; Orme

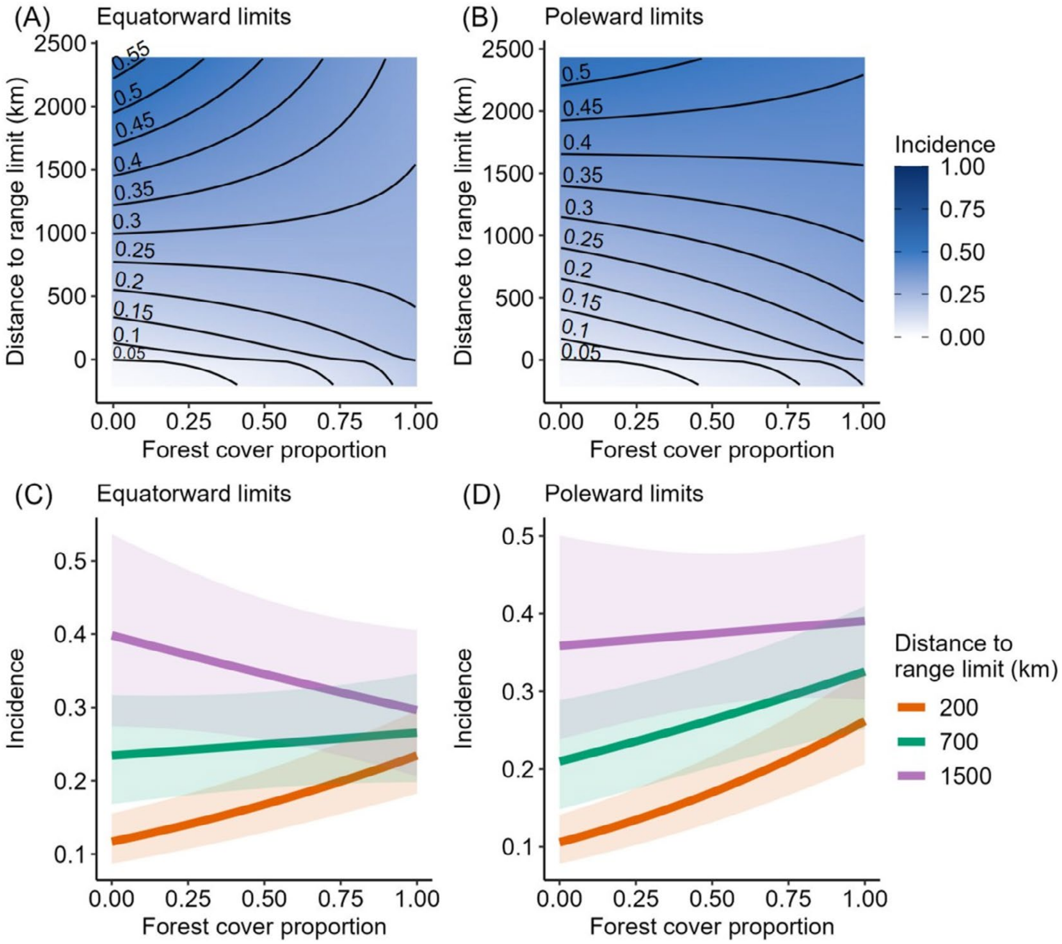

FIGURE 3 | Distance to equatorward- and poleward-facing soft range limits both modulate the relationship between species incidence and forest cover. Panels (A) and (B) are heatmaps showing how the average predicted probability of species incidence (represented by the contour lines and colour hue) varies with forest cover proportion (*x*-axis) and distance to range limit (*y*-axis). Panels (C) and (D) highlight the effects of forest cover on incidence at selected distances to range limit.

et al. 2019). In contrast, studies that did not make this distinction and instead measured the distance to any nearest range limit reported less conclusive results (Betts et al. 2019; Hasui et al. 2024), as hard limits may not exhibit the same declines in abiotic and biotic niche suitability as soft limits. More generally, many studies of ecological patterns across species' ranges tend to examine both hard and soft range limits together (e.g., Lomolino and Channell 1995; Channell and Lomolino 2000; Pironon et al. 2017). Our empirical results highlight that not all range limits are equal. We emphasise the importance of accounting for the hardness of a range limit in future studies of species' ranges. Future studies could explore how sensitivity to forest cover varies at other types of limits, such as those limited by rivers or steep elevational changes, such as mountains, which could present abrupt truncations ('hard' limits) for some species' ranges (Banks-Leite et al. 2022). Abundance-based measures of hardness could also be used to test whether rivers and mountains are hard limits (Gilbert et al. 2024).

Biotic interactions could also produce abrupt range limits (Freeman et al. 2022). Our results did not support the hypothesis that the effect of distance to range limit on sensitivity to forest cover would be stronger at poleward-facing soft range limits, where more gradual changes in abiotic constraints are expected, compared to equatorward-facing soft range limits which are suggested to be more likely to be driven by biotic factors (Paquette and Hargreaves 2021). In general, our results showed that the increase in sensitivity to forest cover was similar at poleward limits compared to equatorward limits (Figure 3, Table S3). There may be different mechanisms driving range limitation at poleward and equatorward limits, such as predominantly biotic limitation at equatorward limits and abiotic limitation at poleward limits (Paquette and Hargreaves 2021). However, if this is the case, it appears that both mechanisms lead to similar effects of distance to range limit on sensitivity to forest cover. The lack of support for the hypothesis could be because the outcome of biotic interactions, such as whether a species' range ends abruptly or overlaps with that of another species at the range limit, can often depend on the climatic conditions (Bothwell et al. 2015; Chamberlain et al. 2014). Therefore, determinants of biotic range limits could be indirectly driven by abiotic factors such as climate (Gross and Price 2000; Srinivasan et al. 2018). Alternatively, it could be that biotic range limits could have more gradual declines in habitat suitability than expected from our hypothesis (Gilbert et al. 2024; Sirén and Morelli 2020).

Our findings offer important insights into how populations may respond to the combined threats of climate and land-use change.

Populations near the soft (inland) limits of their species' range are likely to be critical for enabling range shifts in response to climate change. If species cannot adapt in place, their survival may depend on shifting their ranges to track suitable climatic conditions (Hargreaves and Eckert 2019; Sexton et al. 2011). However, because hard limits act as barriers to expansion, soft-limit populations are expected to lead these shifts (Gibson et al. 2009; Gilbert et al. 2024). This makes it especially concerning that these same populations are also more vulnerable to forest loss from land-use change. Studies on climate-driven range shifts should therefore consider how heightened sensitivity to land-use change at soft limits may interact with climate change to affect populations.

Heightened sensitivity to deforestation closer to species' soft range limits, which we have shown to be a generalisable pattern across the world, could have important implications for conserving biodiversity. Species with small ranges will always be close to their range limit, so they are likely to be highly sensitive to deforestation throughout their range, while species with larger ranges show more variation in sensitivity to deforestation (Figure S3; Table S5). Current approaches to conservation that tend to focus on species-level classifications of responses to threats may be overlooking important intraspecific variation in these responses, particularly for species with large ranges. Further research on this intraspecific variation would help improve the accuracy of predictions of biodiversity change and could help inform effective prioritisation of conservation actions.

Author Contributions

N.R.G., A.L.P. and C.B.-L. designed the study. N.R.G. conducted analyses with input from B.H., A.L.P. and C.B.-L. L.dA., V.A.-R., L.B., J.B., M.G.B., A.C., P.F.D., J.H.H., H.J., J.K., U.G.K., J.R.L., C.J.M., L.A.M.M., J.C.M.-F., P.O., A.M.P., H.P., V.P., J.T., A.U., E.M.W. and C.B.-L. contributed data. C.B.-L. and A.L.P. supervised N.R.G. N.R.G. drafted the manuscript and all authors contributed to revisions and approved the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The R scripts used to process data and conduct analyses are openly available in a Dryad repository: https://doi.org/10.5061/dryad.m905qfvd2. The PREDICTS Project database can be downloaded from: https://data.nhm.ac.uk/dataset/the-2016-release-of-the-predicts-database-v1-1 and https://data.nhm.ac.uk/dataset/release-of-data-added-to-the-predicts-database-november-2022. The Atlantic Bird data can be downloaded from: http://onlinelibrary.wiley.com/doi/10.1002/ecy.2119/suppinfo. The BIOFRAG data can be requested from: https://biofrag.wordpress.com/biofrag-measuring-biodiversity-response-to-forest-fragmentation/. The species' range maps can be requested from BirdLife International via: http://datazone.birdlife.org/species/requestdis. The global tree cover maps can be downloaded from: https://storage.googleapis.com/earthenginepartners-hansen/GFC-2022-v1.10/download.html.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Map of sites included in analysis of hard vs. soft range limits. **Figure S2:** Heatmap from model testing how position in equatorward vs. poleward half of range affects response to forest cover. **Figure S3:** Heatmap from model testing how distance to soft range limit affects sensitivity to forest cover, when accounting for range size. **Figure S4:** Distribution of residuals for hard limit model. **Figure S5:** Distribution of residuals for soft limit model. **Figure S6:** Distribution of residuals for equatorward vs. poleward model. **Table S1:** List of studies. **Table S2:** Model coefficients from analysis of hard vs. soft range limits. **Table S3:** Model coefficients from analysis of equatorward vs. poleward range limits. **Table S4:** Coefficients from model testing how position in equatorward vs. poleward half of range affects response to forest cover. **Table S5:** Coefficients from model testing how distance to soft range limit affects sensitivity to forest cover, when accounting for range size. **Table S6:** Coefficients from model using 400 m buffer to calculate forest cover. **Table S7:** Coefficients from model using 800 m buffer to calculate forest cover. **Table S8:** AIC scores of models reported in main text, compared to models with simpler fixed effects.