RESEARCH ARTICLE

Large-scale spatial variability in urban tolerance of birds

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Abstract

1. Quantifying intraspecific and interspecific trait variability is critical to our understanding of biogeography, ecology and conservation. But quantifying such variability and understanding the importance of intraspecific and interspecific variability remain challenging. This is especially true of large geographic scales as this is where the differences between intraspecific and interspecific variability are likely to be greatest.

2. Our goal is to address this research gap using broad-scale citizen science data to quantify intraspecific variability and compare it with interspecific variability, using the example of bird responses to urbanization across the continental United States.

3. Using more than 100 million observations, we quantified urban tolerance for 338 species within randomly sampled spatial regions and then calculated the standard deviation of each species' urban tolerance.

4. We found that species' spatial variability in urban tolerance (i.e. standard deviation) was largely explained by the variability of urban cover throughout a species' range ($R^2 = 0.70$). Variability in urban tolerance was greater in species that were more tolerant of urban cover (i.e. the average urban tolerance throughout their range), suggesting that generalist life histories are better suited to adapt to novel anthropogenic environments. Overall, species differences explained most of the variability in urban tolerance across spatial regions.

5. Together, our results indicate that (1) intraspecific variability is largely predicted by local environmental variability in urban cover at a large spatial scale and (2) interspecific variability is greater than intraspecific variability, supporting the common use of mean values (i.e. collapsing observations across a species' range) when assessing species–environment relationships. Further studies, across

different taxa, traits and species–environment relationships are needed to test the role of intraspecific variability, but nevertheless, we recommend that when possible, ecologists should avoid using discrete categories to classify species in how they respond to the environment.

KEYWORDS
avian, interspecific variability, intraspecific variability, urban ecology

1 | INTRODUCTION

Interspecific differences in species–environment relationships can sometimes be explained by traits, which can be associated with adaptive capacity or flexibility (Beever et al., 2016). For instance, differences in species traits or characteristics (e.g. body size, habitat or diet generalism, dispersal ability) can translate into differences in species–environment relationships (trait–environment relationships). Commonly, trait-based analyses are performed by collapsing the variation within a species—measured across its distribution range or at least from multiple populations—into a single value (Bolnick et al., 2011; Violle et al., 2012). For example, thermal tolerance (i.e. a value used to capture the varied responses in how species responds to an abiotic variable such as temperature) of birds or butterflies is often measured as the mean value of temperature throughout a species range (Devictor et al., 2012), or pH tolerance of leaves is measured as a mean at the species level (Cornelissen et al., 2011). Similarly, a species' habitat preference, or use, is often categorized as a single categorical variable (e.g. in species distribution models), assuming species respond to the environment similarly across their ranges (e.g. Storchová & Hořák, 2018). Interspecific patterns (e.g. population trends, range shifts or abundance) are often related to the variation in assigned traits to examine the explanatory role of traits in environmental filtering. And this association is then used to predict changes in community composition or ecosystem functioning in response to anthropogenic modification (Jiguet et al., 2010; Webb et al., 2010). However, many studies have found the explanatory power of traits to be rather low (e.g. Angert et al., 2011; Yang et al., 2018), begging the question of what information is missing from traditional trait-based interspecific analyses.

While ecology is often focused on the search for general patterns at the interspecific (i.e. species) level, there remains debate as to what extent intraspecific trait variability needs to be accounted for in interspecific analyses (Albert et al., 2010, 2011; Bolnick et al., 2011; Kraft et al., 2008; Palacio et al., 2019). Intraspecific trait variability can encompass (Albert et al., 2011) population-level variability or between-individual variability. While much is known about between-individual variability (e.g. de Bello et al., 2011; Raffard et al., 2017; Thompson et al., 2018), relatively little is known about population-level variability and how this compares with interspecific variability. This is likely in part because of the longstanding precedent to assume that interspecific variation exceeds intraspecific variation (i.e. the mean field approach; MacArthur & Levins, 1967).

Population-level variability may be advantageous for coping with anthropogenic environmental changes, but can be achieved in different ways: species broadly adapted throughout their range (i.e. high levels of variability) have low sensitivity to local environmental changes compared with species that have locally adapted niches and thus high sensitivity to local environmental changes (Bennett et al., 2019). For example, variability of responses in an invasive grass enabled adaptation to urban environments (Weston et al., 2021), representing a species with low sensitivity to local change and/or a species with locally adapted populations. Quantifying the differences between interspecific variability and potential intraspecific variability (i.e. population-level variability) is, therefore, important for future work aiming to assess interspecific differences in species–environment relationships and improve the predictive power of trait-based analyses (Webb et al., 2010).

Quantifying both intra- and interspecific measures in a given species–environment relationship at a population level is a laborious task. This is because it requires species characteristics to be measured multiple times for many individuals, or populations, of many species throughout a species' range and different ecosystem types within that range (Albert et al., 2011). With the uptick in large-scale biodiversity data (Hampton et al., 2013), gathered through camera-trapping or citizen science initiatives such as iNaturalist (Seltzer, 2019), combined with increasingly available remote sensing layers of environmental variables, there is a push towards a continuous refinement of measuring species–environment relationships (Callaghan, Bowler, et al., 2021; Liu et al., 2021; Santini et al., 2019; Winchell et al., 2020). For example, drivers such as urbanization, the process by which land use is converted into urban areas, can have many negative impacts on fauna and flora (Aronson et al., 2014; Croci et al., 2008; McKinney, 2006; Piano et al., 2020), highlighting the importance of measuring species–environment relationships. This approach has already helped move species habitat classification beyond categorical responses (e.g. urban 'avoider' or 'exploiter') to quantify how a species responds to the urban environment through a continuous quantitative metric of species' tolerance to urbanization (Callaghan, Bowler, et al., 2021). Large-scale datasets are increasingly used to quantify species–environment relationships and the variability among a species' response to an environmental driver (e.g. Fidino et al., 2021; Magle et al., 2021; Winchell et al., 2020). But quantifying intraspecific trait variability, and how this compares with interspecific trait variability, across a species' range remains a missed opportunity with these growing datasets.

Our goal was to address this research gap using broad-scale citizen science data to quantify and examine differences in inter- and intraspecific urban tolerance variability. We used the model of species-specific responses to urbanization, given the increasing role of urbanization in shaping biological communities (Fenoglio et al., 2021). Additionally, there are known interspecific (Jokimäki et al., 2016) and intraspecific (Evans & Gawlik, 2020) differences that occur in response to urbanization and a number of examples of within-species differences in the use of urban habitat (see Evans, 2010). Here, we measure spatial variability in urban tolerance (i.e. how urban tolerance changes in space across the United States and a proxy for differential species responses to urbanization across the continental United States). In a strict sense, a trait is defined as something measurable at the individual level (e.g. body size). But here we use a broader definition to encompass species-specific characteristics, such as habitat preference, recognizing the complexity in defining a trait (Violle et al., 2007), where habitat preference is measured at the population level.

Our first objective was to quantify the extent that urban tolerance spatial variability is a function of the variability of urban habitat that a species experiences across the continental United States (Figure 1). We assessed this because urban use can vary according to the availability of urban habitat. Species may track their environmental niche in regards to urban use (Zurell et al., 2018). For example, a species that is strictly urban intolerant (i.e. low variability in urban tolerance) will likely occupy areas with low urban habitat variability, but in contrast a generalist species (i.e. able to use or avoid urban areas and thus have high variability in urban tolerance) will likely occupy areas with high urban habitat variability. Our second objective was to test whether a species' urban tolerance was associated with the overall prevalence of habitat (i.e. median) where that species was found. Third, we compared the magnitude of intraspecific and interspecific (i.e. species-level) variability, as this difference has important implications for studies using traits as a fixed value (Albert et al., 2011). Our results have implications for any analysis of interspecific and/or intraspecific comparisons in which species–environment relationships are the focus.

2 | MATERIALS AND METHODS

2.1 | Bird occurrence data

We used eBird data (Sullivan et al., 2014, 2017) as our source of bird occurrence data throughout the continental United States. eBird is a semi-structured citizen science project with over a billion observations globally that enlists birdwatchers to submit 'checklists' of birds seen and/or heard while birding. These checklists collect information such as the date, time of day, duration spent birding and distance travelled birding, as well as different protocols indicating the extensiveness of the survey. For example, a checklist is marked as 'complete' only if the observer recorded all birds able to be identified. We used the eBird basic dataset (version ebd_vrs_May2020)

and further subsetted the data by (1) using only complete checklists, (2) that were stationary (i.e. the observer's birding activity occurred at a single, fixed location), (3) that were between 20 and 30 min in duration and (4) were from May, June, July or August to temporally match the breeding season in the continental United States. Some exploratory analyses showed that there was minimal bias in the sampling duration of a checklist across an urbanization gradient (Figure S1) and that urban tolerance scores were robust to any potential sampling biases in terms of duration of a checklist (Figure S2). We used bird occurrence data from 2015 to 2017.

2.2 | Calculating urban tolerance

We used a workflow to quantify bird urban tolerance, accounting for the occurrence of a species in urban areas versus urban availability and sampled urban habitat, within regions across the whole of their range, which was applied to each species. First, we randomly assigned 2000 points throughout the continental United States and created a 500km buffer (radius) around each point (Figure 1). We chose 500km as exploratory qualitative analyses showed that it was an appropriate grain size to balance (a) a reasonable number of eBird samples allowing us to maximize the number of species that met our criteria for inclusion (see below) and (b) small enough to assume that the common species within a buffer (the ones with at least 100 observations) can equally occur throughout the buffer or have a similar percent area overlap of a species' range with the buffer polygon. This helps to tease apart the difference between an ecological signal (i.e. a species avoiding urban habitat) or a methodological signal where by chance alone a buffer intersects a species' range limiting the possibility that a species can use all the urban habitat available in that buffer. There may be edge cases still, even at our chosen grain size, but we are confident that our random sampling approach can overcome potential noise (see Figure S3).

Second, for each buffer, we collated all eBird checklists and assigned each eBird checklist to a value of Visible and Infrared Imaging Suite (VIIRS) night-time lights from a geospatial data product (~500m resolution), representing a continuous proxy for relative urbanization levels (Elvidge et al., 2017) using Google Earth Engine (Gorelick et al., 2017). Here, we consider VIIRS night-time lights as a broad proxy for 'urban habitat', measured at the regional scale and focused on a macro-ecological scale. We acknowledge that urbanization is dynamic and can act at smaller spatial resolutions (e.g. patches of green area at the scale of tens m^2) and many other habitat types (e.g. forest, water, grassland) can be encompassed within an urban landscape. Our metric is not intended to capture such fine-scale patterns of urban habitat, but rather compare broad-scale patterns of 'urban' habitat to other habitat types, measured as the anthropogenic pressure on species that reside there. For example, we use VIIRS night-time light values to differentiate between a downtown city (very urban and high VIIRS night-time light values) and a remote national park (non-urban and low VIIRS night-time light values). This metric has been used extensively to quantify urbanization in
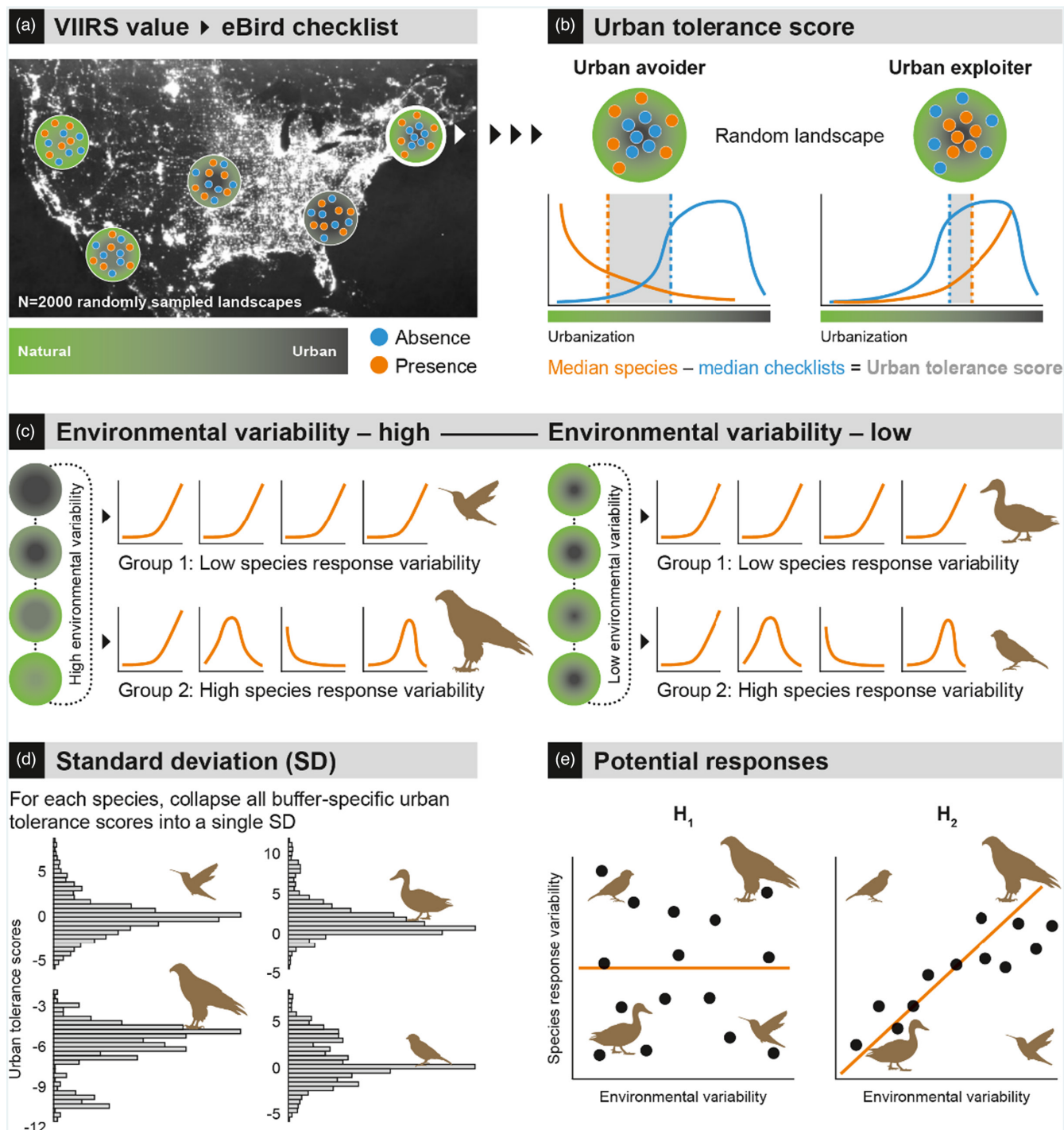
FIGURE 1 Our methodological overview. First (a) we placed 2000 random points throughout the contiguous United States and created a 500 km buffer surrounding each point, and aggregated all eBird data within each buffer. Second (b) we calculated urban tolerance within each buffer for every species with >100 observations as the median VIIRS value at bird occurrence locations subtracted by the median VIIRS value of all eBird checklists sampled in that buffer. Third (c) we calculated the environmental variability (or buffer-level variability) for every buffer and then collapsed these to species-specific distributions of urban tolerance for which we calculated the standard deviation across all buffers. Similarly (d) we calculated the standard deviation of species tolerance scores across all buffers. There were four theorized typical scenarios of responses for a species, which can be seen in (c–e). We hypothesized two potential relationships (e): Environmental variability would (H2), or would not (H1), predict species response variability.

the remote sensing literature (Ma et al., 2012; Stokes & Seto, 2019; Xie et al., 2019; Zhang & Seto, 2013). Moreover, previous work has shown a strong correlation between urban tolerance measured

using VIIRS night-time lights and population density and global human modification (Liu et al., 2021). We temporally collapsed the measures by taking a median value across all monthly VIIRS images

from 1 January 2014 to 1 January 2020. This timeframe temporally extends the timeframe of our bird occurrence data to assess an overall level of urbanization for each point, and we assume that any underlying changes in urbanization level during this time-frame would be negligible.

For each buffer, we then calculated urban tolerance for any species with at least 100 observations (sensu Callaghan et al., 2020; Callaghan, Sayol, et al., 2021). Urban tolerance was defined for each species within each buffer as the median VIIRS value at bird occurrence locations (i.e. the subset of checklists that a species occurred on; Figure 1) subtracted by the median VIIRS value of all eBird checklists sampled in that buffer, where both distributions were first log10-transformed (sensu Callaghan et al., 2020; Callaghan, Bowler, et al., 2021). This provided a quantitative metric where the most 'urban tolerant' species had the highest (positive) values and the least urban tolerant species had the lowest (negative) values (Figure 1). Importantly, this measure of urban tolerance is a relative measure and has been used to provide a quantitative continuous ranking of species on a relative scale (i.e. species A is more urban tolerant than species B). This approach assumes that if the bias in citizen science samples towards urban areas (Mair & Ruete, 2016) is systematic among species, we can still infer which species are relatively more or less common in urban areas given the sampling across an urbanization gradient is relatively consistent. Moreover, this method allows us to compare urban tolerance over a species range by having independent samples of urban tolerance within each of our random buffers that are standardized by subtracting the median VIIRS value of all eBird checklists. To ensure that this process was robust, we performed a resampling procedure where each species' urban tolerance was calculated 100 times, using 50 randomly sampled checklists in each buffer and this was strongly correlated with the overall urban tolerance measure (Figure S4). Additionally, we performed a traditional presence/absence modelling exercise for the species in a subset of buffers and found strong qualitative and quantitative agreement with our measures of urban tolerance (Figure S5).

A total of 338 unique species met sampling criteria in our randomly sampled 2000 buffers, with the maximum number of species included in a buffer being 173 and the minimum 5 (Figure S6). Some species were found in relatively few buffers, such as Hermit Warbler *Setophaga occidentalis* ($N = 3$) and Franklin's Gull *Leucophaeus pipixcan* ($N = 6$) whereas in contrast some species were found in all, or nearly all buffers, such as House Sparrow *Passer domesticus* ($N = 2000$) and Mourning Dove *Zenaida macroura* ($N = 2000$). Across all species, the average number of buffers a species was present in was 549 ± 505 (Figure S7).

2.3 | Intraspecific variability of urban tolerance as a function of urban habitat variability

To test whether spatial variability of urban tolerance is a function of environmental variability of urban habitat across the contiguous

United States, we calculated the standard deviation (SD) using urban tolerance scores of each species individually (urban tolerance SD) and the SD of the buffer urbanization level (i.e. the median VIIRS night-time light value) that each species occurred in (buffer level SD; Figure 1). Our null hypothesis (i.e. urban tolerance SD is explained by buffer level SD) would be supported when species' urban use was related to urban availability, leading to a positive relationship between urban tolerance SD and buffer level SD. To test this hypothesis, we fit a linear model. The response variable was the species' SD of urban tolerance, log10-transformed, and the predictor variable was the buffer level SD. We also included in the model the number of buffers a species was found in as a fixed effect, as a proxy for range size, and because it positively correlated with urban tolerance SD ($R^2 = 0.40$, estimate = 0.37, $t = 15.16$, $p < 0.001$; Figure S8). After fitting our initial model, we tested the robustness of this model when accounting for the phylogenetic relatedness among species, by fitting a phylogenetic linear regression model (Pagel, 1999). Our phylogenetic tree used 1000 trees from Jetz et al., 2012 and building a 50% consensus tree with our species in our analysis.

2.4 | Intraspecific variability of urban tolerance as a function of the median urbanization level

Next, we quantified the strength of the relationship between a species' urban tolerance and the overall urbanization level (i.e. the median VIIRS night-time lights) within each buffer for every species. This was a species-specific analysis, where each species was treated separately. For each species, we used a generalized additive model (GAM) where the response variable was the urban tolerance, and the predictor variable (as a simple additive parametric term) was the total urbanization level (i.e. median VIIRS night-time lights of all samples in that buffer). We also included a bivariate spline for longitude and latitude to include the nonlinear effect of location (i.e. spatial autocorrelation) on the relationship between the response and predictor variable.

2.5 | Comparing interspecific and intraspecific differences in urban tolerance

To meet our third objective aimed at comparing the magnitude of interspecific and intraspecific differences in urban tolerance, we first summarized whether a species-level urban tolerance (i.e. the value that would be used in interspecific analyses) was greater than a species' intraspecific urban tolerance. Species-level tolerance was defined as the mean of their urban tolerance scores. In contrast, intraspecific urban tolerance was defined as the SD of their urban tolerance scores across all buffers that a species occupied. To test for any statistically significant difference we used a linear model with a gaussian distribution where the response variable was urban tolerance and a categorical predictor variable for whether the value was an intraspecific or interspecific measure of urban tolerance.

Additionally, we quantified the urban tolerance variability explained by (1) interspecific differences, (2) available urban habitat in the environment and (3) intraspecific differences in a mixed-effects model. The response variable was the urban tolerance of a species in a specific buffer, and we had two random intercepts, one for species and one for the buffer (i.e. spatial region). The estimated variance of this mixed-effects model was interpreted as the effect of interspecific differences (for the species-level random intercept), available urban habitat in the environment (for the buffer-level random intercept) and intraspecific differences (the remaining residual variance). We complemented this random-effects model by performing a variance decomposition analysis to estimate the repeatability of urban tolerance at a species level (sensu Sol et al., 2014) using a generalized linear-mixed effects model by performing parametric bootstrapping with 1000 replicates. The analysis was performed with the rptGaussian function from the rpt package (Stoffel et al., 2017).

2.6 | Contextual analyses

To provide additional context to our main three objectives, above, we performed some additional analyses. First, from the relationship between urban tolerance SD and buffer level SD we calculated the orthogonal distance from the 1:1 line of the relationship between the buffer level SD and the urban tolerance SD for every species, and this distance was used as a proxy for how much that species uses urban habitat over or under proportional to what is available. We then tested whether the extent of spatial variability of urban tolerance is explained by a species' mean urban tolerance, that is, whether higher intraspecific variability is more typical of urban tolerant bird species than intolerant bird species, which would be consistent with previous studies suggesting that urban use is associated with more generalist species (Bonier et al., 2007). To do this, we tested the relationship between a species SD in urban tolerance and a species' mean urban tolerance, using a linear regression. Lastly, we tested the robustness of collapsing spatial variability into a mean urban tolerance by randomly sampling species' urban tolerances from their corresponding buffers and fit a linear model between these randomly sampled measures of urban tolerance and the mean urban tolerance 1000 times, calculating the R^2 for each linear model fit.

2.7 | Data analysis and availability

All data analysis was conducted in R version 4.1.2 (R Core Team, 2021) statistical software and relied heavily on the tidyverse (Wickham et al., 2019). The sf package (Pebesma, 2018) was used for spatial resampling and spatial handling of data and the lme4 package (Bates et al., 2015) was used for fitting linear mixed effects models. GAMs were fit using 'mgcv' (Wood, 2011). Our phylogenetic linear model was fit using the phylolm package (Ho & Ane, 2014) and phylogenetic trees were handled using the phytools package (Revell, 2012).

Statistical significance, in the case of multiple linear regressions, was concluded at $\alpha < 0.05$. We consider an R^2 value >0.6 to be a strong correlation and an $R^2 > 0.4$ to be a moderate correlation. We follow the eBird/Clements taxonomy v2019 (Clements et al., 2019). Code and data to reproduce these analyses are available here: https://doi.org/10.5281/zenodo.7351955.

3 | RESULTS

3.1 | Overview of variability in urban tolerance

Averaged across all buffers, the mean urban tolerance was negative for 75% of species ($N = 255$) and positive for 25% of species ($N = 83$). We found a wide array of spatial variability in urban tolerance responses across species, with a minimum SD of 0.125 (Hermit Warbler), a maximum SD of 8.19 (Costa's Hummingbird *Calypte costae*) and a mean SD across all species of 1.91. Some species (e.g. Mallard *Anas platyrhynchos*, Mourning Dove) showed spatial variation in urban tolerance over their geographic range (Figure 2). By contrast, some species had relatively low variability in urban tolerance (Figure 2), consistently avoiding urbanization throughout their range (e.g. Northern Bobwhite *Colinus virginianus*) and sometimes consistently using urban cover throughout their range (e.g. Peregrine Falcon *Falco peregrinus*). Species-specific urban tolerance variability estimates for all 338 species can be found in Table S1.

3.2 | Intraspecific variability of urban tolerance as a function of urban habitat variability

Consistent with our expectation that species' variability of urban tolerance was predicted by environmental variability of urban habitat across all species (Figure 1e), variability in a species' response to urbanization throughout a species' range (urban tolerance SD) was strongly correlated with the buffer-level variability (buffer level SD) of where a species occurred ($R^2 = 0.70$, estimate = 1.05, t value = 18.56, p-value<0.001; Table S2; Figure 3). This relationship was robust when considering the phylogenetic relatedness of the species in the model (Table S3). Most species (88%) fell within an orthogonal 'distance of 1' from the 1:1 line (i.e. a smaller than 1 SD change in intraspecific variability with 1 SD change in urban cover), supporting our finding that urban tolerance is a function of urban habitat availability.

3.3 | Intraspecific variability of urban tolerance as a function of the median urbanization level

Our analysis also revealed some patterns on how variability was distributed across space and across species. Ninety percent ($N = 305$) of species showed a negative relationship between the urban tolerance of a buffer and the median urban cover in that buffer, such
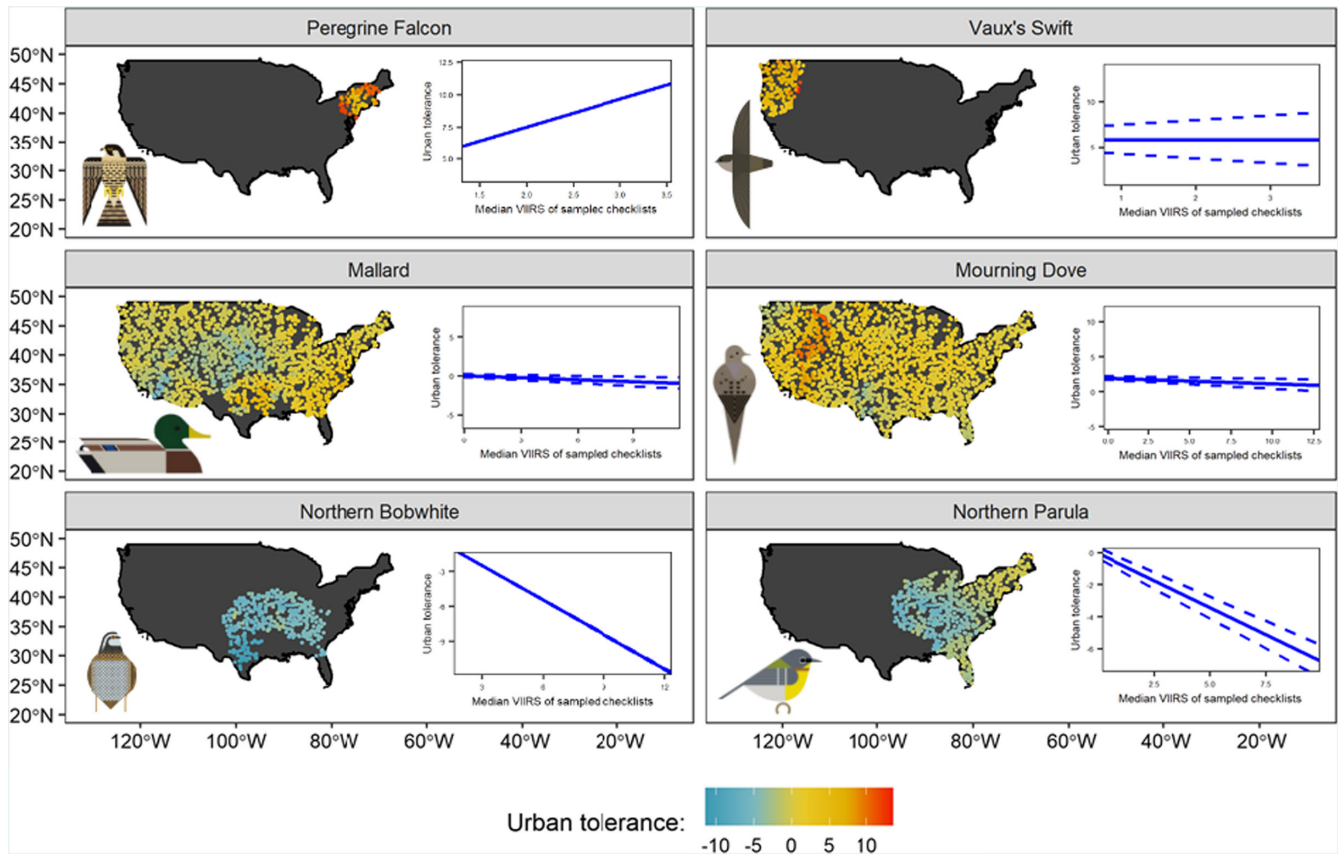
FIGURE 2 Six example species and their distribution throughout the continental United States and their urban tolerance scores, showing the variability of a species throughout its range, where bright red corresponds to 'urban tolerant' and bright blue corresponds to 'urban intolerant'. The inset panels represent the modelled relationship (i.e. the slope and the 95% confidence interval of the slope) between the median VIIRS of the buffers and the species' urban tolerance of that buffer.

that urban areas were more avoided within more urbanized buffers (Figure 2; Table S1). In addition, the mean urban tolerance of a species (i.e. interspecific value) was moderately related to the variability of urban tolerance of a species (i.e. intraspecific value; estimate = 1.31, t-value = 13.62, $p < 0.0001$, $R^2 = 0.35$).

3.4 | Comparing interspecific and intraspecific differences in urban tolerance

Intraspecific variability (SD of all species' urban tolerance measures) was less than interspecific variability (mean of all species' urban tolerance measures; estimate = −0.09, t-value = −8.60, $p < 0.001$; Figure 4). And species with an overall positive response to urbanization had greater variability in their urban tolerance scores than species with an overall negative response to urbanization (Figure 4c). The relationship between the full distribution of species urban tolerances (i.e. randomly sampling a single buffer for each species) and the fixed mean urban tolerance was strongly positive (mean $R^2 = 0.60$, from 1000 resamples), suggesting that the species mean values capture most of the important variability in urban tolerance among species (Figure S9). Our mixed-effect model (Table S4) showed that interspecific variability was the highest source of variability

in our estimated model (variance = 7.643; estimated SD = 2.765), followed by intraspecific variability (variance = 5.505; estimated SD = 2.346) and environmental variability (variance = 1.172; estimated SD = 1.083). Our variance decomposition analysis showed that the repeatability of urban tolerance (i.e. intraclass correlation) was 0.534 (95% CI: 0.494–0.569).

4 | DISCUSSION

4.1 | Drivers of spatial variability in urban tolerance

We showed that there is spatial variability in urban tolerance of birds but this is largely a function of the variability of the available urban habitat throughout a species' environment (Figure 3). The variability in urban tolerance was greater in species that, on average, were more tolerant of urbanization, indicating that generalist life histories (i.e. a species' that can use urban and non-urban habitat types) are better-suited to cope with novel anthropogenic environments (Bonier et al., 2007; Callaghan et al., 2020; Franzén et al., 2020; Palacio, 2020). We also found that a species' urban tolerance was negatively related with increased levels of urbanization (i.e. species selected against urban areas stronger in more highly urbanized
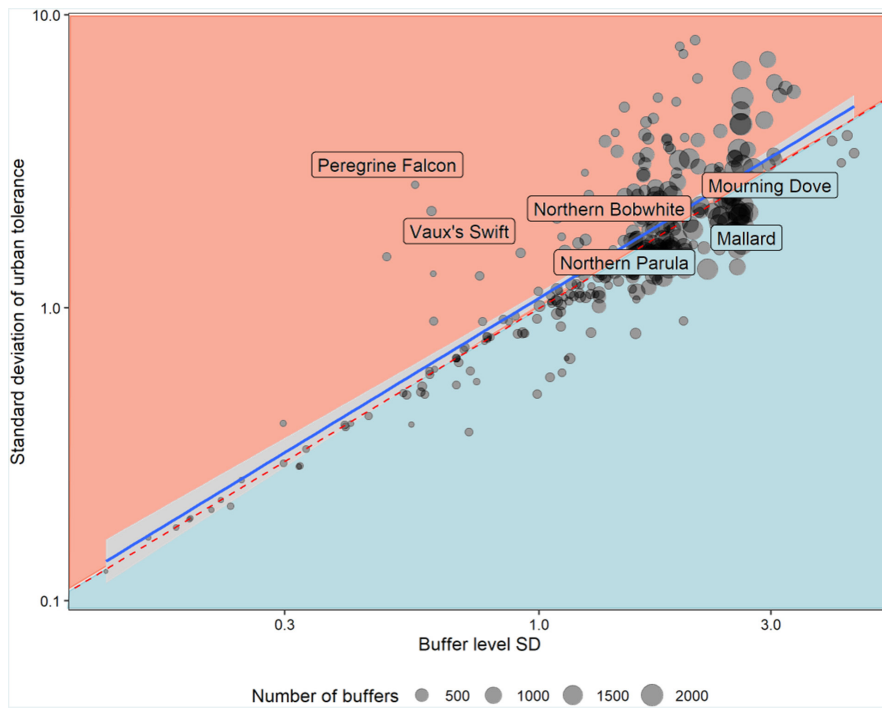
FIGURE 3 The relationship between species-specific variability in urban tolerance (y-axis) and environmental variability in urbanization (x-axis). Each point represents a species (N = 338), and the size of the point corresponds to the number of buffers that species was found in. This relationship was robust when phylogenetic relatedness was accounted for as well (Table S3). The red dashed line represents a 1:1 line and the blue line is a linear model fit, with the shaded area representing the 95% confidence interval of the model fit. The blue region represents species that are below the 1:1 line and the red region represents species that are above the 1:1 line.
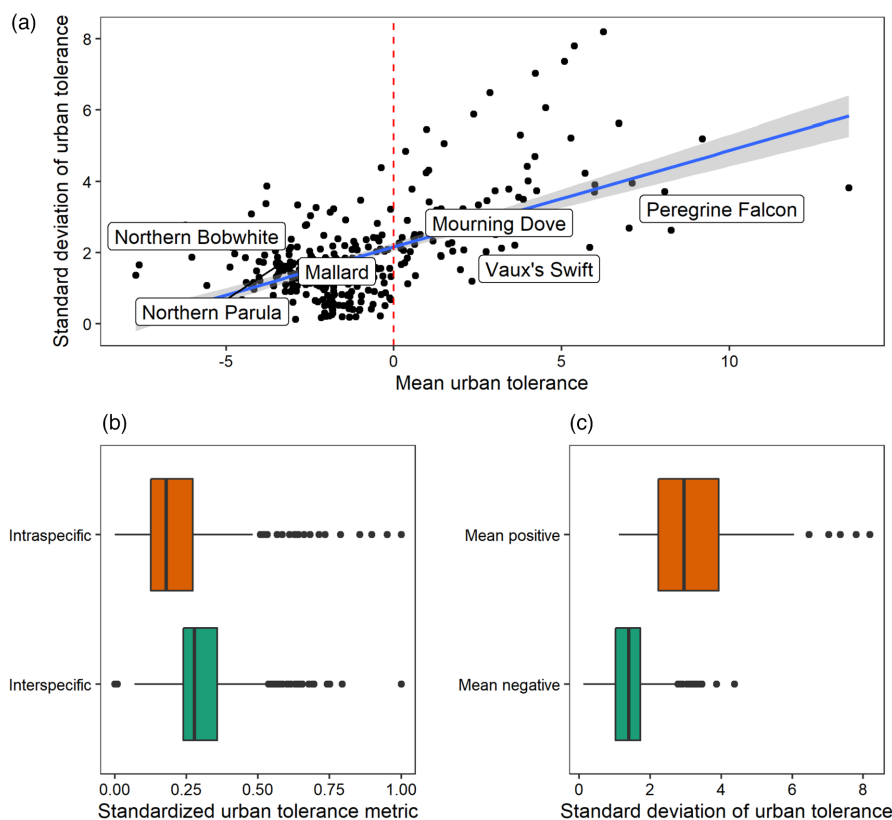

FIGURE 4 (a) The relationship between mean urban tolerance and variability of urban tolerance for 338 species across the continental United States. (b) Scaled responses from (a), where the species' mean represents interspecific measurements and the variability represents intraspecific measurements. (c) The results from (a) visualized by splitting the mean urban tolerance into those species that respond positively to urbanization and those that respond negatively to urbanization.

areas) for most species (90%). Together, our results indicate (1) that intraspecific variability is a consequence of local environmental variability in urban cover and (2) interspecific variability is greater than intraspecific variability, providing some support to the common use of mean trait values when assessing species–environment relationships.

Use of urban habitat by birds is known to vary spatially (see Evans, 2010 and Wesolowski & Fuller, 2012 for some examples), but we showed that this variability is largely a result of the variability in the available urban habitat in space—something that previous studies have rarely assessed quantitatively (Evans, 2010). Hence, species with large variation in urban tolerance were also

the species occupying regions with large variation in urban cover. These species sometimes actively used urban cover (i.e. used more urban cover than expected) while at other times avoided urban cover (i.e. used less urban cover than expected). Our finding that spatial variability of urban tolerance is strongly predicted by environmental variability in urban habitat suggests that (1) urbanization may act as a strong abiotic environmental filter of local community composition (Marcacci et al., 2021) and/or (2) species track the available niches in the environment where they adaptively avoid unsuitable regions (Zurell et al., 2018). For most species (90%), we also found that urban tolerance declined with increasing local levels of urbanization, providing further support that species are broadly tracking their environmental niche in regards to the level of urban cover throughout a species' range. These forms of niche tracking can occur at the species (Tingley et al., 2009; Zurell et al., 2018), population (e.g. climatic niche tracking of White Storks; Fandos et al., 2020) or individual level (e.g. climatic niche tracking of Yellow Warblers; Bay et al., 2021). Our work provides support to the finding that species respond consistently to urbanization and species are consistently classified as urban avoiders or exploiters (sensu Blair, 1996; Sol et al., 2014), and other work that has found consistent densities of species in urban and suburban environments (Evans et al., 2011).

Although we only demonstrate that spatial variability of urban tolerance is related with the environmental variability of where that species is found, we speculate that this is a sum of individual-choices—in terms of movement as well as differences in demographic rates affecting local population persistence. Population-level tracking may be caused by environmental trait filtering affecting the composition of biological communities whereas individual-level tracking can be caused by localized movement decisions. Indeed, Trevail et al. (2021) found that individual specializations (i.e. individual variability) were more likely in heterogeneous environments, providing support to this individual to species speculation. This also makes sense given that a species–environment relationship, such as species' urban habitat use, is theoretically predicted by a collection of individual choices (Johnson, 1980), including the within-individual variability due to plasticity, personality and behaviour (Hertel et al., 2020). Behavioural plasticity at the individual-level is associated with reduced extinction risks (Ducatez et al., 2020; Gilmour et al., 2018) and traits associated with adaptive capacity at the species-level are often included in assessments of species' vulnerability to anthropogenic drivers (e.g. Foden et al., 2013; Santini et al., 2019; Winchell et al., 2020). Thus, a species' adaptive capacity, caused by individual, population or species-level attributes, may be important for conservation since it is one component that can make a species vulnerable to environmental change (e.g. Foden et al., 2013; Lawton et al., 2012). We suggest that species which are less flexible in their ability to use urban habitat are likely at higher risk due to increasing urbanization (Bonier et al., 2007; Sol et al., 2014), but the relationship between species' urban tolerance and in particular predictors of that urban tolerance can vary within and among taxonomic groups (Santini et al., 2019).

Alternatively, spatial variability of urban tolerance could be driven from top-down effects such as large macroecological patterns influencing the local-level adaptations to urban environments. In other words, macroecological variables such as aridity, climate, temperature, precipitation, which influence a species' niche (Gouveia et al., 2014; Lynn et al., 2021) also work in concert to lead to spatial variability in urban tolerance across the United States. We explored this using an analysis where species were nested within ecoregion and found that indeed, ecoregion explained a large portion of the intraspecific variability, but interspecific variability was still greater than intra-ecoregion effects (see Tables S4 and S5 for details). While our research here was focused on describing patterns of variability, further work should look to explain mechanisms leading to such patterns in variability of urban tolerance or species–environment relationships more generally.

4.2 | Considering interspecific and intraspecific variability in urban tolerance

As trait-based ecology has grown, so has the recognition that intraspecific variation might be important for trait-based models (e.g. Des Roches et al., 2018; He et al., 2021; Lajoie & Vellend, 2015). While we found the largest source of variation in urban tolerances was associated with species-level differences, we also found a large amount of intraspecific variability of urban tolerance (e.g. Figure 2). But when this intraspecific variability needs to be accounted for in interspecific analyses remains a pressing question (Albert et al., 2010, 2011; Bolnick et al., 2011). First, our results highlight that caution should be used when generalizing a response across a species' range as is commonly done in the implementation of species distribution models. Second, we found a relatively strong relationship between the mean species urban tolerance (i.e. interspecific comparisons) and the full distributions of species urban tolerances across buffers (Figure S9), highlighting that collapsing intraspecific variability to a mean value may be largely sufficient in some instances (i.e. we found an average R^2 of 0.60). But understanding when, and at what scales, this pattern holds true remains an important avenue for future research. However, this is in direct contrast to studies which have shown the importance of considering intraspecific variation (Des Roches et al., 2018; Wong & Carmona, 2021). To further illustrate the influence of accounting for potential spatial variability in a species–environment relationship analysis we performed an illustrative analysis using two different modelling approaches, both aimed at answering the question: how do traits influence urban tolerance (sensu Evans et al., 2011; Kark et al., 2007; Santini et al., 2019; Sol et al., 2014; Winchell et al., 2020)? Using two different approaches, first simply using the mean urban tolerance as the response variable, and second, using a mixed-effects model with a random intercept to account for spatial variability in a species' urban tolerance, we found qualitatively and quantitatively similar results (see details in Figure S10). These results suggest that in the case of species using, or avoiding, urban habitats, using the mean values from across a

species' range is sufficient to understand interspecific variability. If the scientific question is focused on interspecific differences, then it may be sufficient to focus on collecting interspecific differences opposed to intraspecific differences, but if possible both intra and interspecific data are the most advisable (Bolnick et al., 2011; Violle et al., 2012).

4.3 | Current limitations and future directions

Our methodological approach here is similar to others, for example, Martin et al., 2020 used a modelling framework to assess the geographical distribution of species' response to climate by dividing the distribution into spatial subsets along occupied climatic conditions. Similarly, we used spatial variability as a proxy for population-level variability. This approach assumes that different populations are being sampled and not individuals because of the large geographic space over which species were sampled (i.e. the United States) and, therefore, individuals are unlikely to be sampled in different parts of this geographic space, especially considering our analysis was performed during the breeding months. Nevertheless, this assumption is strongest for wide-ranging species, and some small-ranged species with randomly sampled patches near one another may still be considered a single population depending on some definitions. But given the difficulty of sampling from known different populations we are confident our approach provides a first step in understanding population level variability. Further work should focus on teasing out any methodological artefacts in our approach for measuring spatial variability of urban tolerance. For plants, for example, it is likely easier to measure multiple traits over many individuals from known different populations compared to animals, where individuals need to be caught and ethics approved. This likely explains why most research on intraspecific variability in traits has been focused on plants (Albert et al., 2010, 2011; Bolnick et al., 2011; Kraft et al., 2008; Zhang et al., 2020). However, our use of broad-scale citizen science data allowed us to quantify intraspecific variability across the entire United States, but for other questions looking at intraspecific variability it may be costly to quantify, for example, variability in traits (e.g. body size) among different populations. Traits, in a strict sense (Violle et al., 2007), are those measurable on individuals, which may be the most difficult to gather data for animals, particularly at large spatial scales. By contrast, a broader suite of traits (or rather species attributes or characteristics), such as habitat and climate preferences, are typically measured at population-levels and hence may be easier targets for studies on intraspecific variation. Because citizen science data are steadily increasing and remotely sensed habitat variables are simultaneously increasing at increasingly fine spatial resolutions, we suggest that these data sources offer a way to further quantify and understand intraspecific and interspecific variability of species–environment relationships and potentially habitat-density associations (e.g. Schaub et al., 2011).

Our analysis was focused on only one specific species–environment relationship: a species' response to urbanization. To what extent our results generalize to other environmental gradients (e.g. agriculture, forest integrity) remains to be formally tested. However, we hypothesize that similar patterns would emerge because environmental filtering, niche construction and trait filtering respond similarly to macroenvironmental filtering, regardless of the specific species–environment relationship (Thakur & Wright, 2017). We also restricted our analysis to birds during the breeding season, and further work should leverage other growing citizen science datasets to test the generality of our findings for other taxa and in different regions of the world. By restricting our analyses to the breeding season, and only the United States (where eBird sampling is most intense) we may underestimate the variability in urban tolerance given the known temporal changes in urban tolerance that can occur in birds (Callaghan, Cornwell, et al., 2021). Furthermore, citizen science data are biased in space, with proportionately more records arising from urban areas, but because this bias is likely to be systematic across species, the relative urban tolerance scores should be robust (Mair & Ruete, 2016; Tang et al., 2021). Another bias with citizen science is one towards more common species (Tulloch et al., 2013), and there may be a lack of rare species, accentuated by our criteria of only including species with at least 100 records in a buffer. While this biases our analysis towards more common species, it is possible that the rarer species may be less urban tolerant (e.g. habitat specialists in remote regions such as grasslands or boreal forests during the breeding seasons). Therefore, our results will depend, to some extent, on the number of species included, as it is expected that the higher the number of species, the larger the interspecific variability, and possibly a lower influence of intraspecific variability, because as the number of species increases, the chances of including rare species constrained to particular habitats increases. As such, our analyses should be interpreted with care and as citizen science data continues to increase, these biases can be minimized (e.g. by subsampling data) in the future. Our method currently assumes that species have an equal likelihood of using urban habitat throughout a randomly sampled buffer (i.e. 500 km radius buffer), but we acknowledge that species–environment relationships can be spatial scale dependent (Cushman & McGarigal, 2002; Thrush et al., 2005) and, therefore, testing how our results change at different spatial scales remains an important future research avenue. Lastly, future research should integrate variability at different organization levels (Albert et al., 2010, 2011), for instance quantifying how variability scales from individuals to populations to species (McCabe et al., 2021; Trevail et al., 2021).

5 | CONCLUSIONS

We have provided a large assessment of spatial variability of urban tolerance, incorporating >300 bird species. Together, our results support the negative consequences of urbanization on biodiversity (Parris, 2016; Piano et al., 2020), but also suggest that generalist species tend to be more variable in their response and hence potentially less vulnerable to anthropogenic changes. Our results illustrate the complexity and nuances of dealing with variability in

species–environment relationships as highlighted by others previously (Evans et al., 2011; Santini et al., 2019; Sol et al., 2014; Winchell et al., 2020). Still, the greater magnitude of interspecific over intraspecific variation supports the use of mean trait values in trait-based ecology, at least for species–environment relationships. Ultimately, growing citizen science data will likely form a major component of future understanding of species–environment relationships for both basic (Soroye et al., 2018) and applied (Hertzog et al., 2021) research. Since species differences may drive evolutionary and ecological change within biological communities (Trevail et al., 2021), citizen science data offers an excellent opportunity to further our understanding of variability in species–environment relationships and how it impacts species' responses to anthropogenic pressures.

AUTHOR CONTRIBUTIONS

Conceptualization: Corey T. Callaghan, Diana E. Bowler. Methodology: Corey T. Callaghan, Diana E. Bowler, Federico Morelli, Facundo X. Palacio, Yanina Benedetti. Investigation: Corey T. Callaghan, Diana E. Bowler, Facundo X. Palacio. Visualization: Corey T. Callaghan, Diana E. Bowler, Federico Morelli, Facundo X. Palacio, Yanina Benedetti. Writing—original draft: Corey T. Callaghan. Writing—review and editing: Corey T. Callaghan, Diana E. Bowler, Federico Morelli, Facundo X. Palacio, Yanina Benedetti.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and code are available from the Zenodo Repository https://doi.org/10.5281/zenodo.7351955 (Callaghan et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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