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RESEARCH ARTICLE

Limited Evidence That Interspecific Nest-Site Competition and Facilitation Drive Range Limits

Neil A. Gilbert[1] | Meghan A. Beatty[2] | Hallie D. Bridgewater[1]

[1]Department of Biology, Oklahoma State University, Stillwater, Oklahoma, USA | [2]K. Lisa Yang Center for Conservation Bioacoustics, Cornell Lab of Ornithology, Cornell University, Ithaca, New York, USA

Correspondence: Neil A. Gilbert (neil.gilbert@okstate.edu)

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ABSTRACT

Aim: Biotic interactions form a pillar of niche concepts but are frequently overlooked as range-limiting factors. At local scales, 'non-excavator' bird species—those that nest in tree cavities but cannot create cavities themselves—experience competition with other non-excavators but experience facilitation by excavators such as woodpeckers. Our objective was to evaluate whether competition and facilitation mediate the range limits of non-excavator species.

Location: USA and Canada.

Time Period: Contemporary.

Group: Cavity-nesting birds (55 non-excavators, 20 excavators).

Methods: Using eBird abundance maps, we modelled abundance of non-excavator species within their non-coastal range limits as a function of either (1) summed abundances of non-excavator heterospecifics, (2) summed abundances of excavator heterospecifics, or (3) abundances of House Sparrows or European Starlings, two invasive 'supercompetitors'. We also evaluated 'edge–core' models that included data for range limits and cores.

Results: At a cross-species level, the effects of heterospecific non-excavator and excavator abundance were not significant for 'edge only' models. At a species level, only 3 species (5% of the total) showed strong (≥ 95% confidence) competitive effects of non-excavators *and* strong facilitative effects of excavators. However, invasive 'supercompetitors' were associated with low range-limit abundance of non-excavators; for example, House Sparrows showed significant negative effects on range-limit abundance for nine out of the 17 (53%) non-excavator species of similar size. 'Edge–core' models showed positive effects of heterospecific abundance (both non-excavators and excavators) within range cores but not edges.

Main Conclusions: Our results are consistent with the 'Eltonian Noise Hypothesis', which suggests that biotic interactions 'wash out' at broadening spatial scales such that only abiotic variables correlate with species distributions at broad scales. Among-species broad-scale similarity and fine-scale variation in habitat selection, as well as variation in phenology, may contribute to the limited evidence we found of competition or facilitation contributing to range limits.

1 | Introduction

Range limits provide ecologists the opportunity to unravel secrets of the niche (Sexton et al. 2009). Niche theory posits that species ranges are limited by dispersal factors such as movement barriers, biotic factors such as competition, and abiotic factors such as climate (Soberón and Nakamura 2009). Of these, abiotic factors take the lion's share of attention in macroecology, likely

because they are easier to quantify and relate to species' distributions at broad scales, and may indeed 'wash out' the signal of biotic interactions (the 'Eltonian Noise Hypothesis'; Soberón and Nakamura 2009; Wisz et al. 2013). However, biotic interactions may contribute to range limits in many species, and understanding the role of these biotic interactions may help explain why many species do not seem to be shifting their ranges to track their thermal niches with climate warming (Lawlor et al. 2024).

As a range-limiting factor, interspecific competition is thought to be disproportionately important in high-diversity regions (Paquette and Hargreaves 2021; Freeman et al. 2022). Beyond such general macroecological expectations, detecting the signature of biotic interactions on range limitation requires identifying the limited resource(s) for which species compete (Louthan et al. 2015; Anderson 2017). For example, the arctic fox (*Vulpes lagopus*) has experienced range retractions following poleward expansion of the red fox (*Vulpes vulpes*), which dominates in contests for food resources and den sites (Tannerfeldt et al. 2002). One example of interspecific competition that has been observed at local scales (Newton 1994) but is seldom evaluated at macroecological scales is competition for nest sites among bird species that use tree cavities.

Cavity-nesting birds are limited by nest-site availability and may thus experience strong biotic interactions with cavity-nesting heterospecifics (Figure 1a; Newton 1994; Holt and Martin 1997; Cockle et al. 2010, 2011; Lima and Garcia 2016). Cavity-nesting birds can be classified into guilds of *excavators* that create cavities (e.g., woodpeckers) or *non-excavators* that rely on existing cavities (Bunnell 2013; van der Hoek et al. 2017). Non-excavator species experience facilitation by excavator heterospecifics but competition with non-excavator heterospecifics (Figure 1b; Martin and Eadie 1999; Blanc and Walters 2008; Trzcinski et al. 2022; Bonaparte et al. 2024). The intensity of these biotic interactions may be mediated by body size; for example, a small non-excavator will likely not compete with a large non-excavator because the two species have different requirements for entrance size. Similarly, a large-bodied non-excavator will not experience facilitation by a small-bodied excavator because it will be unable to enter the cavity (Figure 1b; Martin et al. 2004; Di Sallo and Cockle 2022). Additionally, species differ in competitive ability, and previous work suggests that several invasive species—especially European Starlings (*Sturnus vulgaris*) and House Sparrows (*Passer domesticus*)—have disproportionately strong competitive effects on other cavity-nesters (Lindell 1996; Charter et al. 2013, 2016; Robillard et al. 2013; Goldshtein et al. 2018). Positive relationships between excavator and non-excavator species richness and indices of abundance have been found at local (Martin and Eadie 1999; Blanc and Walters 2008; Segura 2017; Trzcinski et al. 2022), regional (Sandoval and Barrantes 2009; Alaniz et al. 2024), and global scales (van der Hoek et al. 2020). Yet, it is unknown if and how biotic interactions drive the range limits of cavity-nesting birds at macroecological scales.

Our objective was to evaluate whether competition and facilitation mediate the non-coastal range limits of non-excavator cavity-nesting birds. We focused on species that breed in the United States and Canada and used eBird Status and Trends products (Strimas-Mackey et al. 2022) and nest-trait databases (van der Hoek et al. 2017; Chia et al. 2023) to determine range limits and identify cavity-nesting bird species. Focusing on the abundance of non-excavators within their non-coastal range limits, we predicted (1) a negative relationship with the abundance of non-excavator heterospecifics (competition), (2) a positive relationship with the abundance of excavator heterospecifics (facilitation), and (3) stronger relationships for heterospecifics of similar body size (Figure 1b). Moreover, we predicted strong competitive effects of two invasive 'supercompetitors', the European Starling and House Sparrow. Our work investigates the role of biotic interactions in understanding species range limits and provides an example for developing predictions about the strength of biotic interactions based on traits such as nest type and body size.

2 | Methods

2.1 | Study Area and Species Selection

We selected 55 non-excavator species that breed in the United States and Canada based on published nest trait data (van der Hoek et al. 2020; Chia et al. 2023). We omitted Mexican and Central American species because breeding strategies may fundamentally differ for temperate-zone species, e.g.,

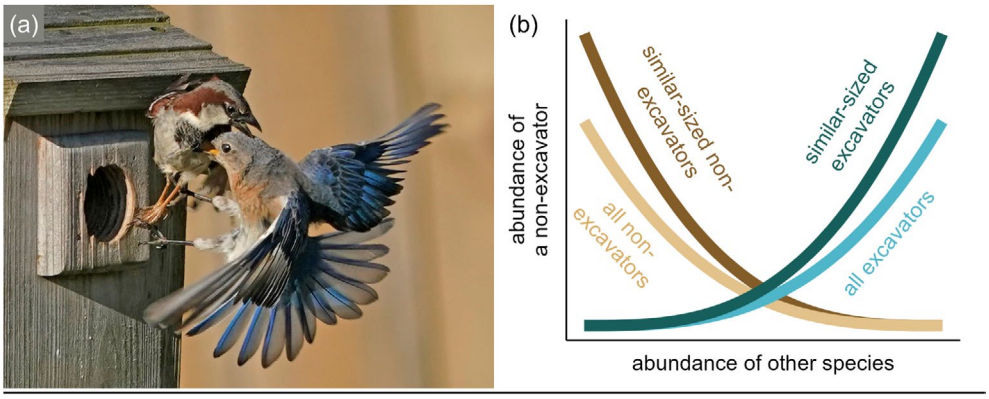

FIGURE 1 | (a) A male House Sparrow (*Passer domesticus*; left) fighting a female Eastern Bluebird (*Sialia sialis*; right) for a nest box, i.e., an artificial cavity. Photo by Mike Dickie Photography and used with permission. (b) For a focal non-excavator cavity-nesting species at its range limits, hypothesized relationships relating to competition with heterospecific non-excavators (brown) and facilitation by heterospecific excavators (teal).

greater use of natural cavities by non-excavators compared to temperate zones (Cockle et al. 2011; Zavala et al. 2025) and also because the eBird Status & Trends products we employed may be less accurate in these regions due to the comparatively lower volume of data (Strimas-Mackey et al. 2022). Because our focus was on terrestrial species that primarily use tree cavities (including nest boxes, which function as artificial tree cavities), we excluded species in families Cathartidae, Alcidae, Oceanitidae, Hydrobatidae, and Procellariidae, and furthermore omitted species coded as cavity nesters but that use non-tree nest structures, e.g., burrows in the ground (Chia et al. 2023). We performed a manual screening of cavity-nesting classification to impute status for species with missing data, omit species that were erroneously classified as cavity-nesters in a published database (e.g., Black-throated Green Warbler *Setophaga virens* was coded as a cavity-nester by Chia et al. (2023) despite building open-cup nests in trees; Billerman et al. 2025), and omit species occurring in North America only as localized feral populations. The first author screened all species and classified each as (1) verified cavity nester, (2) not a cavity nester, or (3) uncertain. The last author reviewed Birds of the World nest site information for each 'uncertain' species to verify them as a cavity nester. Finally, the first author made a final judgement call for species with limited information based on nest information in Birds of the World (Billerman et al. 2025) and on nesting habits of similar species. Finally, we used classifications from van der Hoek et al. (2017) to define non-excavator and excavator guilds; we grouped their 'non-excavator' and 'facultative excavator' (species that can excavate or modify cavities but often do not) categories into a non-excavator category and used their 'primary excavator' category to define excavators. This resulted in a final list of 55 non-excavator species representing 14 families (Table S1).

2.2 | Abundance Maps and Identifying Non-Coastal Range Edges

We used the ebirdst R package to download breeding-season abundance rasters (based on 2023 eBird data) for the 55 focal non-excavator species, as well as 20 excavator species occurring within the region (Table S1; Strimas-Mackey et al. 2022; Fink et al. 2025). The abundance maps have 27 × 27 km spatial resolution and are based on 2023 data from eBird (Fink et al. 2025), a global community-science effort in which observers submit checklists of birds they detect (Sullivan et al. 2009). Metadata regarding effort (e.g., time-of-day, distance travelled, number of observers) are collected but sampling locations are not randomized (Sullivan et al. 2009). To be used in models, the data are subjected to filtering rules to retain only checklists that report counts of all bird species detected, have complete effort information, are 6 h or less in duration, and cover distances less than 10 km; the data are then spatially subsampled to reduce bias from non-random sampling (Strimas-Mackey et al. 2022). The machine-learning models used to predict relative abundance incorporate environmental variables (e.g., elevation, land cover) that may influence bird abundance, as well as variables such as time-of-day and observer skill that influence detectability (Fink et al. 2010). The model predictions represent the expected count of a species by an experienced birdwatcher during a 1-h, 1-km checklist during the morning hours on a day with favourable weather conditions at a random location within a given 27 × 27 km pixel (Strimas-Mackey et al. 2022). We omitted pixels that were within 100 km of coastlines because hard dispersal barriers like coastlines may mask the range-limiting influences of biotic and abiotic factors (Banks-Leite et al. 2022; Gilbert et al. 2024). Finally, using the smoothed range polygons from ebirdst (based on the abundance maps described above, i.e., areas with nonzero relative abundance; Strimas-Mackey et al. 2022), we calculated the distance between each pixel centroid and the nearest range polygon boundary and defined range edges as those within the 10th percentile of range-edge distance and range cores as those greater than the 90th percentile of range-edge distance, producing equal numbers of edge and core cells (Figure 2).

2.3 | Data Formatting and Analysis

We fit two sets of models: 'edge only' models that only considered the range-edge cells for an individual non-excavator species, and 'edge–core' models that included both edge and core cells. For both model sets, the response variable was the abundance of an individual non-excavator species within cells included for a given model

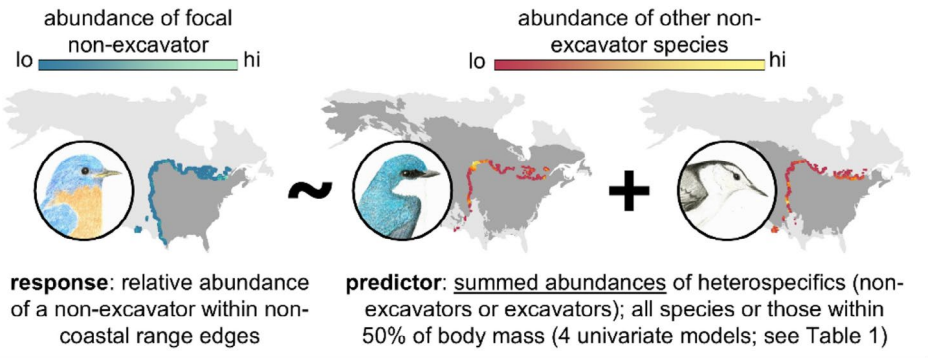

FIGURE 2 | Summary of approach. We used relative abundance maps from the eBird Status and Trends product to identify abundances of non-excavators in their non-coastal range limits (response variable) and calculated the summed abundance of heterospecifics within the same grid cells as the predictor variable. Example maps for Eastern Bluebird (*Silia sialis*), Tree Swallow (*Tachycineta bicolor*), and White-breasted Nuthatch (*Sitta carolinensis*) are shown; see Table 1 for a summary of the models evaluated.

TABLE 1 | The four models used to assess our hypotheses regarding competition, facilitation, and body-size effects.

Model	Predictor
1	Abundance of *all non-excavator* cavity-nesting heterospecifics
2	Abundance of *non-excavator* cavity-nesting heterospecifics *within 50% of the body mass* of the focal non-excavator species
3	Abundance of *all excavator* cavity-nesting heterospecifics
4	Abundance of *excavator* cavity-nesting heterospecifics *within 50% of the body mass* of the focal non-excavator species

(Figure 2). For 'edge only' models, the only predictor variable was the summed abundances of other cavity-nesting species within range-edge cells of a given non-excavator cavity-nester (Figure 2). For the 'edge–core' models, we included a predictor variable for the summed abundances of other cavity-nesting species within each focal cell, along with a binary predictor for range position (1 = edge, 0 = core) and an interaction between range position and heterospecific abundance. For each model set, we calculated four predictors to evaluate our hypotheses (Table 1): (1) summed abundance of all other non-excavator cavity nesters, (2) summed abundance of all excavator cavity nesters, (3) summed abundance of other non-excavator cavity nesters within 50% of the body mass of a given species, (4) and summed abundance of excavator cavity-nesters within 50% of body mass of a given species (Figure 2). We also calculated heterospecific abundance within 25% of body mass for a supplemental analysis testing whether signatures of competition or facilitation only appear for species very similar in size. We used body-mass information from the AVONET database (Tobias et al. 2022). We used generalized linear mixed-effects models with a Gamma response and log link because the relative abundance estimates provided by eBird are positive and continuous. The models had a random-effects structure such that the intercept and slope(s) varied by species. We fit the models using the R packages glmmTMB and brms, using a Bayesian framework for the 'edge only' models to obtain estimates of species-level slope parameters with uncertainty (Brooks et al. 2017; Bürkner 2017; R Core Team 2026). We classified a species as showing weak or strong support for the predicted patterns (Figure 1) if the 68% or 95% credible intervals for the effect of heterospecific abundance did not overlap zero, respectively. To evaluate sensitivity to how range edges were defined, we evaluated supplemental models in which species' range edges were defined as the 5th and 20th percentile (rather than 10th percentile) of distance-to-range-edge. Finally, to evaluate sensitivity to how non-coastal cells were defined, we evaluated supplemental models in which non-coastal cells were defined as those > 50 km (rather than 100 km) from the nearest coastline.

2.4 | Effects of Invasive 'Supercompetitors'

Our primary analysis involved summing the abundances of other cavity-nesting birds present in a location (Figure 2), which might conceal range-limiting effects if individual co-occurring species exert strong effects while other species do not (Louthan et al. 2015). Therefore, we conducted an additional analysis in which the range-limit abundance of non-excavators (response variable) was predicted by the abundance of either House Sparrows or European Starlings, two non-excavator species that were introduced to North America in the mid-to-late 19th century and are frequently considered aggressive competitors for nest sites (Figure 1a; Robillard et al. 2013; Charter et al. 2016). We analysed species that were within 50% body mass of sparrows ($n = 17$) or starlings ($n = 8$) and also completed an auxiliary analysis with all non-excavator species ($n = 53$). We fit generalized linear models (Gamma response and log link) for each species individually using the R package glmmTMB (Brooks et al. 2017). Because these 'supercompetitor' species may have opposing habitat preferences to many of the focal non-excavator species (e.g., preference for human-modified habitats versus forests), we also evaluated supplemental models in which we also included the mean amount of human modification (Kennedy et al. 2019) in the grid cell as a predictor (Supporting Information).

3 | Results

3.1 | Cross-Species Level: No Evidence of Competition or Facilitation

At a cross-species level, the 'edge only' models indicated that abundance of heterospecific cavity-nesters did not show a clear relationship with abundance of non-excavator species at their range limits (Figure 3). For all guild–size combinations, the coefficient for the abundance of heterospecifics had both 68% and 95% credible intervals overlapping zero. We interpret these results as providing no evidence of broad-scale competition for or facilitation of nest sites limiting the ranges of non-excavator cavity nesters (Figure 3). In all cases except for the non-excavators within 50% of body mass, the 'edge–core' models identified strong positive relationships between focal non-excavator abundance and heterospecific abundance (for both non-excavator and excavator guilds) but significant interactions with range position such that these relationships were only apparent within the cores of species' ranges (Figure 4). Because the models estimated positive relationships for both non-excavator (opposing prediction) and excavator (supporting prediction) heterospecifics, we are hesitant to interpret the latter pattern as support for facilitation (Figure 1). In all 'edge–core' models, the main effect of range position was strong and significant, with range edges having lower abundance than range cores (Figure 4). Supplemental models that defined range limits based on 5th and 20th percentiles of distance-to-range-edge, and models that defined non-coastal range cells as > 50 km from a coastline (rather than 100 km), did not find different results from the main models (Tables S2–S4). Results from models that defined range limits based on the 20th percentile of distance-to-range-edge estimated positive relationships between focal non-excavator abundance and abundance of all non-excavators and excavators (but not those of similar size; Table S3), likely due to a greater inclusion of range-core areas. Finally, supplemental models that considered species within 25% body mass did not find significant effects (Table S5).

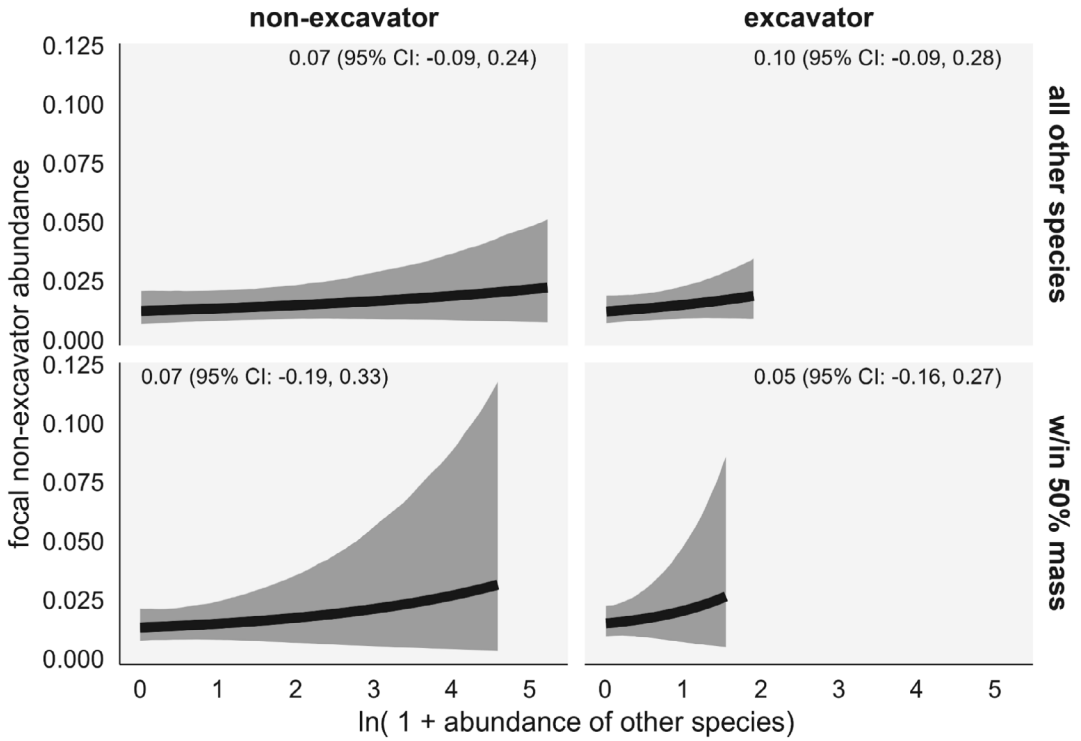

FIGURE 3 | Results from 'edge only' models: No evidence that abundance of cavity-nesting heterospecifics limits ranges of non-excavator cavity-nesting birds. Columns represent whether non-excavator (left) or excavator (right) heterospecifics were used as predictors of range-limit abundance of individual non-excavator species. Rows represent models for which abundance of all heterospecifics (top) or similar-sized heterospecifics (bottom; within 50% of body mass of focal species) were used. The lines and bands are the means and 95% credible intervals of cross-species model predictions (i.e., estimates for a hypothetical species with average parameter values).

3.2 | Most Species Do Not Show Hypothesized Patterns of Competition or Facilitation

Focusing on 'edge only' models, most non-excavator species did not show support for the hypothesized patterns of competition or facilitation (Figures 1 and 4). Nearly equal numbers of species showed negative (supporting competition hypothesis) and positive (opposing competition hypothesis) associations with the abundance of heterospecific non-excavators (Figure 5; 10 vs. 11 species for similar-sized heterospecifics, 14 vs. 14 species for all heterospecifics). Moreover, similar numbers of species showed negative (opposing facilitation hypothesis) and positive (supporting facilitation hypothesis) associations with the abundance of heterospecific excavators (Figure 5; 4 vs. 5 species for similar-sized heterospecifics, 12 vs. 15 species for all heterospecifics). In addition, 4 species (7% of the total) showed strong effects of the same sign across guilds—e.g., either all positive effects (e.g., Eastern Bluebird *Sialia sialis*) or all negative effects (e.g., Tree Swallow *Tachycineta bicolor*). Only three species (5% of the total) showed strong (≥95% confidence) competitive effects of non-excavators of either size group *and* strong (≥95% confidence) facilitative effects of excavators of either size group (Figure 5): Eastern Screech-Owl (*Megascops asio*), Great Crested Flycatcher (*Myiarchus crinitus*), and Carolina Chickadee (*Poecile carolinensis*). For example, range-limit abundance of Great Crested Flycatcher showed a clear negative relationship (competition) with abundance of similar-sized non-excavator heterospecifics but positive relationships with abundance of other guild–size combinations (Figure S1).

3.3 | 'Supercompetitors' Associated With Low Range-Limit Abundance of Non-Excavators

Range-limit abundance of non-excavators tended to be lower in locations where House Sparrows or European Starlings were abundant (Figure 6). Nine out of the 17 (53%) non-excavator species within 50% body mass of House Sparrows showed significant negative effects of sparrow abundance on range-limit abundance, while two species (12%; White-breasted Nuthatch *Sitta carolinensis* and Prothonotary Warbler *Protonotaria citrea*) showed a significant positive effect (Figure 6). Three out of the eight (38%) non-excavators within 50% body mass of starlings showed significant negative effects of starling abundance on range-limit abundance, and two species (20%; American Kestrel *Falco sparverius* and Purple Martin *Progne subis*) showed significant positive effects (Figure 6). When accounting for human modification in the landscape, the number of species showing significant negative effects of 'supercompetitor' abundance dropped to 6 (35%) for House Sparrow and 2 (25%) for European Starling (Figure S2). Expanding the basic analysis (no habitat effect) to all non-excavators, 45% and 43% of species, respectively, showed significant negative associations between range-limit abundance and abundance of European Starlings and House

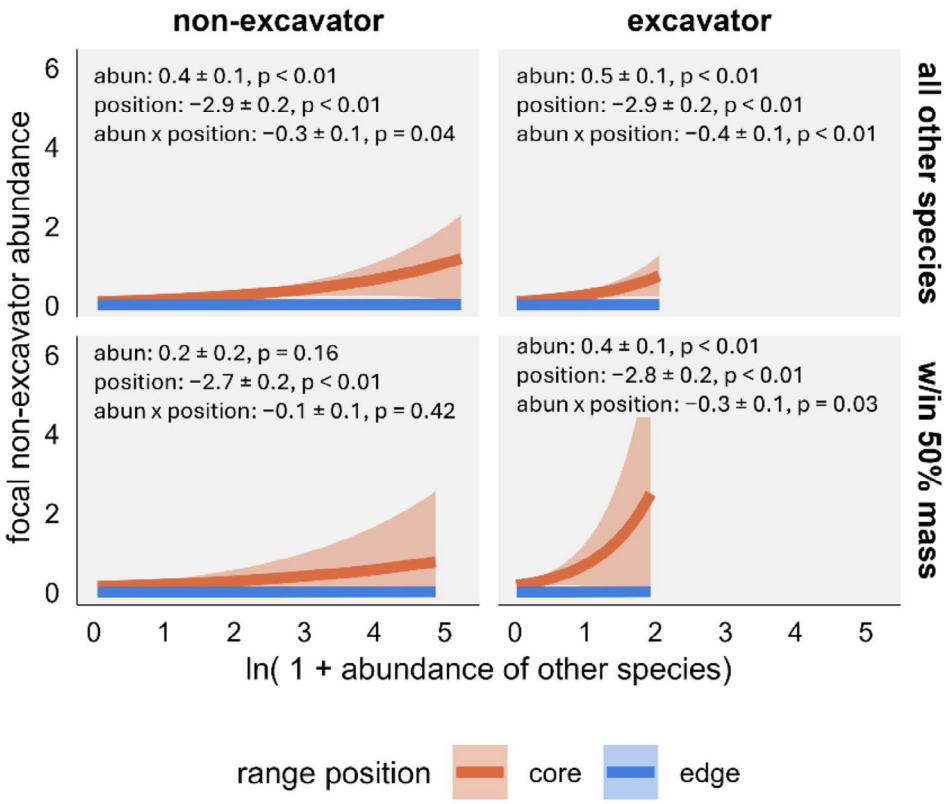

FIGURE 4 | Results from 'edge–core' models: Predicted associations between abundance of non-excavator species and heterospecific abundance within range cores (red) and range edges (blue). Rows represent models for which abundance of all heterospecifics (top) or similar-sized heterospecifics (bottom; within 50% of body mass of focal species) were used. The lines and bands are the means and 95% confidence intervals of cross-species model predictions (i.e., estimates for a hypothetical species with average parameter values).

Sparrows (9% and 15% showed significant positive effects; Table S6).

4 | Discussion

The goal of this paper was to evaluate whether nest-site competition and facilitation contribute to the range limits of cavity-nesting birds. We found limited evidence that nest-site competition or facilitation influences range limits of non-excavator cavity-nesters (Figures 3–5). The 'edge only' models found no effects of heterospecific abundance (Figure 3), while the 'edge–core' models found positive effects of heterospecific non-excavators (opposing prediction) and excavators (supporting prediction), but only in range cores (Figure 4). Beyond these across-species effects, the abundance of two non-native 'supercompetitors' showed negative effects on the range-limit abundance of many non-excavator heterospecifics (Figure 6). Our work supports the 'Eltonian Noise Hypothesis' which suggests that biotic interactions are primarily detectable at local scales, whereas abiotic variables explain the broad distributions of organisms (Soberón and Nakamura 2009). Moreover, our analysis focused on data from the United States and Canada, and if biotic interactions truly are more important as a range-limiting factor in tropical regions (Paquette and Hargreaves 2021; Freeman et al. 2022), alternative results might emerge if quality abundance maps were available for full assemblages of excavators in low-latitude regions. Beyond these generalities, we believe there are specific processes that explain why nest-site competition and facilitation were not apparent at broad scales.

Shared broad-scale habitat preferences paired with microhabitat niche partitioning could obscure and/or diminish the signal of competition at broad scales. In the 'edge only' models, 34% of non-excavator species showed unexpected *positive* associations (across either size category) with abundance of non-excavator heterospecifics, and the 'edge–core' models estimated positive effects of heterospecific abundance (for both excavators and non-excavators) within range cores but not edges, results that may reflect shared habitat preferences (e.g., forests comprised of similar tree species) at broad scales (Figure 5; Li and Martin 1991; Martin et al. 2004; Bunnell 2013). Even with such broad-scale positive associations, co-occurring non-excavators may alleviate competition via fine-scale habitat partitioning (Colwell and Fuentes 1975; Price 1978) such as selection of cavities at different heights or within trees of different sizes within the same small area (Gutzwiller and Anderson 1987). Our study suggests that competition for cavities among non-excavator species is generally not strong enough to be detectable in abundance patterns at range limits at a relatively coarse spatial resolution (Yackulic 2017).

Beyond spatial partitioning of nest sites, differences in breeding phenology among non-excavator species may relieve competition (i.e., temporal partitioning; Post 2019). In extreme cases, an early-breeding species may fledge young and vacate a cavity such that it can be used by a late-breeding species (or a species attempting a second brood) within the same season (Newton 1994). Alternatively, a would-be competitor species may be deterred from initiating a contest for a cavity with another species that has already made a significant parental

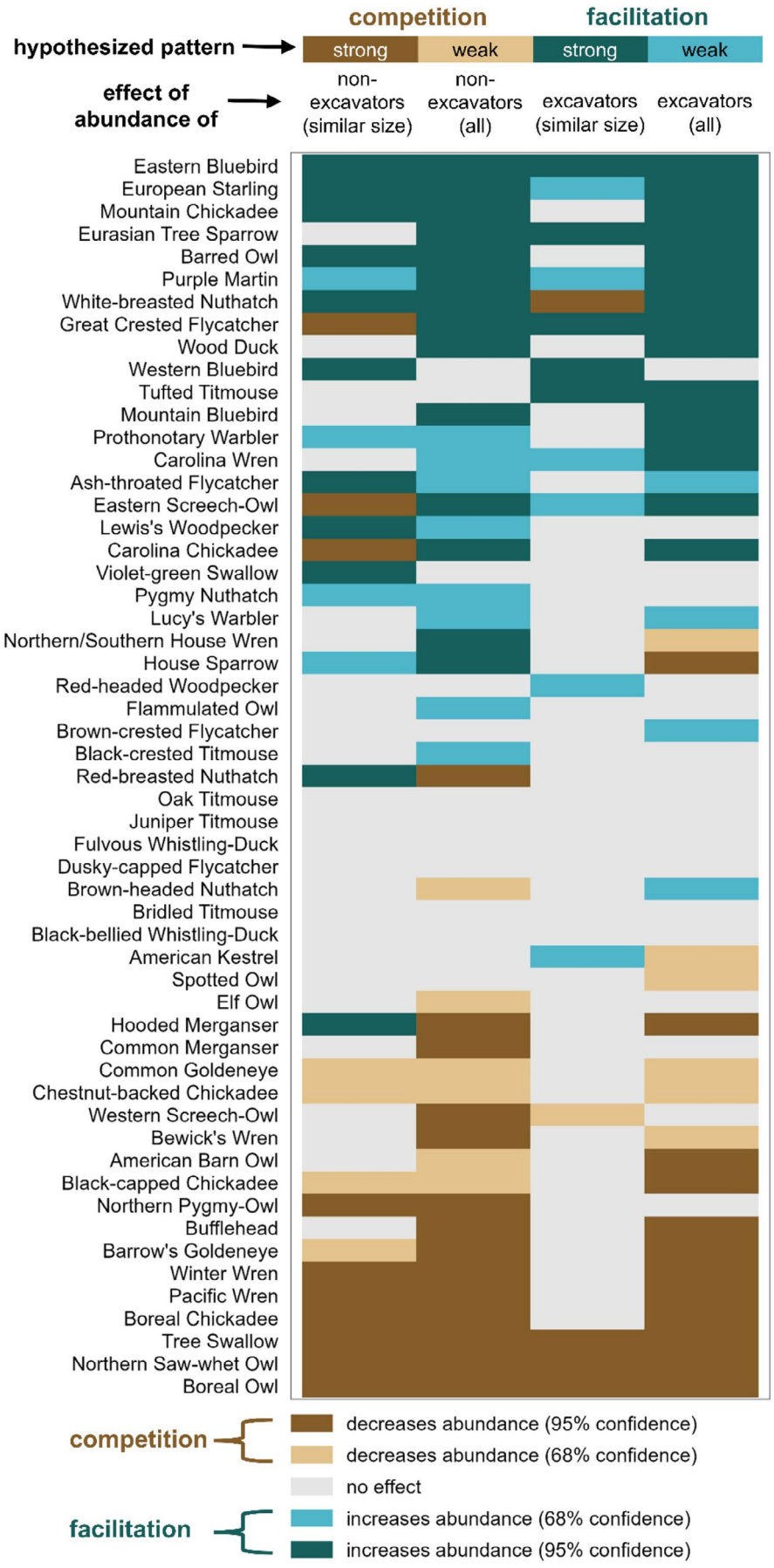

FIGURE 5 | Legend on next page.

FIGURE 5 | Few non-excavator species showed support for the hypothesized patterns of competition from other non-excavators and facilitation by excavators. Each cell reports the effect of heterospecific non-excavator abundance (left two columns) and excavator abundance (right two columns) on the abundance of non-excavator species (*y*-axis) within their range limits.

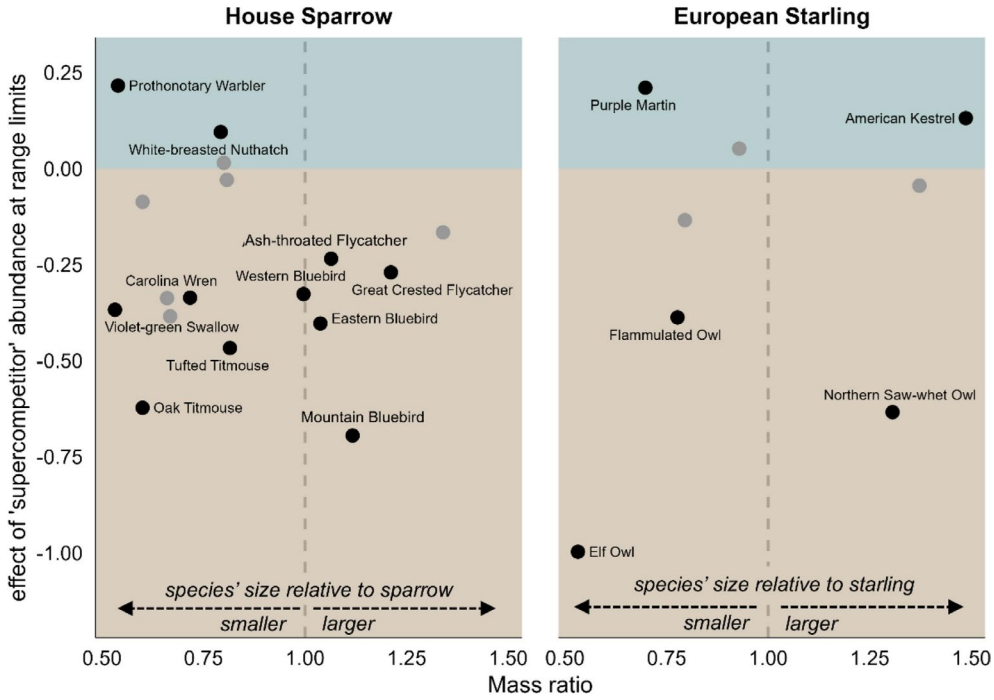

FIGURE 6 | Estimated effects of two 'supercompetitor' invasive cavity-nesters on the range-limit abundances of similar-sized non-excavator species. The y-axis is the estimated slope for 'supercompetitor' abundance and the *x*-axis is the mass ratio between species. Unlabeled species in grey did not show significant effects of the 'supercompetitor'.

investment (e.g., producing eggs or feeding young) and is therefore motivated to aggressively defend the cavity (Biermann and Robertson 1981). Focusing on abundances of resident versus migratory species may be a fruitful avenue for future research, as residents often initiate nests before migrants (Grist et al. 2017; Søraker et al. 2022). Ultimately, incorporating these phenological nuances is challenging because breeding seasons can vary significantly within the ranges of individual species; for example, southern populations of Eastern Bluebirds may begin nesting in early March, while northern populations may not begin until mid-to-late April (Billerman et al. 2025).

While previous studies have detected positive associations between species richness of excavator and non-excavator species at regional and global scales (van der Hoek et al. 2020; Alaniz et al. 2024), we found no evidence of excavators facilitating non-excavators at range edges, as measured by relative abundance (Figure 3). This disparity may arise because facilitation may be more apparent when considering entire species ranges. The 'edge–core' models that included range-core data found positive associations between focal non-excavator abundance and excavator abundance (Figure 4), with the strong caveat that abundance of heterospecific non-excavators also showed positive effects, contradicting our expectations (Figure 1). Alternatively, this disparity with other studies may arise due to limitations of species richness as a biodiversity metric (Fletcher Jr. et al. 2025). Moreover, reliance of individual non-excavator species on just one or a few 'keystone' excavator species (Aitken et al. 2002; Martin et al. 2004) might not be detectable using our approach of aggregating abundances across excavator species. Finally, facilitation by excavators for non-excavators may be lagged such that, for a given location, several years are required for excavators to provide enough cavities to influence abundance of non-excavators (Trzcinski et al. 2022). In this case, snapshot correlations of excavator and non-excavator abundances from a single year may not reveal facilitation.

Abundance may not always be a reliable instrument for measuring biotic interactions (Van Horne 1983; Vickery et al. 1992). Underpinning our analysis is the assumption that competition for nest sites reduces fecundity and eventually population abundance, contributing to the formation of range limits (Sexton et al. 2009). Local-scale studies corroborate the first portion of this assumption; for example, relaxed interspecific competition increased the number and mass of Collared Flycatcher (*Ficedula albicollis*) fledglings, presumably due to increased access to nest sites and food (Gustafsson 1987). However, immigration may cancel out reductions in fecundity and conceal competition when viewed through the lens of abundance (Van Horne 1983; Vickery et al. 1992). Indeed, theoretical modelling suggests that many decades to millennia of biotic interactions are required for one species to influence the abundance of another over broad spatial scales (Yackulic 2017). Future efforts might go beyond abundance as the response variable and analyse macrodemography databases to assess whether heterospecific abundance influences nest success (Senzaki et al. 2020).

5 | Conclusions

Given our results, it is tempting to abandon hope of quantifying biotic interactions at macroscales. However, we maintain that such efforts are valuable despite the challenges because they can provide mechanistic understanding of biodiversity patterns (Freeman et al. 2022) and explain departures from expected range shifts based on thermal niche tracking (Lawlor et al. 2024). Because we found the most compelling evidence of range-limit cavity competition when focusing on invasive 'supercompetitors'—especially the House Sparrow—our best advice is to tailor analyses to individual species (e.g., keystone excavators, 'supercompetitor' non-excavators) when seeking macroecological signal of biotic interactions (Louthan et al. 2015). Range limitation will likely continue to stymie ecologists far into the future, but biotic interactions like nest-site competition can enrich our understanding of why species occur where they do.

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The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data and code to reproduce the study are available at: https://doi.org/10.5061/dryad.zkh1893qm.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** The Great Crested Flycatcher was one of the few species to show range-limit abundance patterns consistent with hypothesized patterns: there was a negative relationship with abundance of similar-sized non-excavator heterospecifics (bottom left; brown) and positive relationships with excavators (right column; green). Points represent the data. Lines represent means and shaded regions (too narrow to be visible in bottom left) represent 95% credible intervals of model predictions. **Figure S2:** Estimated effects of two 'supercompetitor' invasive cavity-nesters on the range-limit abundances of similar-sized non-excavator species from models including the average level of human modification in the landscape. The y-axis is the estimated slope for 'supercompetitor' abundance and the x-axis is the mass ratio between species. Unlabeled translucent points represent species that did not show significant effects of the 'supercompetitor'. **Table S1:** Species in analysis. type_vdh is the classification for van der Hoek et al. (2017); type is the classification used in this paper. **Table S2:** Results from sensitivity analysis evaluating if results change if range edges are defined based on the 5th percentile (rather than 10th) of distance-to-range edge. **Table S3:** Results from sensitivity analysis evaluating if results change if range edges are defined based on the 20th percentile (rather than 10th) of distance-to-range edge. **Table S4:**

Results from sensitivity analysis evaluating if results change if non-coastal cells were defined as > 50 km from a coast, rather than 100 km. **Table S5:** Estimated effect of the summed abundances of heterospecifics with mass ratios between 0.7 and 1.3 on the range-limit abundance of focal non-excavators. **Table S6:** Expanded 'supercompetitor' analysis to all non-excavator species, regardless of body size. The latter two columns report the number and proportion of non-excavator species that showed significant associations between range-limit abundance and the abundance of two 'supercompetitors', the European Starling and House Sparrow.