eLife

Ecology
Evolutionary Biology

Decoupling both local and global abundance from global range size: challenging the abundance-occupancy relationship in birds

Reviewed Preprint
v2 • May 12, 2025
Revised by authors

Reviewed Preprint
v1 • August 30, 2024

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eLife assessment

This study offers a **useful** discussion of the well-accepted abundance-occupancy relationship in macroecology. While using the ebird large dataset to revisit the theme is interesting, multiple unresolved confounding factors exist, leaving the results **inadequate** to overturn the repeatedly confirmed abundancy-occupancy relationship.

https://doi.org/10.7554/eLife.95857.2.sa2

Abstract

In macroecology, a classic empirical observation has been positive relationships between local abundance and species' range, known as the abundance-occupancy relationships (AORs). The existence of this empirical relationship has informed both theory development and applied questions. Notably, the spatial neutral model of biodiversity predicts AORs. Yet, based on the largest known meta-analysis of 16,562,995 correlations from ~3 billion bird observations, this relationship was indistinguishable from zero. Further, in a phylogenetic comparative analysis, species range had no predictive power over the global mean abundance of 7,464 bird species. We suggest that publication and confirmation biases may have created AORs, an illusion of a 'universal' pattern. This nullification highlights the need for ecologists to instigate a credibility revolution like psychology, where many classic phenomena have been nullified.

Main

A positive interspecific relationship between abundance and distribution —abundanceoccupancy relationships (AORs) — is considered one of the most general and robust patterns in ecology (1–4). Sometimes referred to as a macroecological law (5, 6), the AOR asserts that empirically locally abundant species tend to be widely distributed, and conversely, locally rare species tend to be geographically restricted in their range. The mechanism driving this relationship was never proven, and it remains unresolved why species distribution should affect per-unit-area abundance (or *vice versa*). Nonetheless, the existence of a pervasive AOR has underpinned many practical applications in ecology and conservation (7), for example, setting harvest rates for fisheries (8), managing invasive species by restricting expansion rather than local elimination and identifying species at high risk of extinction in biodiversity inventories such as the IUCN Red List Criteria (9). Given the increasing human-induced land-use changes in the Anthropocene (10), concomitantly with increasing debate about global biodiversity change [cf. (11)], fully understanding the relationship between abundance and range size is increasingly important.

Many plausible biological mechanisms have been proposed for AORs, yet none of them has unequivocal support (*3, 4, 12, 13*). Among all mechanisms, it is noteworthy that a spatially explicit neutral model of biodiversity and biogeography can generate AORs (14, 15). Specifically, this macroecological 'null' model can produce a positive correlation between species range (or occupancy) and their per-unit-area local as well as total global abundance. This observation, in turn, supports the utility of neutral theory as a null model of community and macroecology (14). Although neutral theory may provide a biological null model, an additional null hypothesis is that AOR does not exist. Indeed, sampling bias can create AORs because locally rare species are more likely to be missed, resulting in an underestimation of range size or occupancy, thereby generating a positive relationship (13, 16). Yet, this sampling explanation has long been discarded as a plausible mechanism leading to observed patterns (2, 3, 17). This is because of substantial empirical evidence for positive interspecific relationships, including a meta-analysis of 279 effect sizes with an overall effect of r = 0.58 (or its Fisher's transformation: Zr = 0.66) in 2006 (1). It does not seem that sampling bias alone could explain this remarkably strong relationship.

Nonetheless, a large amount of variation does exist in empirical patterns of AORs, including strikingly negative relationships (12, 18–20). Some of the observed heterogeneity is likely to be due to different aspects of sampling, such as the number of species and spatial and temporal coverage (3, 4, 12). Also, other types of bias could generate artefactual AORs: namely 'confirmation bias', where sampling is prejudiced to support one's hypothesis and 'publication bias', where statistically significant relationships are preferentially reported and published. Although both biases are widespread, including in ecological studies (21–23), no studies so far systematically considered or quantified both biases in the context of AORs [cf. (1)].

Furthermore, there has, until recently, been a lack of large and methodologically consistent data resources, therefore leaving a traditional meta-analytic approach as the best available option for testing the validity and generality of the AOR.

A citizen science dataset to test AORs

Here, we use data from eBird — a global citizen science dataset aimed at counting birds — to quantify the relationship between local-scale (and global-scale) abundance and global-scale range size as a proxy for occupancy (AOR). This approach is similar to previous works [e.g, (16)]; they pointed out that the use of arbitrary cut-offs in many AOR studies can lead to artifactual positive AOR relationships). By examining this relationship across a global dataset, we aim to test whether the classic AOR pattern holds at a broader scale using citizen science data, which provides a more

comprehensive spatial coverage than traditional studies. Previous AOR studies often focused on local or regional scales, defining occupancy within specific patches or habitats. In contrast, our approach uses global range size to explore how generalizable AOR patterns are when scaled up to global datasets, providing insights into whether the same positive relationship persists across diverse environments and species distributions.

Large citizen science datasets collected for non-hypothesis-driven purposes are not random samples [see (24)], but they have the advantage of avoiding biases such as confirmation and publication bias. Also, using the eBird dataset allows us to estimate heterogeneity due to sampling intensity (e.g., the duration of a sampling event directly influences the number of species recorded). Specifically, we can quantify how AOR will change in relation to increases in species richness and sampling duration, both of which are predicted to reduce the magnitude of AORs (3, 4, 19).

For occupancy, we use global range size not only because global range size should be relatively stable — 'local' range sizes for one species could vary dramatically — but also because different types of occupancy measures were deemed to contribute less to the observation heterogeneity (25, 26). Fortunately, for birds, a large database of global range sizes has already been compiled (27). For abundance, we use two different measurements: local species counts and local mean density, as follows. First, we carry out the largest known meta-analysis by synthesizing correlations between global range sizes of 7,635 species and local species counts collected across 16,562,995 eBird checklists (resulting in 16,562,995 *Zr* values and corresponding sampling variances; **Fig. 1**). These checklists all included counts of each species present and the duration of observation (hereafter, effort time).

Second, we conduct a phylogenetically controlled comparative analysis, regressing species range sizes on 7,464 estimates of globally derived species' mean density, equivalent to mean local density (per 5-degree grid cell), estimated in earlier work (28) (see Methods for more details). Given the different potential biases mentioned before, we expected a more modest relationship in relation to that of the previous meta-analysis (r = 0.58; note that this relationship included many different taxa; if restricted to bird species, it was even stronger r = 0.74 or Zr = 0.95) (17). Also, although no such empirical evidence appears to exist, it seems feasible that in filling in an eBird checklist, some people may undercount common and widespread species while they may overcount rare and geographically restricted species. If this is the case, the relationship (AORs) could be further weakened. Yet, if such overcounting and undercounting were present, we expect it would introduce large heterogeneity into our dataset because that type of behaviour would not be consistent across all contributors, and they would sometimes result in negative AORs, increasing variability among the 16,562,995 *Zr* values.

Overwhelming support against AOR

Surprisingly, the overall (aggregated) relationship between local abundance and global occupancy was near-zero (r = 0.015), although this relationship was statistically significant due to our extremely large sample size (p = 0.0005, z = 2.805, $Z_r = b_{[\text{overall mean}]}$ = 0.015, 95% confidence interval, CI = [0.004, 0.025]; **Fig. 2**, **Table S1**). However, this significant relationship disappeared (r = 0.0009) once we controlled for species number and effort time (p = 0.863, z = 0.173, $Z_r = b_{[\text{overall mean}]}$ = 0.0009, 95% CI = [-0.0092, 0.0111]); both variables were statistically significant predictors of the effect. As expected, the increase in species number (modelled as the inverse of species number - 3, which is equivalent to sampling error for Z_r) and effort time on the natural log scale, decreased the strength of the relationship (sampling variance: $p < 0.0001$, z = 140.29; $b_{[\text{sampling variance}]}$ = 0.0147, 95% CI = [-0.0149, -0.0145]); ln(effort time): $p < 0.0001$, z = -183.45, $b_{[\ln(\text{effort time})]}$ = 0.230, 95% CI = [0.226, 0.233]; marginal R^2 = 5.1% for the model with these two predictors; (29); **Table S2**–**4**). These observations are consistent with the explanation that sampling protocols can create positive artifactual relationships between range and abundance.

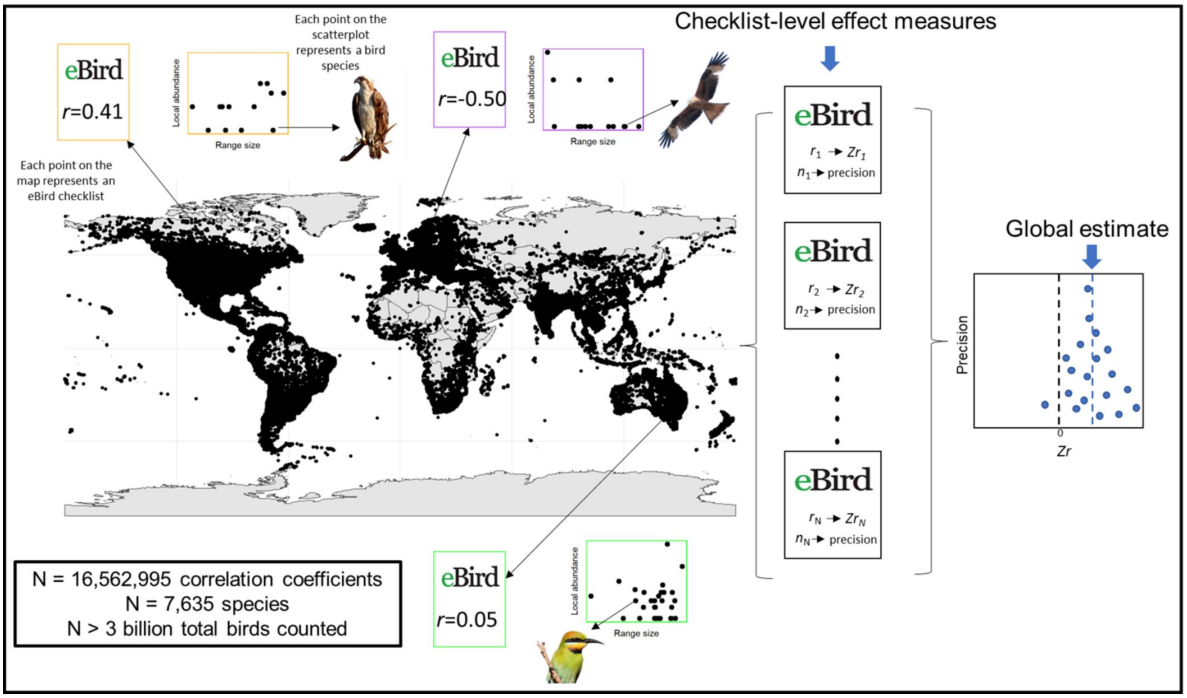

Figure 1.

A conceptual overview of our methods.

We aggregated individual eBird checklists across the world (shown on the map), represented by the three colored insets which show the relationship between global range size (x-axis) and local abundance (y-axis) and the associated correlation value. We then aggregated these checklist level measures for 16,562,995 eBird checklists into the largest-ever meta-analysis to find the global level relationship between global range size and local abundance.

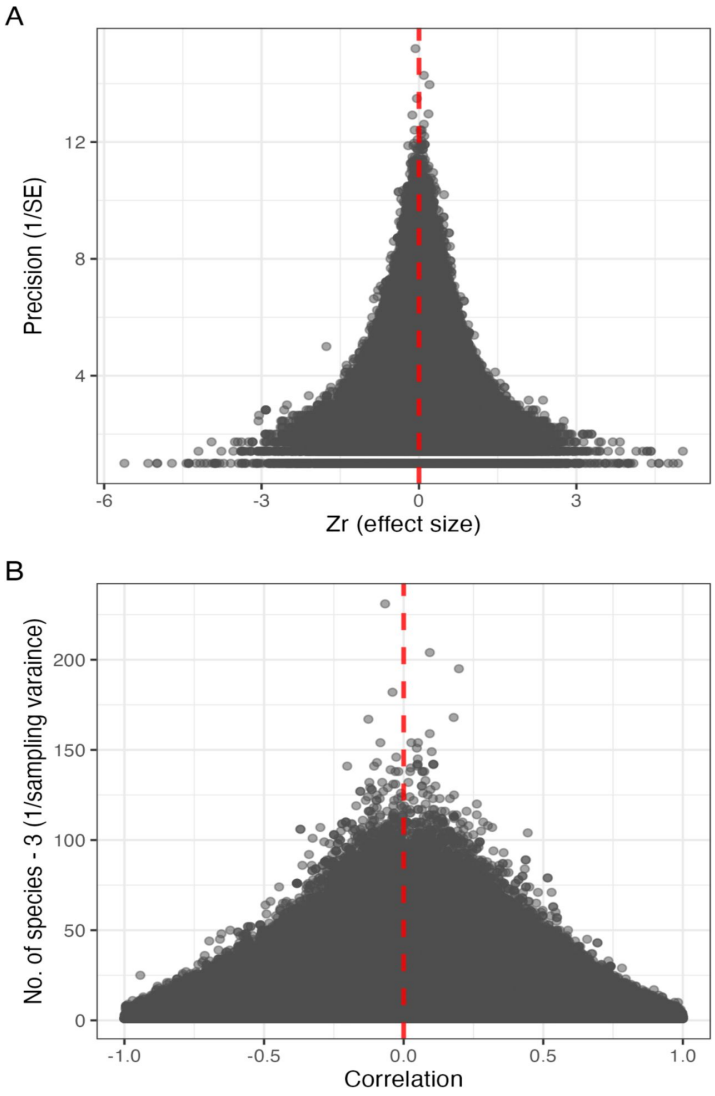

Figure 2.

Funnel plots.

(A) the relationship between 16,562,995 effect sizes (Fisher's; *x*-axis) and their precision (the square root of the inverse of the sampling variance; *y*-axis). (B) the relationship between 16,562,995 correlations based on 3,005,668,285 observations of 7,635 species (Pearson's correlation coefficients; *x*-axis) and the number of species - 3, which is the inverse of the sampling variances for Z_r (*y*-axis). Both plots consist of data points with the red dashed line indicating zero effect.

Even more remarkably, our meta-analysis suggested that the AOR is likely indistinguishable from zero even with a larger dataset because the observed heterogeneity among effect sizes was very small (i.e., most effect sizes were effectively zero after accounting for sample size). A measure of relative heterogeneity $I^2_{[total]}$ was 13.5%, meaning that 86.5% of all the observed variation (in **Fig. 2**) is due to sampling error, therefore, is neither biological nor ecological (country level; I^2 = 5.5%, σ^2 = 0.005; state level: I^2 = 6.3%, σ^2 = 0.005; effect-size level; I^2 = 1.5%, σ^2 = 0.001); in contrast, the average I^2 [total] across 86 ecological meta-analyses was approximately 92% (30), making our observed heterogeneity unusually low. Low relative heterogeneity, however, does not necessarily mean absolute heterogeneity is also low (31). We found the absolute heterogeneity, $\sigma^2_{[total]}$ = 0.011, approximately one-thirtieth of the heterogeneity ($\sigma^2_{[total]}$ = 0.323) found in the previous meta-analysis (1). Also, this is around one-tenth of the average heterogeneity ($\sigma^2_{[total]}$ = 0.125; median = 0.105), found in 31 meta-analyses in ecology and evolution (23). Overall, low relative and absolute heterogeneities indicate that our dataset of 16,562,995 effect sizes does not have much variability left to be explained despite our observations coming from many different locations across the globe and contributed by tens of thousands of individual birdwatchers. Importantly, we emphasize that this combination of zero effect and very small heterogeneity is only expected when a particular phenomenon is not real.

Moreover, our phylogenetic comparative analysis, which accounted for phylogenetic uncertainty (32), corroborated our meta-analytic results [cf. (33)]. The global range sizes had little predictive power on mean species density (both on log10; p = 0.808, $t_{99.6}$ = 0.0227, $b_{[slope]}$ = 0.0928, 95% CI = [-0.1615, 0.2068]; **Fig. 3**, **Table S5**). Taken together, our results provide overwhelming evidence against the fundamental relationship between species range and local abundance, while the results are consistent with this relationship as a sampling artifact. Nevertheless, our results are also consistent with previously published empirical evidence. This is because we have shown that relationships between global species ranges and local counts can be null, strongly negative, or strongly positive, which can be generated primarily by sampling (error) variance (shown in **Fig. 2**).

Lawless macroecology and non-neutral theory: implications

Our results demonstrate clearly that the AOR is not observed in a very large global dataset, with both applied and theoretical ramifications. First, we must reconsider fishing quotas, conservation priorities, and invasive species control strategies based on AORs [cf. (7)]. Second, it may be futile to pursue all ecological or biological mechanisms proposed for AORs [see (3, 13)]. We cannot exclude, however, the possibility of AORs occasionally emerging in some restricted areas because there was a small unexplained variance in the meta-analytic dataset. Most notably, our near-zero results with small heterogeneity suggest that contrary to earlier suggestions (14, 15), the spatial neutral model is not a suitable null model of macroecology. Within the neutral theoretical framework, AORs can be broken by local adaptation (an alternative hypothesis) (14). If local adaptation were to disrupt a predicted positive relationship (AOR), we would have observed substantial heterogeneity and a reduced relationship, not a near-zero relationship. This is because it is extremely unlikely that local adaptation and neutral processes are in a perfect balance, resulting in an exact-zero relationship with little heterogeneity. In other words, local adaptions are expected to create local specificities and global variability/heterogeneity; our metaanalysis did not find such variability.

We point out that any model of a positive AOR posits a mechanism that connects species range and local abundance on the one hand. Rabinowitz, on the other hand, effectively decoupled these two variables (34) although studies using her framework found positive correlations between species range and local abundance (35). Our results are consistent with this decoupling. By adding habit specificity to species range and abundance, she suggests seven forms of rarity, which could reflect different underlying macroecological mechanisms; for example, two forms of rarity are geographically restricted but locally abundant with narrow or broad habitat types. Unlike the

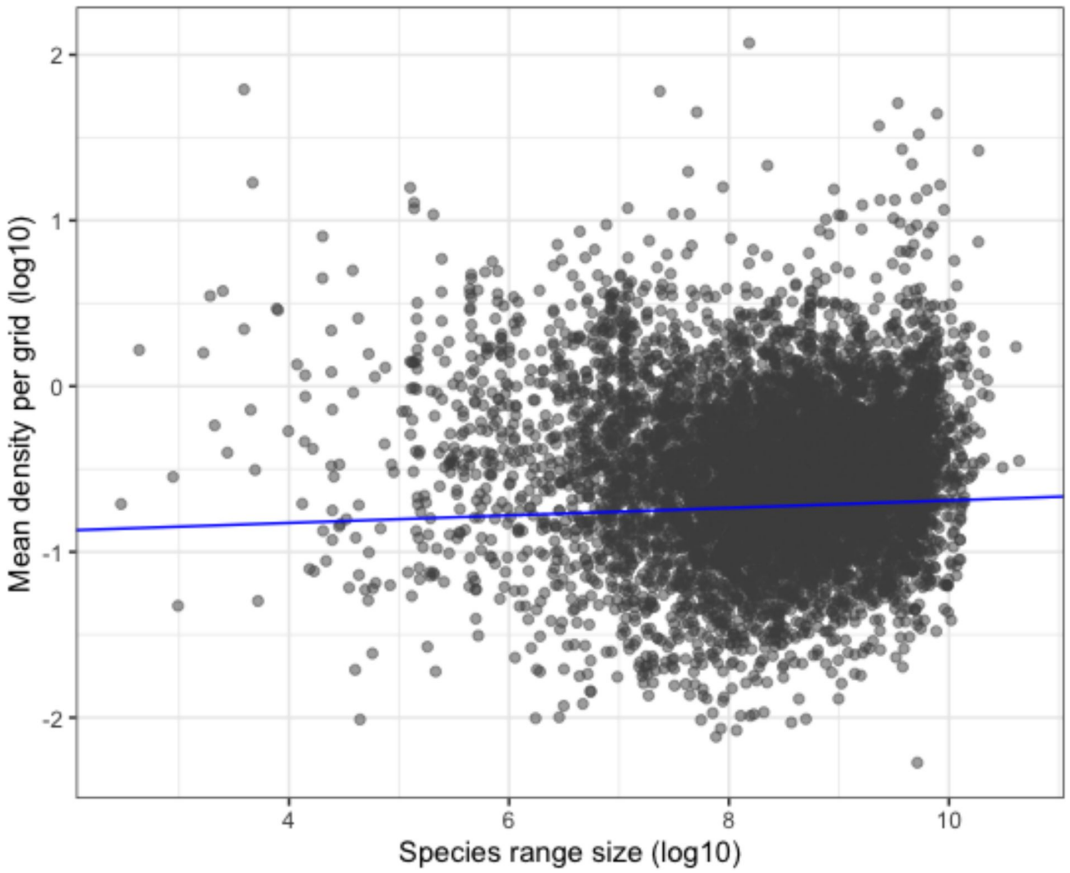

Figure 3.

The relationship between species average (mean) density and species range size.

We calculated the mean density of a species in 5-degree grids where species occurred (*y*-axis) while the species range size (*x*-axis) was estimated by the sum of the percentage occurrence of the species multiplied by the grid size (km^2) across all the 575 grids (7,464 species). The blue line indicates an average slope line from phylogenetic comparative models with 100 different posterior phylogenetic trees.

world created by the spatial neutral model, our results support many such 'rare' species (35). In this regard, it is no longer surprising that AORs do not exist. Therefore, we believe Rabinowitz's framework, rather than the AOR, has more empirical support from global-scale patterns of species abundance and provides a useful conceptual structure for future theoretical and applied work, although this line of work is still limited.

Potential limitations of current work and future work

The primary aim of our study was to demonstrate the potential of large-scale citizen science datasets, such as eBird, to revisit and refine longstanding macroecological relationships. These data, with their global coverage and unprecedented spatial resolution, offer unique opportunities to explore broad-scale patterns beyond the scope of traditional, localized studies [e.g., (4)], Although our findings challenge some long-held assumptions about the consistency of the abundance-occupancy relationship, our work only deals with interspecific AORs among birds, synthesizing observations from potentially heterogeneous locations, ecological contexts, and data quality. Therefore, we hope this work serves as we view this study as a foundation for further investigations that utilize such comprehensive datasets.

Future studies could delve deeper into specific ecological factors that may shape interspecific AORs if they do exist. For instance, investigating how islands might influence abundancedensity patterns could shed light on density release, where species on islands achieve higher densities due to reduced competition and predation. Additionally, exploring the impact of latitude and climate, such as how Rapoport's rule may lead to more extensive ranges and population sizes in temperate regions (9) could provide valuable insights into the variability of AORs across geographic and climatic gradients. Similarly, examining species-specific traits, including body size or wing morphology, may uncover correlations with range size and abundance. We further acknowledge that we did not account for anthropogenic changes in populations or range sizes in our analyses and, therefore, we included alien species without separating them from native ones. More precise range-size estimates would also improve the accuracy of AOR assessments since species range data are often overestimated due to the failure to capture gaps in actual distributions (36).

Beyond these biological and ecological factors, methodological refinements using citizen science data are also needed (37). Our approach, which relies on relative abundance measures, provides a starting point. While our approach relies on relative abundance measures as a starting point, more sophisticated methods are needed to account for known biases (e.g., differences in species detectability, observer experience) in citizen science data so as to enhance the precision of future macroecological studies. We therefore encourage further work to explore novel analytical approaches and statistical frameworks designed to handle these inherent biases, including variation in both observer effort and detectability across species and habitats. Such improvements should help clarify the conditions under which AORs may emerge, remain weak, or are fully decoupled.

A credibility revolution in ecology beyond biases and crises

Whilst we provided an explanation for the non-existence of AOR with our work's limitations in mind, it still feels hard to comprehend the extent of overestimation in the previous meta-analysis (r = 0.58 for all taxa; r = 0.74 for birds) (1, 17). We have shown that some bias may be due to sampling bias. However, we speculate that much of the overestimation originates from publication bias and confirmation bias, which is supported by mounting evidence from metaresearch studies (21–23). Although we do not have direct evidence, our eBird datasets are free from these two types of biases (i.e., birdwatchers generally do not think of the macroecological patterns that would later be tested with the data they submit), while the literature-based meta analyses are not. Regarding publication bias, the original meta-analysis of AOR states, "the failsafe number indicates that more than half a million unpublished null results would be required to nullify an effect of this magnitude" (1). Indeed, we provided much more

than a half million null effects to reach our null conclusion (**Fig. 2**). However, we should note that large datasets like eBird have other biases than publication or confirmation biases (24). For example, it is possible that by excluding checklists with a single 'X' (see Methods), we are preferentially removing abundant species as birdwatchers may report 'X' for more common species with high abundances.

A recent study reexamining 86 ecological and evolutionary meta-analyses demonstrated a 23% reduction in overall effects due to publication bias, turning 33 of 50 statistically significant meta-analytic conclusions (66%) into non-significant (23). Similarly, a study examining 83 topics in life sciences showed that the effect size of non-blind studies, which are at risk of confirmation bias, was twice as large as blinded counterparts protected against confirmation bias (21). Metaresearch on behavioral ecology identified 79 studies on nestmate recognition, 23 of which were conducted blind (22). Non-blind studies confirmed a hypothesis of no aggression towards nestmates nearly three times more often. It is possible that confirmation bias was at play in earlier AOR studies.

We finish with an intriguing parallel topic to AORs in psychology, where the current replication crisis started (38, 39). There have been over 100 studies, and many theoretical models support the hypothesis of 'ego depletion' where self-control is a finite resource, so self-control will decrease once it is exerted (40). The first meta-analysis of ego depletion, like AOR, suggested a very strong support for it (standardized mean difference, or $d = 0.62$). Yet a subsequent multi-lab replication found that ego-depletion does not exist and is so weak as to be negligible ($d = 0.04$) (41). Indeed, a series of multi-lab replications has indicated that several psychological phenomena, which were once believed to be real beyond a reasonable doubt, are too weak to be useful or are nonexistent (42). In ecology, recently collated large datasets collected for nonhypothesis-driven purposes offer a unique opportunity to revisit and retest longstanding ideas.

Taken together, we call for reexamining all ecological laws, rules, and patterns, as very few topics are free from sampling, confirmation, and publication biases [cf. (43)]. To counter such biases, we urgently require a 'credibility revolution', a more optimistic name for a replication crisis, turning this crisis into an opportunity to improve science. A credibility revolution in ecology, like in psychology, needs to embrace non-traditional to avoid confirmation and publication bias, such as pre-registration (44), registered reports (45), prospective and living meta-analyses, open synthesis communities (46), and big-team-science collaborations (47) involving community (citizen) scientists (37).

Methods

Quantifying abundance-occupancy relationship at the local-scale

We used the eBird dataset (48, 49) to assess the relationship between local-scale abundance and occupancy (i.e., global range size). eBird, launched in 2002 by the Cornell Lab of Ornithology, is a global citizen science project that enlists volunteer birdwatchers to submit 'checklists' of birds seen and/or heard while birdwatching. Data undergo a semi-automated filtering process before being entered into the dataset, and expert reviewers additionally review species (or counts of species) that surpass pre-set filters before being accepted into the dataset (50). Importantly, birdwatchers must indicate whether they are submitting a 'complete' checklist representing all birds that an individual birdwatcher was able to identify during their birdwatching outing. Further, birdwatchers can either submit the count of a species during their birding, or they can submit an 'X' to signify that a species was present but not estimate the number of individuals present during their birdwatching outing.

We downloaded the eBird basic dataset (version ebd_rel-May2020) and considered all eBird checklists between January 1st, 2005 and May 31st 2020. We then performed some quality assurance, applying an additional set of filters to the data, potentially removing any 'outliers' that could produce undue leverage on our results. The following filtering was completed [*sensu* (24, 51)]. We only included: (1) complete checklists; (2) checklists that were <240 minutes and >5 minutes; (3) checklists that travelled < 5km; and (4) checklists that travelled < 500 ha. Because birdwatchers will sometimes use an 'X' to signify presence, and this is most likely to happen for more abundant species, we excluded any checklist that had at least an "X" on it, as this could potentially influence the correlation between the abundance of a species and range size by disproportionately removing the most abundant species from the correlation. This exclusion aimed to ensure that correlations between local abundance and range size were not distorted by the lack of abundance data for highly observable, widespread species, and providing all species on a checklist with an abundance estimate maximizes the interpretability of the relative abundance measure in our work. We further only considered checklists that had at least ten species recorded on them, and a correlation test was performed only if we had range size data (see below) for a minimum of 4 species on the checklist.

We used range size maps from BirdLife International (27), using their global range, ignoring the differences between resident and breeding ranges. We chose to use the global range because of the difficulty of defining species occupancies using grid cells (i.e., almost infinite ways of defining occupancy) and the importance of using the entire species distribution range pointed out by earlier studies (e.g., (16)) due to sampling artifacts. When an eBird checklist met the aforementioned criteria, we performed a correlation test using Pearson's correlation coefficient from the *cor.test* function in *R* (52). Both the counts of every species and the range size were log-transformed before estimating a correlation (for a workflow, see **Fig. 1**). We obtained 16,562,995 correlations based on 3,005,668,285 individual bird observations, including 7,635 species. We note that we conducted all computational and statistical work using *R* and we created plots using the R package, *ggplot2* (53), patchwork (54) and their dependencies.

Meta-analysis of Big Data

We transformed correlations between species abundance and range into Fisher's Z o Z_r to unbound and calculated sampling variance for each Z_r value; note that the inverse of the sampling variance of Z_r is N (the number of species in a checklist) - 3 (see **Fig 1**). We used the *R* package, *asreml* (55) to run a multilevel random-effects model (56); note the *asreml* is a commercial package, so it is not free. Our large meta-analyses with ~17 million effect sizes were only able to run with *asreml* given the computational time required for such a large dataset. We had 'country' (245 levels) and state code (2,871 levels) as random factors in the model to control for non-independence. In addition, to quantify the variance component for these two clustering factors and also at the level of effect sizes (16,562,995 levels), we modelled 'units' (the effect size level random effect or residuals) in the *asreml* function with 'the number of species - 3' as the 'weights' argument and *asr_gaussian(dispersion = 1)* as the 'family' argument. We also obtained the multilevel versions of I^2 (30, 57) to obtain relative heterogeneity for our meta-analytic model (**Table S1**; also, all models used in this study are summarized in **Table S6**).

To gauge the impacts of potential biases, we fitted two moderators: 1) the z-transformed version of ln(checklist duration) as a surrogate for the amount of effort for observation and 2) sampling variance, which is usually used to detect publication bias, more specifically, small study bias where effect sizes from small studies can create 'funnel asymmetry', creating bias in meta-analytic overall mean (58) (cf. **Fig. 2**). We ran two uni-moderator models and one multimoderator model with both moderators (three meta-regression models in total; **Table S2**–**4**). We estimated the multilevel model versions of R^2 (29).

Quantifying the abundance-occupancy relationship at the macro-scale

To corroborate our local-level analysis described above, we quantified an additional macro-scale analysis of the relationship between abundance (i.e., density) and occupancy (global range size). For this, we used data from a recently published analysis of global abundances for birds within 5-degree grid cells (28). This dataset was derived by integrating expert-derived abundance measures with a large, less structured global citizen science dataset using a multiple-imputation technique to estimate density within 5-degree grids for 9,700 bird species (575 girds). We used these predicted density estimates from each grid cell and, for each species, took the mean of all density estimates in the grid cells for which a species was found. This mean density was then our measure of macro-scale abundance. For our measure of occupancy, we used a summation of all range sizes for the grids a species was found in, calculated by using range maps from BirdLife International focusing on the entire extent of a species' extant range, ignoring the effect of transient species. Our analysis incorporated a total of 7,464 species of bird species, corresponding to the species for which we had both range maps and estimated density, along with phylogenetic information included in (59).

Phylogenetic comparative analysis

To statistically test whether there was an effect of abundance and occupancy at the macro-scale, we used phylogenetic comparative analysis. This analysis also addresses the issue of positive interspecific AORs potentially arising from not accounting for phylogenetic relatedness among species examined (9). We used avian phylogeny from Jez et al. (59), and analysed 100 phylogenetic trees using the R function *phylolm* (60). Resulting estimates from the 100 models were merged using Rubin's rules, as described in (32), to obtain current estimates and errors that accounted for phylogenetic uncertainty (**Table S5**); we implemented this procedure using the R function *miInference* from the *norm2* package (61).

Data and materials availability

All data, code, and materials are available online unless they are too large to be archived (*https://github.com/itchyshin/AORs*), and they are archived in a public repository, Zenodo (*https://doi.org/10.5281/zenodo.14019900*).

Acknowledgements

We thank Szymek Drobniak for helping run large meta-analytic models on a cluster computer system. We are also grateful to Malgorzata Lagisz, Tim Parker, Daniel Noble, Tim Blackburn, and Diana Bowler, and Luís Borda de Agua for their comments on earlier versions of this manuscript.

Table S1.

Results of the intercept meta-analytic model using the *asreml* function

Effect	Name	Effect	SE	z value
Fixed	Intercept	0.0145081	5.17e-03	2.80459
Random	Country	-0.528	5.76e-04	7.915738
Random	State code	0.005161983	1.96e-04	26.331084
Random	Effect size (units)	0.001597069	2.22e-05	71.864656

Table S2.

Results of the meta-regression model with 'checklist duration' as a moderator, using the *asreml* function

Effect	Name	Effect	SE	z value
Fixed	Intercept	0.02314897	5.16E-03	4.490484
Fixed	z(ln(checklist duration))	-0.019646	7.20E-05	-272.88526
Random	Country	0.00451859	5.72E-04	7.894702
Random	State code	0.00519698	1.97E-04	26.372854
Random	Effect size (units)	0.00127717	2.20E-05	57.961243

Table S3.

Results of the meta-regression model with 'sampling variance' as a moderator, using the *asreml* function

Effect	Name	Effect	SE	z value
Fixed	Intercept	-0.0171537	5.23E-03	-3.279982
Fixed	Sampling variance	0.36149029	1.47E-03	245.747022
Random	Country	0.00466502	5.89E-04	7.91356
Random	State code	0.00530528	2.01E-04	26.4252
Random	Effect size (units)	0.00143218	2.21E-05	64.76545

Table S4.

Results of the meta-regression model with 'checklist duration' and 'sampling variance' as moderators, using the *asreml* function

Effect	Name	Effect	SE	z value
Fixed	Intercept	0.00089738	5.19E-03	0.1728713
Fixed	z(ln(checklist duration))	-0.0147034	8.01E-05	-183.44948
Fixed	Sampling variance	0.22952897	1.64E-03	140.287413
Random	Country	0.004581054	5.80E-04	7.896078
Random	State code	0.005273559	2.00E-04	26.418513
Random	Effect size (units)	0.001272852	2.20E-05	57.801132

Effect	Name	Effect	SE	t value (df)
Fixed	Intercept	-0.91553	1.6476	-0.556 (1776.3)
Fixed	log10(range size)	0.022645	0.092832	0.244 (99.6)

Table S5.

Results of the phylogenetic regression using the *phylolm* and *miInference* functions

Model (results)	Fromula	Variance components (normally distributed with the mean of 0 and given σ^2 values
Table S1	$Zr_i = \beta_0 + \text{County}_{k[i]} + \text{State-code}_{j[i]} + \text{Effect-size}_i$	$\text{County}_k \sim \mathcal{N}(0, \sigma^2_{country})$ $\text{State-code}_j \sim \mathcal{N}(0, \sigma^2_{State-code})$ $\text{Effect-size}_i \sim \mathcal{N}(0, \sigma^2_{Effect-size})$ $\text{Sampling-error}_i \sim \mathcal{N}(0, \sigma^2_{Sampling-error_i})$
Table S2	$Zr_i = \beta_0 + \beta_1 * \text{z(ln(checklist duration))}_i + \text{County}_{k[i]} + \text{State-code}_{j[i]} + \text{Effect-size}_i$	$\text{County}_k \sim \mathcal{N}(0, \sigma^2_{country})$ $\text{State-code}_j \sim \mathcal{N}(0, \sigma^2_{State-code})$ $\text{Effect-size}_i \sim \mathcal{N}(0, \sigma^2_{Effect-size})$ $\text{Sampling-error}_i \sim \mathcal{N}(0, \sigma^2_{Sampling-error_i})$
Table S3	$Zr_i = \beta_0 + \beta_1 * \text{Sampling-variance}_i + \text{County}_{k[i]} + \text{State-code}_{j[i]} + \text{Effect-size}_i$	$\text{County}_k \sim \mathcal{N}(0, \sigma^2_{country})$ $\text{State-code}_j \sim \mathcal{N}(0, \sigma^2_{State-code})$ $\text{Effect-size}_i \sim \mathcal{N}(0, \sigma^2_{Effect-size})$ $\text{Sampling-error}_i \sim \mathcal{N}(0, \sigma^2_{Sampling-error_i})$
Table S4	$Zr_i = \beta_0 + \beta_1 * \text{z(ln(checklist duration))}_i + \beta_2 * \text{Sampling-variance}_i + \text{County}_{k[i]} + \text{State-code}_{j[i]} + \text{Effect-size}_i$	$\text{County}_k \sim \mathcal{N}(0, \sigma^2_{country})$ $\text{State-code}_j \sim \mathcal{N}(0, \sigma^2_{State-code})$ $\text{Effect-size}_i \sim \mathcal{N}(0, \sigma^2_{Effect-size})$ $\text{Sampling-error}_i \sim \mathcal{N}(0, \sigma^2_{Sampling-error_i})$
Table S5	$\text{Abundance}_i = \beta_0 + \beta_1 * \text{log10(range size)} + \text{Error}_i$	$\text{Error}_i \sim \mathcal{N}(0, \sigma^2_{error}\mathbf{A})$

Table S6.

Notations of statistical models used in this study (results of these models are in Table S1–5)

Additional information

Funding

Australian Research Council Discovery Project Grant, DP210100812 (SN)

Author contributions

Conceptualization: SN, WKC & CTC

Methodology: SN, WKC & CTC

Investigation: SN, WKC & CTC

Visualization: SN & CTC

Project administration: SN

Writing - original draft: SN, WKC & CTC

Writing - review & editing: SN, WKC & CTC

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Reviewer #1 (Public review):

Summary:

This article presents an analysis that challenges established abundance-occupancy relationships (AORs) by utilizing the largest known bird observation database. The analysis yields contentious outcomes, raising the question of whether these findings could potentially refute AORs.

Strengths:

The study employed an extensive aggregation of datasets to date to scrutinize the abundance-occupancy relationships (AORs).

Weaknesses:

The authors should thoroughly address the correlation between checklist data and global range data, ensuring that the foundational assumptions and potential confounding factors are explicitly examined and articulated within the study's context.

In the revision, the authors have refined their findings to birds and provided additional clarifications and discussion. However, the primary concerns raised by reviewers remain inadequately addressed. My main concern continues to be whether testing AOR at a global scale is meaningful given the numerous confounding factors involved. With the current data

and analytical approach, these confounders appear inseparable. The study would be significantly strengthened if the authors identified specific conditions under which AORs are valid.

https://doi.org/10.7554/eLife.95857.2.sa1

Author response:

The following is the authors' response to the original reviews

> ***Public Reviews:***
>
> ***Reviewer #1 (Public Review):***
>
> *Summary:*
>
> *This article presents a meta-analysis that challenges established abundance-occupancy relationships (AORs) by utilizing the largest known bird observation database. The analysis yields contentious outcomes, raising the question of whether these findings could potentially refute AORs.*

We thank the Reviewer for their positive comments.

> *Strengths:*
>
> *The study employed an extensive aggregation of datasets to date to scrutinize the abundance-occupancy relationships (AORs).*

We thank the Reviewer for their positive comments.

> *Weaknesses:*
>
> *While the dataset employed in this research holds promise, a rigorous justification of the core assumptions underpinning the analytical framework is inadequate. The authors should thoroughly address the correlation between checklist data and global range data, ensuring that the foundational assumptions and potential confounding factors are explicitly examined and articulated within the study's context.*

We thank the Reviewer for these comments. We agree that more justification and transparency is needed of the core assumptions that form the foundation of our methods. In our revised version, we have taken the following steps to achieve this:

- Altered the title to be more explicit about the core assumptions, which now reads: "Local-scale relative abundance is decoupled from global range size"

- We have added more details on why and how we treat global range size as a measure of 'occupancy.'

- We have added a section that discusses the limitations of using eBird relative abundance

> ***Reviewer #2 (Public Review):***
>
> *Summary:*
>
> *The goal is to ask if common species when studied across their range tend to have larger ranges in total. To do this the authors examined a very large citizen science database which gives estimates of numbers, and correlated that with the total range size, available*

> *from Birdlife. The average correlation is positive but close to zero, and the distribution around zero is also narrow, leading to the conclusion that, even if applicable in some cases, there is no evidence for consistent trends in one or other direction.*

We thank the Reviewer for these comments.

> *Strengths:*
>
> *The study raises a dormant question, with a large dataset.*

We thank the Reviewer for these comments. We intended to take a longstanding question and attempt to apply novel datasets that were not available mere decades ago. While we do not imply that we have 'solved' the question, we hope this work highlights the potential for further interrogation using these large datasets.

> *Weaknesses:*
>
> *This study combines information from across the whole world, with many different habitats, taxa, and observations, which surely leads to a quite heterogeneous collection.*

We agree that there is a heterogeneous collection of data across many habitats, taxa, and observations. However, rather than as a weakness, we see this as a significant strength. Our work assumes we are averaging over this variability to assess for a large-scale pattern in the relationship - something that was potentially a limitation of previous work, as these large datasets were often focused on particular contexts (e.g., much work focused solely on the UK), which we believe could limit some of the generalizability of the previous work. However, the reviewer makes a fair point in regard to the heterogeneity of data collection. We have now added some text in the discussion which is explicit about this - see the new section named "Potential limitations of current work and future work —although our findings challenge some long-held assumptions about the consistency of the abundance-occupancy relationship, our work only deals with interspecific AORs among birds, synthesizing observations of potentially heterogeneous locations, context and quality".

> *First, scale. Many of the earlier analyses were within smaller areas, and for example, ranges are not obviously bounded by a physical barrier. I assume this study is only looking at breeding ranges; that should be stated, as 40% of all bird species migrate, and winter limitation of populations is important. Also are abundances only breeding abundances or are they measured through the year? Are alien distributions removed?*
>
> *Second, consider various reasons why abundance and range size may be correlated (sometimes positively and sometimes negatively) at large scales. Combining studies across such a large diversity of ecological situations seems to create many possibilities to miss interesting patterns. For example:*
>
> *(1) Islands are small and often show density release.*

See comment below.

> *(2) North temperate regions have large ranges (Rapoport's rule) and higher population sizes than the tropics.*

See comment below.

> *(3) Body size correlates with global range size (I am unsure if this has recently been tested but is present in older papers) and with density. For example, cosmopolitan*

> *species (barn owl, osprey, peregrine) are relatively large and relatively rare.*

See comment below.

> *(4) In the consideration of alien species, it certainly looks to me as if the law is followed, with pigeon, starling, and sparrow both common and widely distributed. I guess one needs to make some sort of statement about anthropogenic influences, given the dramatic changes in both populations and environments over the past 50 years.*

See comment below. We also added a sentence in the methods that highlighted we did not remove alien ranges and provided reasons why. Still, we do acknowledge the dramatic changes in populations and environments over the past 50 years (see the new section "Potential limitations of current work and futur work")

> *(5) Wing shape correlates with ecological niche and range size (e.g. White, American Naturalist). Aerial foraging species with pointed wings are likely to be easily detected, and several have large ranges reflecting dispersal (e.g. barn swallow).*

We agree that all of the points above are interesting data explorations. As said above, our main purpose was to highlight the potential for further interrogation using these large datasets. However, we have added some additional text in the discussion that explicitly mentions/encourages these additional data explorations. We hope people will pick up on the potential for these data and explore them further.

> *Third, biases. I am not conversant with ebird methodology, but the number appearing on checklists seems a very poor estimate of local abundance. As noted in the paper, common species may be underestimated in their abundance. Flocking species must generate large numbers, skulking species few. The survey is often likely to be in areas favorable to some species and not others. The alternative approach in the paper comes from an earlier study, based on ebird but then creating densities within grids and surely comes with similar issues.*

We agree that if we were interested in the absolute abundance of a given species, the local number on an eBird checklist would be a poor representation. However, our study aims not to estimate absolute abundance but to examine relative abundance among species on each checklist. By focusing on relative abundance, we leverage eBird data's strengths in detecting the presence and frequency of species across diverse locations and times, thereby capturing community composition trends that can provide meaningful insights despite individual checklist biases. This approach allows us to assess the comparative prominence of species in the community as reported by the observer, providing a consistent metric of relative abundance. Despite detectability biases, the structure of eBird checklists reflects the observer's encounter rates with each species under similar conditions, offering a valuable snapshot of relative species composition across sites and times. The key to our assumption is that these biases discussed are not directional and, therefore, random throughout the sampling process, which would translate to no 'real' bias in our effect size of interest.

> *Range biases are also present. Notably, tropical mountain-occupying species have range sizes overestimated because holes in the range are not generally accounted for (Ocampo-Peñuela et al., Nature Communications). These species are often quite rare, too.*

We thanks the reviewer for pointing to this issue and reference. We included a discussion on these biases in our limitations section and reference Ocampo-Peñuela et al. to emphasize the need for improved spatial resolution in range data for more accurate AOR assessments."More

precise range-size estimates would also improve the accuracy of AOR assessments, since species range data are often overestimated due to the failure to capture gaps in actual distributions ”

> *Fourth, random error. Random error in ebird assessments is likely to be large, with differences among observers, seasons, days, and weather (e.g. Callaghan et al. 2021, PNAS). Range sizes also come with many errors, which is why occupancy is usually seen as the more appropriate measure.*
>
> *If we consider both range and abundance measurements to be subject to random error in any one species list, then the removal of all these errors will surely increase the correlation for that list (the covariance shouldn't change but the variances will decrease). I think (but am not sure) that this will affect the mean correlation because more of the positive correlations appear 'real' given the overall mean is positive. It will definitely affect the variance of the correlations; the low variance is one of the main points in the paper. A high variance would point to the operation of multiple mechanisms, some perhaps producing negative correlations (Blackburn et al. 2006).*

We agree random errors can affect estimates, but as we wrote above, random errors, regardless of magnitudes, would not bias estimates. After accounting for sampling error (a part of random errors), little variance is left to be explained as we have shown in the MS. This suggests that many of the random errors were part of the sampling errors. And this is where meta-analysis really shines.

> *On P.80 it is stated: "Specifically, we can quantify how AOR will change in relation to increases in species richness and sampling duration, both of which are predicted to reduce the magnitude of AORs" I haven't checked the references that make this statement, but intuitively the opposite is expected? More species and longer durations should both increase the accuracy of the estimate, so removing them introduces more error? Perhaps dividing by an uncertain estimate introduces more error anyway. At any rate, the authors should explain the quoted statement in this paper.*
>
> *It would be of considerable interest to look at the extreme negative and extreme positive correlations: do they make any biological sense?*

Extremely high correlations would not make any biological sense if these observations were based on large sample sizes. However, as shown in Figure 2, all extreme correlations come from small sample sizes (i.e., low precision), as sampling theory expects (actually our Fig 2 a text-book example of the funnel shape). Therefore, we do not need to invoke any biological explanations here.

> *Discussion:*
>
> *I can see how publication bias can affect meta-analyses (addressed in the Gaston et al. 2006 paper) but less easily see how confirmation bias can. It seems to me that some of the points made above must explain the difference between this study and Blackburn et al. 2006's strong result.*

We agree. Now, we extended an explanation of why confirmation bias could result in positive AOR. Yet, we point out confirmation bias is a very common phenomena which we cite relevant citations in the original MS. The only way to avoid confirmation bias is to conduct a study blind but this is not often possible in ecological work.

“Meta-research on behavioural ecology identified 79 studies on nestmate recognition, 23 of which were conducted blind. Non-blind studies confirmed a hypothesis of no aggression

towards nestmates nearly three times more often. It is possible that confirmation bias was at play in earlier AOR studies."

> *Certainly, AOR really does seem to be present in at least some cases (e.g. British breeding birds) and a discussion of individual cases would be valuable. Previous studies have also noted that there are at least some negative and some non-significant associations, and understanding the underlying causes is of great interest (e.g. Kotiaho et al. Biology Letters).*

We agree. And yes, we pointed out these in our introduction.

> ***Reviewer #3 (Public Review):***
>
> *Summary:*
>
> *This paper claims to overturn the longstanding abundance occupancy relationship.*
>
> *Strengths:*
>
> *(1) The above would be important if true.*
>
> *(2) The dataset is large.*

We have clarified this point by changing the title to emphasize that we do not suggest overturning AORs entirely but instead provide a refined view of the relationship at a global scale. Our results suggest a weaker and more context-dependent AOR than previously documented. We hope our revised title and additional clarifications in the text convey our intent to contribute to a more nuanced understanding rather than a whole overturning of the AOR framework.

> *Weaknesses:*
>
> *(1) The authors are not really measuring the abundance-occupancy relationship (AOR). They are measuring abundance-range size. The AOR typically measures patches in a metapopulation, i.e. at a local scale. Range size is not an interchangeable notion with local occupancy.*

We have refined this in our revision to be more explicitly focused on global range size. However, we note that the classic paper by Bock and Richlefs (1983, Am Nat) also refers to global (species entire) range size in the context of the AOR. Importantly, Bock and Richlefs pointed out the importance of using species' entire ranges; without such uses, there will be sampling artifacts creating positive AORs when using arbitrary geographical ranges, which were used in some studies of AORs. So we highlight that our work is well in line with the previous work, allowing us to question the longstanding macroecological work. One of the issues of AOR has been how to define occupancy and global range size, which provides a relatively ambiguous measure, which is why we used this measure.

> *(2) Ebird is a poor dataset for this. The sampling unit is non-standard. So abundance can at best be estimated by controlling for sampling effort. Comparisons across space are also likely to be highly heterogenous. They also threw out checklists in which abundances were too high to be estimated (reported as "X"). As evidence of the biases in using eBird for this pattern, the North American Breeding Bird Survey, a very similar taxonomic and geographic scope but with a consistent sampling protocol across space does show clear support for the AOR.*

Yes, we agree the sampling unit is non-standard. However, this is a significant strength in that it samples across much heterogeneity (as discussed in response to Reviewer 2, above). We were interested in relative abundance and not direct absolute abundance per se, which is accurate, especially since we did control for sampling effort.

We appreciate the reviewer's attention to our data selection criteria. We excluded checklists containing 'X' entries to minimize biases in our abundance estimates. The 'X' notation is often used for the most common species, reflecting the observer's identification of presence without specifying a count. This approach was chosen to avoid disproportionately inflating presence data for these abundant species, which could distort the relative abundance calculations in our analysis. By excluding such checklists, we aimed to retain consistency and ensure that local abundance estimates were representative across all species on each checklist. We have revised our manuscript to clarify this methodological choice and hope this explanation addresses the reviewer's concern. We modified our text in the methods to make the entries 'X' clearer (see the Method section).

> *(3) In general, I wonder if a pattern demonstrated in thousands of data sets can be overturned by findings in one data set. It may be a big dataset but any biases in the dataset are repeated across all of those observations.*

Overturning a major conclusion requires careful work. This paper did not rise to this level.

We appreciate the reviewer's caution regarding broad conclusions based on a single dataset, even one as large as eBird. Our intention was not to definitively overturn the abundance-occupancy relationship (AOR) but to re-evaluate it with the most extensive and globally representative dataset currently available. We recognise that potential biases in citizen science data, such as observer variation, may influence our findings, and we have taken steps to address these in our methodology and limitations sections. We see this work as a contribution to an ongoing discourse, suggesting that AOR may be less universally consistent than previously believed, mainly when tested with large-scale citizen science data. We hope this study will encourage additional research that tests AORs using other expansive datasets and approaches, further refining our understanding of this classic macroecological relationship. However, we have left our broad message about instigating credible revolution and also re-examining ecological laws.

> ***Recommendations for the authors:***
>
> ***Reviewer #1 (Recommendations For The Authors):***
>
> *(1) The investigation focuses solely on interspecific relationships among birds; thus, the extrapolation of these conclusions to broader ecological contexts requires further validation.*

We have now added this point to our new section: "Although our findings challenge some long-held assumptions about the consistency of the abundance-occupancy relationship, our work only deals with interspecific AORs among birds, so we hope this work serves as a foundation for further investigations that utilize such comprehensive datasets."

> *(2) The rationale for combining data from eBird - a platform predominantly representing individual observations from urban North America - with the more globally comprehensive BirdLife International database needs to be substantiated. The potential underrepresentation of global abundance in the eBird checklist data could introduce a sampling bias, undermining the foundational premises of AORs.*

We agree with the limitation of ebird sampling coverage, but it should not bias our results. In statistical definitions, bias is directional, and if not directional, it will become statistical noise, making it difficult to detect the signal. In fact, our meta-analyses adjust what statisticians call sampling bias and it is the strength of meta-analysis.

> *(3) In the full mixed-effect model, checklist duration and sampling variance (inversely proportional to sample size N) are treated as fixed effects. However, these variables are likely to be negatively correlated, which could introduce multicollinearity, inflating standard errors and diminishing the statistical significance of other factors, such as the intercept. This calls into question the interpretation of insignificance in the results.*

Multicollinearity is an issue with sample sizes. For example, with small datasets, correlations of 0.5 could be an issue, and such an issue would usually show up as a large SE. We do not have such an issue with ~ 17 million data points. Please refer to this paper.

Freckleton, Robert P. "Dealing with collinearity in behavioural and ecological data: model averaging and the problems of measurement error." *Behavioral Ecology and Sociobiology* 65 (2011): 91-101.

> *(4) The observed low heterogeneity may stem from discrepancies in sampling for abundance versus occupancy, compounded by uncertainties in reporting behavior.*

If we assume everybody underreports common species or overreports rare species, this could happen. However, such an assumption is unlikely. If some people report accurately (but not others), we should see high heterogeneity, which we do not observe). We have touched upon this point in our original MS.

> *(5) The contribution and implementation of phylogenetic comparative analysis remain ambiguous and were not sufficiently clarified within the study.*

We need to add more explanation for the global abundance analysis

“To statistically test whether there was an effect of abundance and occupancy at the macro-scale, we used phylogenetic comparative analysis. This analysis also addresses the issue of positive interspecific AORs potentially arising from not accounting for phylogenetic relatedness among species examined ”

> *(6) The use of large N checklists could skew the perceived rarity or commonality of species, potentially diminishing the positive correlation observed in AORs. A consistent observer effect could lead to a near-zero effect with high precision.*

Regardless of the number of N species in checklists (seen in Fig 2), correlations are distributed around zero. This means there is nothing special about large N checklists.

> *(7) The study should acknowledge and discuss any discrepancies or deviations from previous literature or expected outcomes.*

We felt we had already done this as we discussed the previous meta-analysis and what we expected from this meta-analysis. Nevertheless, we have added some relevant sentences in the new version of MS.

> *In addition to these major points, there are several minor concerns:*

> *(1) Figure 2B lacks discussion, and the metric for the number of observations is not clarified. Furthermore, the labeling of the y-axis appears to be incorrect.*

Thank you very much for pointing out this shortcoming. Now, the y-axis label has been fixed and we mention 2B in the main text.

> *(2) The study should provide a clear, mathematical expression of the multilevel random effect models for greater transparency.*

Many thanks for this point, and now we have added relevant mathematical expressions in Table S6.

> *(3) On Line 260, the term "number of species" should be refined to "number of species in a checklist," ideally represented by a formula for precision.*

This ambiguity has been mended as suggested.

> *Please provide the data and R code linked to the outputs.*

The referee must have missed the link (https://github.com/itchyshin/AORs) in our original MS. In addition to our GitHub repository link, we now have added a link to our Zenodo repository (https://doi.org/10.5281/zenodo.14019900).

> ***Reviewer #3 (Recommendations For The Authors):***
>
> *The authors cite Rabinowitz's 7 forms of rarity paper as a suggestion that previous findings also break the AOR. In fact empirical studies of the 7 forms of rarity typically find that all three forms of rareness vs commonness are heavily correlated (e.g. Yu & Dobson 2000).*

We thank the reviewer for drawing attention to Yu & Dobson (2000) and similar studies that find positive correlations among the axes of rarity. Ref 3 is correct in that Rabinowitz's (1981) framework does not require that local abundance and geographic range size be uncorrelated for every species; instead, it highlights conceptual scenarios where a species may be common locally yet have a restricted distribution (or vice versa).

Empirical analyses such as Yu & Dobson (2000) show that, on average, these axes can be correlated, which *may* align with conventional AOR findings in some taxonomic groups. However, Rabinowitz's key insight was that exceptions do occur, so these exceptions demonstrate that strong positive AORs may not be universally applicable. Our results do not claim that Rabinowitz's framework "breaks" the AOR outright; instead, we use it to underscore that local abundance can, in principle, be "decoupled" from global occupancy. Whether the correlation found by Yu & Dobson (2000) implies a positive AOR, requires a detailed simulation study, which is an interesting avenue for future research.

Thus, citing Rabinowitz serves to highlight the potential heterogeneity and complexity of abundance–occupancy relationships rather than to refute every positive correlation reported in the literature. Our findings suggest that when examined at large spatiotemporal scales (with unbiased sampling), the overall AOR signal may be less robust than traditionally believed. This is consistent with Rabinowitz's view that local abundance and global range can vary along independent axes. Now we added

"Although studies using her framework found positive correlations between species range and local abundance."

https://doi.org/10.7554/eLife.95857.2.sa0