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Alexander H. Murray

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Biodiversity in the Anthropocene, understanding the impacts of land-use change, and species interactions.

By
Alexander Hennessy Murray

Supervising Committee:
Luke Frishkoff, Supervising Professor
Matt Fujita
Alison Ravenscraft
Eric Smith
Matt Walsh

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Abstract

The extent of human influences on the environment and biodiversity has led to naming our current time period the Anthropocene. A primary way in which humans impact biodiversity is through habitat modification. Despite the knowledge that habitat modification is negative for many species, we still don't understand why some species are able to persist despite habitat modification while others do not. In my first chapter I used a trait-based approach to understand what determines species' sensitivity to habitat modification. Trait-based approaches from different regions often disagree on the importance of the same traits, and I thought climate and land use change severity may account for some of these discrepancies. I set out to test the role of microhabitat use, climate and land use change severity in determining how species respond to habitat modifications. I used anuran abundance data from 18 studies across tropical forests, in conjunction with trait data (microhabitat use and reproductive mode). I found that microhabitat use greatly impacts species' sensitivity to habitat modification, particularly that species vertical niche is important as species' abundance tends to track the availability of their preferred vegetative strata. Arboreal anurans are most sensitive to conversion to land uses which lack vegetative strata, however the extent to which arboreal anurans are sensitive varies with climate. In warmer regions arboreal species are not as sensitive to habitat modification as terrestrial species, as their arboreal nature may have pre-adapted them to the warmer conditions associated with habitat loss. The finding that climate influences trait-based responses to habitat modification is novel and shows that conservation efforts need to incorporate climate context into planning. In my next chapter (chapter 3) I assess what accounts for variation between communities in sensitivity to habitat modification. Previous research has demonstrated that populations and communities vary in their sensitivity to habitat modification, and contemporary factors such as climate account for some of this variation. Here I focus on how historical factors may also contribute to this variation, I test if early humans have contributed to the variation in community sensitivity to land use change. I test the extinction filter hypothesis, using early humans as a filter, which may have already removed sensitive species from communities. I used the PREDICTS database to obtain bird community in different land uses from 54 studies across the world. I found that early humans impact community sensitivity, areas with a greater history of human presence, tend to be less sensitive to habitat modification. This reduced sensitivity to habitat modification comes from a decrease in the number of species found in primary vegetation, rather than an increase in species able to tolerate habitat modification. These results suggest that it is important to consider human history when considering patterns of diversity and/or assessing which communities are most critical to protect, as sensitive species are more likely to occur in areas with low histories of human presence. In my last chapter (chapter 4), I focus on species interactions, as a potential factor which may be causing species to decline. I assessed the population trends of a common lizard, the prairie lizard (*S. consobrinus*), which appears to be in decline, and a closely related species, the Texas Spiny Lizard (*S. olivaceus*). Occurrence data from the last 100 years reveals that *S. consobrinus* is declining, while *S. olivaceus* is increasing in relative abundance. I grouped the data into pseudo-sites to assess the role of climate change, land-use change, and species interactions in the decline of *S. consobrinus*. I found that climate alone does a poor job of predicting the current distribution of *S. consobrinus*, and that presence of *S. olivaceus* and amount urbanization are much better predictors of *S. consobrinus* occurrence. *S. olivaceus* seems to be critical in contributing to the decline of *S. consobrinus*, and co-occurrence between the two species has become increasingly infrequent through time. To validate that these results in patterns of co-occurrence are representative of natural communities, I performed 176 surveys spread across the distribution of *S. consobrinus* in

Texas. Community surveys mirrored occurrence data and suggest that presence of *S. olivaceus* leads to absence of *S. consobrinus* in habitat it would otherwise likely occupy. Observations of the two species in the field revealed major shifts in habitat use by S. *consobrinus* in the presence of *S. olivaceus*, occupying habitat three times as open in areas which also possess *S. olivaceus* when compared to alone. Finally, to confirm that competition is occurring I conducted competition trials between the two species and found that *S. olivaceus* is the superior competitor when compared to *S. consobrinus*. Aggressive behaviour by *S. olivaceus* leads to frequent retreats by *S. consobrinus*, and greatly increased frequency of *S. consobrinus* hiding compared to when *S. consobrinus* is not present. Across all data, results suggest that *S. olivaceus* is competing with *S. consobrinus*, and that this contributes to the decline *S. consobrinus* in central and south Texas.

Dedication

I am dedicating this dissertation to my amazing parents, Anne and Gary Murray, as their continued sacrifice through the years of putting my brothers and I above themselves has allowed us to pursue our passions in life. Their support has been constant regardless of the distance between us, and this work would not have been possible without them, it is as much a result of their efforts as it is of mine. Beyond my parents, my brothers Matthew and Patrick are awesome and have been always interested and supportive of my work . The entire Murray and Hennessy families have contributed to my dissertation, and encouraged me to pursue my interests through the years. In particular, my grandfather John Hennessy, was pivotal in me developing an interest in wildlife and the outdoors, without our time together I may never have pursued a career focused on understanding and protecting nature.

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Chapter 1

General Introduction

One of the most concerning issues in the world right now is the continual loss of biodiversity, primarily resulting from anthropogenic influences. However, our ability to slow down and stop such declines is hindered by our lack of both resources and an understanding of the mechanisms by which species and ultimately communities decline. Habitat modification, climate change, and introductions of invasive species all contribute to these declines (Pereira *et al.*, 2012) yet the specific ways by which these factors ultimately lead to species' demise are often not well understood. Amongst these, habitat modification is responsible for the greatest number of declines(Pereira *et al.*, 2012), thus understanding how habitat modification is responsible for species declines is of the highest priority. Particularly because the solution to deal with habitat modification is the most straightforward of the threats, in that if we avoid habitat modification declines associated with direct habitat modification are often minimized. Yet not all species decline when habitat is converted from natural landscapes to those for human use, with some species being deemed "winners" while others are considered "losers" (McKinney & Lockwood, 1999). Successful conservation efforts will rely on our ability to identify which areas are most important to protect based on the conservation value of the communities within, and the threat of decline for those populations if habitat were modified. A growing amount of literature highlights that the impacts of habitat modification are not equal on all species or populations (Frishkoff *et al.*, 2014; Frishkoff *et al.*, 2015; Nowakowski *et al.*, 2018; Williams *et al.*, 2021), and so understanding the mechanisms responsible for species' declines is one of the most important tasks at hand for conservation biology.

Trait-based approaches are frequently used to estimate species' sensitivity to habitat modification, and have identified traits/properties of species which frequently lead them to decline following habitat conversion (Almeida-Gomes & Rocha, 2015; Nowakowski *et al.*, 2017). Yet trait-based approaches often fail to identify the mechanism by which species are excluded from disturbed habitats, and instead simply identify a correlation between a trait and sensitivity. Further a great deal of disagreement can exist between studies in the traits which make species susceptible to change suggesting a need to add transferability across studies using trait-based approaches (HATFIELD *et al.*, 2018). Some of this inability to achieve consistency with trait-based approaches may stem from an influence of climate over species' responses, as climate can impact the outcome of habitat modification (Mantyka-pringle *et al.*, 2012). Further not all forms of habitat modification are equal and so consideration of the degree to which habitat has been modified and in what ways it differs from natural habitat is critical to understanding how species response (Newbold *et al.*, 2015). This led me to focus my 1st chapter on understanding how traits, climate and land use change severity combine to alter species responses to habitat modification in tropical rainforests. To accomplish this I used the PREDICTS database (Hudson *et al.*, 2017) to obtain abundance data in natural and disturbed sites across the world. I chose to focus the study on anurans, as amphibians are the most threatened group of terrestrial vertebrates and scoring of traits across different taxonomic groups can be difficult. For each species I scored trait data for vertical niche and reproductive habitat based off all information available in the literature. The two main questions I wanted to address were: 1) Does the vertical niche of a species act as a limiting axis of species niche, that is to say, as vegetative strata is removed do species which depend upon it see decreases in abundance corresponding to this loss? 2) Do traits predispose species equally in sensitivity across the different climate regions? I found that the vertical niche does act as a limiting axis of species niche in that for arboreal frogs, their abundance tends to track the availability of vegetative strata, with abundance highest in primary forest and declining through complex and simple agriculture. Climate does indeed impact trait-based responses to habitat modification, and predictions are greatly improved by including such interactions. The finding that trait-based responses to habitat modification change with climatic conditions explains in part why trait-based studies from different regions often find different results, and highlights the need to consider the climate of regions in conservation planning.

A growing body of research suggests the importance of context in determining how species and populations respond to habitat modification (Frishkoff *et al.*, 2015; Orme *et al.*, 2019; Williams *et al.*, 2021). However, sensitivity of entire communities may differ as well, if common factors which impact sensitivity to disturbance are shared within a community. The extinction filter hypothesis (Balmford, 1996) proposes a scenario in which exposure to past disturbances leads those communities to appear to be less sensitive to similar disturbances in the future. Support for this hypothesis can be found in areas with high levels of natural disturbance are less sensitive to disturbance than communities that haven't experienced such disturbances (Betts *et al.*, 2019). This may stem from species being lost as a result of previous disturbances, and so areas which have been subject to such disturbances may have fewer sensitive species remaining. Modern humans have drastic impacts on biodiversity, yet little is known about how prehistoric human populations impacted communities, and if these impacts are still found in communities today. In my third chapter I ask if prehistoric human populations alter community response to habitat modification. This may be possible if prehistoric humans caused extinctions or if they increased species ability to cope with human threats such as habitat loss through adaptation over time. I used the PREDICTS database (Hudson *et al.*, 2017) to obtain abundance data in natural and disturbed sites across the world for birds. I found strong support that historical human populations have altered natural communities, which leads communities with large human populations 12,000 YBP (years before present) to be less sensitive to contemporary habitat modification. This decreased sensitivity to habitat modification stems from a decrease in the number of species in the natural vegetation, rather than an increase in the number of species which can tolerate habitat modification, suggesting we may be responsible for many "dark extinctions" we previously did not appreciate. This finding is important, as it informs us of the need to prioritize conservation efforts in areas which have had low human populations through time, as these are the areas most likely to contain species which are sensitive to habitat loss and could be lost if not protected.

While habitat modification is responsible for threatening the greatest number of species it is not the only threat: species interactions can also influence the success of species. Invasive species have received a great deal of attention for the role they have played in the declines of many species (Bradley *et al.*, 2019). However native species can also play a role in species declines, particularly as climate change alters the conditions under which species occur, and habitat modification can change the outcome of competitive interactions. Yet very little is known as to how species interactions are changing as a result of human activities, although they undoubtedly are being impacted (Blois *et al.*, 2013; Alexander *et al.*, 2016). To address this glaring need for study, I focused my fourth chapter on understanding the populations trends and distribution of a common lizard species, the Prairie lizard (*Sceloporus consobrinus*). This species was chosen as it appears to be absent in many areas where it was formerly found (AHM personal observation), and yet no documentation about populations trends or potential reduction in its distribution exists in the literature. Further, this species appears to be declining primarily in region inhabited by a much larger, closely related species the Texas Spiny Lizard (*Sceloporus olivaceus*). Given the similarity between the two species, and the high abundance of *S. olivaceus* in the present, it seems possible that interactions between the two species may be contributing to the potential decline of *S. consobrinus*. The main objectives were: 1) To establish if *S. consobrinus* is indeed declining, and if so where. 2) To determine the role of climate, contemporary land use, and species interactions on the occurrence of *S. consobrinus*. 3) Assess if competition is playing a role in changing patterns of distribution, and if so what mechanism has brought about the change. To accomplish these goals I used three different data sources: occurrence data from the last 100 years, transects across Texas, and behavioral trials. I found that *S. consobrinus* is declining through time, however this decline is not range wide, the declines are concentrated in central Texas where it co-occurs with *S. olivaceus*. Increasing urbanization and presence *S. olivaceus* reduce the occurrence of *S. consobrinus*. Yet *S. consobrinus* is absent in areas which remain natural landscapes, suggesting that urbanization alone cannot explain their decline. Behavioral trials revealed high levels of competition between the two species, with *S. olivaceus* being the superior competitor, changing habitat use of *S. consobrinus*. We find that co-occurrence between the two species is infrequent today. In areas where *S. olivaceus* is widespread throughout the landscape *S. consobrinus* is absent, suggesting that habitat heterogeneity is beneficial for allowing co-occurrence of these species at the landscape level. Determining the true mechanism by which the strength of competition has been increasing between the two species is not fully resolved and future studies could focus on this.

This work may act as a springboard for a variety of future research, and adds value to the current research on the importance of biotic interactions. It is especially influential as it provides a great example of how competition can exclude species from otherwise suitable habitat and is unique amongst studies in that it combines occurrence data, transects and behavioral trials as support. It establishes a geographically concentrated decline of a species which was previously not known to be in decline, and competition as one of the primary causes.

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Chapter 2

Climate and land-use change severity alter trait-based responses to habitat conversion

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Alexander H. Murray[1], A. Justin Nowakowski[2,3], Luke O. Frishkoff[1]

[1]Department of Quantitative Biology, University of Texas at Arlington, Arlington, Texas, USA
[2]Conservation Commons, Smithsonian Conservation Biology Institute, Washington, DC, USA
[3]Moore Center for Science, Conservation International, Arlington, Virginia, USA

Abstract:

Aim: A major goal in modern ecology is understanding the source of variation in species responses to anthropogenic change. Trait-based approaches show promise, but traits found to be predictive in one study often fail in others. We seek to understand whether variation in traits' explanatory power comes about due to interaction effects—between multiple traits and between traits and the environment. We assess the context-dependence of trait-based responses to habitat conversion by testing the hypothesis that abundance in converted habitats decreases with arboreality, while including interactions with, reproductive mode, a trait of known importance, and biologically relevant climate variables.

Location: Global Tropical Forest Biomes

Time Period: 1997-2018

Major taxa studied: Amphibians

Methods: Using 18 studies of amphibian communities from across the globe, we evaluate the role of vertical niche position and reproductive mode in determining abundance within primary forest, structurally complex agriculture, and structurally simple agriculture. We examined interactions between traits, land-use types and climate variables.

Results: Average abundance steadily declined from primary forest, through complex agriculture, and was lowest in simple agriculture. Arboreality (high vertical niche position) leads to increased sensitivity to conversion of forest to simple agriculture, while terrestrial species are more sensitive when habitat is converted to complex agriculture. We found no evidence that trait-by-trait interactions determined abundance after habitat conversion. However, the effects of climate can alter how species' traits determine abundance patterns—while lentic amphibians maintain abundance after conversion regardless of climate zone, direct developers and lotic species become increasingly sensitive to habitat modification in warmer climates.

Major Conclusions: Vertical niche position acts as a limiting axis in modified environments, with response to conversion dependent on the availability of vegetative strata. Interactions between traits and the environment play a strong and underappreciated role in defining community composition in converted habitats. Such interactions may underlie the difficulties past studies have had in achieving generality across study locations and faunas.

Keywords: biodiversity, niche, community change, habitat loss, traits, anura, microhabitat, global change, conservation, countryside biogeography.

Introduction:

Biodiversity loss has progressed toward a state of crisis: species are vanishing at unprecedented rates, causing some to suggest that we are entering Earth's sixth mass extinction event (Wake & Vredenburg, 2008; Barnosky *et al.*, 2011). Climate change, disease, and invasive species all contribute to species declines, but habitat loss threatens the greatest number (Pereira *et al.*, 2012). Nevertheless, not all species decline when natural habitats are converted; many species persist or thrive in converted habitats (McKinney & Lockwood, 1999; Daily *et al.*, 2001; Mendenhall *et al.*, 2016; Elsen *et al.*, 2017). A major goal in conservation and ecology is therefore to understand and predict how species will respond to habitat conversion, since doing so can help target and prioritize conservation towards species at greatest risk.

Species response to conversion of natural vegetation to human land uses such as agriculture can be predictable. For example, closely related species often respond similarly to habitat conversion (Frishkoff *et al.*, 2014; Sol *et al.*, 2017; Nowakowski *et al.*, 2018a). This phylogenetic signal in species response suggests that there exists some set of phylogenetically conserved traits that dictate species responses to habitat conversion. Prior trait-based studies have often sought to understand broad scale extinction risk. These studies have found correlations between traits and extinction risk in mammals (Purvis *et al.*, 2000; Cardillo *et al.*, 2005; Fritz *et al.*, 2009), birds (Owens & Bennett, 2000), amphibians (Cooper *et al.*, 2008), reptiles (Böhm *et al.*, 2016), and butterflies (Kotiaho *et al.*, 2005). Result of comparative analyses generally point to small geographic range size and habitat specialization as the primary causes of high extinction risk (usually measured as IUCN status)(Chichorro *et al.*, 2019). However, species responses to the individual threats driving extinctions – such as habitat conversion, disease, and climate change – may be mediated by different suites of traits (Murray *et al.*, 2014). Elucidating which traits underlie responses to specific threats will ultimately grant greater resolution to predict the communities of the future and the actions needed to preserve them.

Global and regional studies have lent us some testable hypotheses to understand how traits mediate species responses to habitat conversion. Several studies of amphibians point to the importance of reproductive mode as strongly influencing sensitivity to habitat conversion, with some reproductive modes greatly reduced or entirely absent from converted habitats such as agriculture, pastures, tree plantations and forest fragments (Almeida-Gomes & Rocha, 2015;

Nowakowski *et al.*, 2017). Lotic (stream) breeding species are especially likely to decline, as loss of natural vegetation leads to extreme changes in the stream structure, altering water flow, and increasing sediment load. In contrast lentic (still water) breeding species tend to be resistant, perhaps due to the increases in still water—cattle ponds, water storage tanks, tire ruts along roadways—that habitat conversion engenders. Other studies link species' declines to changes in the structural complexity of the physical environment. Removal of a layer of vegetation results in loss of species associated with that layer. For example understory birds are particularly dependent on that strata's availability—because mango plantations lack understory vegetation, species inhabiting this stratum are lost from these orchards (Ehlers Smith *et al.*, 2015). Fossorial reptiles and amphibians are among the most sensitive, as well as arboreal amphibians which lay eggs in vegetation (Trimble & van Aarde, 2014). Traits that tie directly into the parts of the habitat which are being converted are likely to be strong links for identifying species which are most sensitive. Since habitat conversion reduces vertical stratification and canopy cover, species sensitivity should scale with arboreality, so that species that dwell in trees are most likely to be impacted by conversion of forest to other land uses.

While many traits have been flagged in individual studies, such regional analyses do not always support one another. As such, the generalizability of findings from these regional studies is unclear. For example, in bees, traits do not generally predict species responses to land-use change, and when they do it is highly dependent on the crop type (Bartomeus *et al.*, 2018). Other studies have found that traits which are significant predictors with one data set are not transferable to other data sets from adjacent geographic regions (Hatfield *et al.*, 2018). There are three possibilities that might explain these inconsistencies. First, most commonly queried traits might have little predictive power because traits that are easy to measure (and therefore included in studies) may be unrelated to the hard-to-measure traits that actually influence habitat affiliation. For example, thermal tolerance appears to be a strong predictor of species' responses to habitat conversion, with warm tolerant species often persisting after land-use change, a consequence of increasing temperatures when natural vegetation is cleared (Nowakowski *et al.*, 2018c). However, measuring thermal tolerances is time intensive, and therefore is not available for most species observed in community datasets. Second, trait-by-trait interactions might be crucial, such that the same trait could yield opposite responses based on the presence or absence of another trait. Third, traits may interact with the environment to influence how species respond, such that a given trait might cause species to be susceptible to habitat conversion in one biome or climate zone, but tolerant elsewhere. Measuring the right traits, trait-by-trait interactions, and trait-by-environment interactions may all play some role in the apparent lack of transferability in trait-based studies of community composition.

Trait-by-trait interactions are frequently ignored in trait-based analyses, in part for fear that the number of all possible interactions within studies with many traits would outstrip the capacity of regional data sets with relatively few species (Doherty *et al.*, 2020). Similarly, trait-by-environment interactions have rarely been assessed because (i) tolerance to habitat conversion is often treated as a property of a species and invariant between populations and (ii) regional studies typically do not span enough geographic space to robustly ask whether traits modulate species responses to habitat conversion across different environmental or climate zones. However, a handful of recent studies have highlighted the tolerance to human habitat does vary across a species' range (Frishkoff *et al.*, 2019; Orme *et al.*, 2019), suggesting the possibility that species traits may govern the degree and directionality of shifts in tolerance to converted habitats. Such trait-by-climate interactions would sit on top of the documented ways that climate affects biodiversity loss within the context of land-use change (independent of traits) where habitat conversion causes the largest declines in the hottest areas, where species may already be living close to their thermal limits (Mantyka-pringle *et al.*, 2012).

We here seek to understand the degree to which interactions—between traits and between traits and the environment—may provide hidden insights into the role that traits play in determining response to habitat conversion. To do so, we examined anuran (frog) response to habitat conversion, compiling a dataset of anuran abundance for the tropical forested regions of the world. Anurans possess substantial trait diversity, including in their vertical habitat usage and their requirements for reproductive habitat. We first test the hypothesis that vertical niche position acts as a limiting axis of a species' niche, in that species' abundance tracks the availability of their preferred vegetative strata: Arboreal species have the most to lose, especially in converted habitat without tree cover. This hypothesis is important to evaluate, given that the most diverse tropical communities contain a large proportion of arboreal species (Oliveira & Scheffers, 2018), with over half of all individuals residing more than a meter off the ground (Scheffers *et al.*, 2013). As such, if arboreal species are most sensitive to habitat conversion, the future will be grim for amphibians, particularly if agricultural intensification accelerates in tropical regions (Lewis *et al.*, 2015). Alternatively, arboreal species may be more resistant to habitat disturbance, as arboreal frogs often have greater dispersal ability and come from areas with greater environmental instability, suggesting a degree of resilience may be associated with life in the canopy (Scheffers *et al.*, 2017). Yet arboreality, as it pertains to sensitivity to habitat conversion, is still not well understood, and even general evidence linking arboreality to high threat status is weak (Sodhi *et al.*, 2008).

Next we examine whether trait-by-trait, and trait-by-environment interactions change the intensity or direction of how species respond to habitat conversion. To avoid problems of exponential numbers of trait-by-trait interactions inherent in many trait-based studies, we examine this issue from a narrowly focused hypothesis testing framework. Specifically, we examine interactions between vertical niche and reproductive mode (preference for still water, moving water, or terrestrial environments for larval (or direct-) development). Reproductive mode is one of the most consistent traits that is associated with anuran response to habitat conversion (Nowakowski *et al.*, 2017), and so provides a good point to assess the influence of trait-by-trait interactions. To address the potential interactions between traits and environmental factors we examined interactions between both vertical niche position and reproductive mode with maximum temperature of the warmest month. We chose to focus on maximum regional temperature because habitat modification often leads to a warmer and drier local environments (Prevedello *et al.*, 2019), and local microclimates are in part governed by regional climates. As ectotherms, amphibians are extremely sensitive to changes in environmental temperature, with thermal tolerances often dictating species responses to habitat modification (Nowakowski *et al.*, 2018c). We predict that these higher order interactions between traits, and between traits and the environment are common in determining species' responses to habitat conversion. Specifically, we predict that:

1). Among frogs that breed in water, arboreal species will be most heavily impacted by habitat conversion. We expect this to occur because habitat conversion may increase the distances between suitable water for reproduction and suitable trees for adult persistence, exposing these species to heightened risk during transit (Becker *et al.,* 2007). In contrast direct developing species may be equivalently sensitive regardless of arboreality, since they do not need to travel to water bodies.

2) Arboreal species will be less sensitive to habitat conversion in warmer areas, because life in the canopy has rendered them preadapted to deal with the hot and dry conditions of human-modified habitats. In contrast, in cooler environments understory dwelling species may be robust to (or potentially even benefit from) decreased canopy cover (and increased warming) associated with habitat conversion, because such temperature increases do not push them above their thermal limits.

3) Direct developing species will be most negatively impacted by habitat modification in warm climates as a result of increased desiccation of eggs in converted habitats, and their typically low thermal tolerances.

We find that reproductive mode and arboreality explain amphibian tolerance towards habitat conversion, and while trait-by-trait interactions are not detected, trait-by-environment interactions alter the magnitude and even direction of the traits' effects.

Methods:

Community composition data:

We compiled a database of 18 studies of amphibian abundance across land-use types, which includes 154 species (see Appendix S1). To do so, we combined previously compiled databases with additional studies seeking site level abundance data for tropical forests. We first used the PREDICTS database (Hudson *et al.*, 2017) as a foundation for obtaining amphibian abundance data across land cover types. We trimmed the data set to only include studies from tropical moist and semi-moist broadleaf forests, in order to restrict comparisons to environmental variation within similar biomes. We excluded studies that did not use standardized sampling methods, or that only provided presence or absence data. We removed studies which did not include primary forest as their natural sites to control for the impacts of any prior habitat conversion. Because our hypotheses were primarily concerning stark changes in habitat structure, we removed secondary forests from the analyzed dataset. This allowed us to focus on the availability of vertical stratification between primary forest and converted land uses. All abundances were corrected for sampling effort within studies. This yielded 14 studies. We then supplemented this database by searching the literature, finding an additional four studies that met our criteria.

We only included modified habitats that were actively being used for production; this included production of food, livestock and timber. We refer to these collectively as agriculture, though we recognize that the production expands further than just food. Not all converted habitats are the same, so we split these habitats into two categories that reflect how simplified the structure of the vegetation was—a likely driving force governing amphibian community composition. Structurally simple agriculture consisted of habitats with minimal vegetative structure, referring to crops, grasses, or otherwise short vegetation with few trees. This category includes corn, sugar cane, sun coffee without trees interspersed, as well as cattle pastures. Structurally complex agriculture contained converted habitat with some degree of vertical stratification remaining; including tree plantations(Malonza & Veith, 2012), mixed cacao and coffee farms (Pearman, 1997), and shade grown coffee plantations (Pineda & Halffter, 2004). The primary forest category consisted of studies in undisturbed forest, and in one case, we reclassified a mature secondary growth plot (as classified by the PREDICTS dataset) to primary forest based on the study referring to the area as a natural forest remnant, and describing the forest's age as being at least 400 years old (Sung *et al.*, 2012). Study locations came from 4 continents, with the greatest number of studies from Central America (Fig. 1).

Amphibian trait data:

We quantified anuran use of vegetative strata to characterize the vertical niche position of each species. To do so we scoured primary literature, amphibiaweb, and detailed regional books on amphibians (Duellman, 1970, 1978; Savage, 2002). Based on the information therein we scored vertical niche position in general microhabitats and calling habitat (when available) based on the proportion of observations or frequency of use of different strata as provided by the literature. Similar to the approach of the Elton traits database (Wilman *et al.*, 2014), we used a standardized protocol for translating descriptions of habitat use into a pseudo-continuous variable representative of the importance of each strata layer in a species overall habitat use (Fig. 2a.). General and calling microhabitat were broken down and scored based on its strata layer above the ground: below ground (-1), on ground (0), in understory (1), in mid-story (2), and in canopy (3). As such, a species could get an index value between -1 (fully fossorial) and 3 (fully canopy dwelling). We calculated, mean vertical niche position for a species as an average of the strata scores of both general habitat and calling habitat usage. For example, a species that spends half of the time in the canopy, a quarter of time in mid-story and a quarter of time in the understory would receive a general habitat score of 2.25 ($2.25 = 3*0.5 + 2*0.25 + 1*0.25$). Next, if the species is found calling half of the time from the mid-story and half of the time from the understory then it would receive a calling score of 1.5 ($1.5 = 2*0.5 + 1*0.5$). We calculated, mean vertical niche position for a species as an average of the strata scores of both general habitat and calling habitat usage, making the example frog have a vertical niche position of 1.875 ($1.875 = (2.25+1.5)/2$). Arboreality need not be constant, and some anurans display a drastic decrease in perch heights from wet to dry season (Basham & Scheffers, 2020). For our metric we were primarily interested in the general level of arboreality, so such intra-annual cycles in arboreality are not considered.

Using the same information sources as for vertical niche position, we also characterized species' reproductive mode, based on a combination of the habitat is which eggs are laid and the habitat where larva develop. Our classification contains three groups, representing a compromise between adequate sample sizes (per category) and representing differences in general habitat requirements for development, which may affect species response to land use. Species were classified as (1) terrestrial direct developers that forgo a larval stage, (2) lotic species, that have aquatic larvae that develop in moving water (lotic habitat), or (3) lentic species, that have aquatic larvae that develop in still waters (lentic habitat). We removed phylotelm (plant held water) breeding species from our study, as our dataset did not contain many. Detailed descriptions of amphibian trait scoring are contained in Appendix S2. All references for data sources can be found in Appendix S1.

Analysis:

To test the hypotheses that (i) species that use higher vegetative strata will be most severely reduced following conversion of tropical forest, and (ii) that this reduction will be most severe in structurally simple agriculture, we implemented a generalized linear mixed effect model. Doing so allowed us to analyze the fixed effects of land use and vertical niche position, along with their interaction. We controlled for impact of species, study, and site within study by including random intercept terms in our models. Models were run using a log link, and a negative binomial distribution (all models contain the same set of species (N = 154), studies (N = 18), sites (N = 462), and total number of observations (N = 6,742).

To accomplish our second goal of assessing trait-by-trait and trait-by-environment interactions we adjusted the fixed effect structure. The resulting fixed effects included land-use, vertical niche position, reproductive mode, and all their two-way interactions, or land-use, vertical niche position, and one of five climate variables (*maximum temperature of warmest month*{bio5}, *mean annual temperature*{bio1*}*, *annual precipitation*{bio12}, *temperature seasonality*{bio4} and *precipitation seasonality*{bio15}) or absolute latitude. For presentation, we focus on maximum temperature of warmest month (hereafter maximum temperature) as these models best predicted amphibian abundance and present results of latitude and the other climate variables in the supplement (Appendix 3). We obtained environmental data from the WorldClim dataset (Fick & Hijmans, 2017). We extracted the climatic variables at the individual sites within studies at a 2.5-minute scale, a resolution suitable for detecting large biogeographical patterns in climate, as is our focus. We examined the strength of the vertical niche position by reproductive mode (or climate) terms, to understand the strength of interactions in affecting community composition. We ran our models in R using the 'glmmTMB' package to implement generalized linear mixed effect models. We conducted model comparison of a full suite of models using AIC, and tested for term significance through likelihood ratio tests of nested models, evaluated against a chi-square distribution (appendix contains full model information). We calculated r^2 values for each model using the r.squaredGLMM function from the 'MuMIn' package in R (Nakagawa *et al.*, 2013; Johnson, 2014; Barton & Barton, 2019). To ensure our results were robust to phylogenetic non-independence, we incorporated phylogeny into our models using the glmmTMB_phylo function in R (Magnusson *et al.,* 2020). All models that included phylogeny were fit with the same basic structure as non-phylogenetic models but with phylogeny included as a random effect. The phylogeny used in the analyses was obtained from VertLife (Jetz & Pyron, 2018). Non-phylo models include a random effect of species, phylo models have an added a random effect structure corresponding to (Brownian motion) evolution along the phylogeny. As such each phylo model contains both a phylogenetic independent source of random variation (the 'species' random effect), and a phylogenetically dependent source of random variation (the 'phylo' random effect). In the phylo model (equivalent to Pagel's lambda model) we use relative variance between the "white noise" species random effect component versus the Brownian phylogenetic component to calculate lambda (i.e., h2) (Table 1,2, S2). All models presented in the main text are phylogeny models, we present AIC values for non-phylogenetic models in the supplement (Table S2). Inclusion of phylogeny does not alter the direction or significance of parameters effects.

Results:

After filtering our data, we retained 18 studies with 154 species, and over 6,700 individual observations of species within sites (Fig. 1). Values for niche position in our final data set ranged from fully fossorial to nearly entirely canopy dwelling species (vertical niche position scores from -0.99 to 2.52) though the average species centered between terrestrial and understory (mean vertical niche position of 0.54; Fig. 2b). Nearly half of the species had reproductive modes requiring still water (N = 75), while a sizeable portion of the tropical faunas were direct developing (N = 60). Fewer species had larvae that developed exclusively in streams (N = 19; Fig. 2b). Regardless of vertical niche position, average amphibian abundance steadily declined from primary forest, through complex agriculture (e.g. tree plantations, and tall perennial crops), and was lowest in simple agriculture (e.g. pastures, or short crops; Fig. 3). We found that high vertical niche position increases sensitivity to habitat conversion, but only in simple agriculture. As forest is converted from primary vegetation to simple agriculture the magnitude of declines increases with arboreality; yet when forest is converted to complex agriculture arboreal species maintain their abundance (*vertical niche* X *land use* interaction, df = 2, χ^2=30.74, p<0.001, Table 1).

To test the role of trait-by-trait interactions in determining species responses to habitat conversion we included interactions between reproductive mode, vertical niche position, and land uses, as well as all 2-way interactions. We find that interactions between traits did not influence how species respond to habitat conversion (*reproductive mode* X *vertical niche* X *land use* interaction, df = 4 χ^2=4.734, p=0.32), even though individual traits had strong stand-alone affects. In addition to niche position's role (described above), reproductive mode strongly impacted species response to habitat modification (*reproductive mode* X *land use* interaction, df = 4, χ^2=277.4, p<0.001, Table 1). Lentic breeding species are least sensitive to habitat conversion, even in the most severely modified habitats. Lotic breeding species and direct developing species are both negatively impacted regardless, and this decline is most severe for direct developing species in simple agriculture (Fig. 4).

Finally, we assessed the influence of environmental context on species response to habitat conversion and found that all tested climate variables interacted with land-use and traits to better explain amphibian abundance (Table 1; additional climate variables reported in Table S1). Maximum temperature interacted with individual traits to yield the best predictions of amphibian abundance of all models examined. Climate temperature strongly impacted how reproductive mode influenced response to habitat modification (*max temperature* X *reproductive mode* X *land use* interaction, df = 4, χ^2=16.323, p=0.0026; Fig. 4, Table 2, Fig 3.7). In contrast to lentic species, which are relatively resistant to habitat modification regardless of climate zone, lotic species suffer extreme declines after modification in hot climates, but are relatively resistant in colder ones. Similarly, direct developing frogs thrive in complex agriculture in colder climates, yet decline in abundance with such modification in hot climates. Direct developing frogs' declines are precipitous in simple agriculture regardless of temperature. Maximum temperature also controls how vertical niche position influences response to habitat modification, with this effect most notable for arboreal species in complex agriculture, which are positively affected by conversion to complex agriculture in warmer environments (*max temperature* X *vertical niche position* X *land use* interaction, df =2, χ^2=26.25, p<0.001 Fig. 5, Table 3, Fig 3.6).

Discussion:

Overall the hypothesis that arboreality leads to increased sensitivity to habitat conversion is supported, as arboreal species decline most severely in converted habitats with only short vegetation remaining (Fig. 3). However, arboreal species do not decline in converted habitats with taller vegetation, such as plantations, or coffee farms—instead abundances of terrestrial and understory species are reduced. As such, responses to habitat conversion seem to be modular—habitat conversion in lower strata can leave arboreal species relatively unharmed. This suggests that vertical niche position acts as a limiting niche axis for amphibians, where species track availability of their preferred vegetative strata. Other studies have found that species respond more to reductions in habitat structure availability than to plant community composition, suggesting that changes in habitat structure may be one of the primary mechanisms causing species declines (Garden *et al.*, 2007). Similarly, arboreal mammals also appear to be more sensitive to habitat conversion than terrestrial mammals, suggesting that this finding is likely not taxonomically restricted (Whitworth *et al.*, 2019).

Structurally complex agriculture, such as timber or oil palm plantations often have the greatest simplification of vegetation close to the ground, resulting in a cleared understory but a physically intact “canopy” environment. This may allow arboreal species to remain relatively unscathed. Alternatively, the increased abundance of arboreal amphibians in complex agriculture compared to primary vegetation may reflect increased detection probability, rather than a change in the number of individuals occurring there. Arboreal species are often more difficult to find compared to terrestrial species, even if they are no less common. The problem of detecting highly arboreal species becomes most severe as vegetation height increases (Vences *et al.*, 2008). Frogs can be considerably easier to find during periods of mating as they often descend from higher vegetation to the understory for egg deposition. During this time, they are more readily observable from the ground—the location that human observers generally station themselves. Tropical forests in particular have high structural complexity and very tall trees, which makes observing canopy dwellings species more difficult. Arboreal species that persist in converted habitats may be easier to find because the canopy height is lower and structural complexity is decreased in comparison to forest. As a result, increased detection probability may mask potential declines in abundance of arboreal species.

We tested the ability of trait-by-trait interactions to improve our understanding of species response to habitat modification but found no support for this hypothesis, at least between vertical niche position and reproductive mode. Despite this lack of evidence, such interactions may still be important in some taxa and between other sets of traits. However, reproductive mode on its own is important. Our findings show that lentic species in general are much less sensitive to habitat conversion than lotic or direct developing species, mirroring results found in other studies (Hirschfeld & Rodel, 2017; Nowakowski *et al.*, 2017). Direct developing species may be especially sensitive to habitat modification because they frequently require leaf litter to keep the eggs sheltered from unfavorable conditions, and potential predators. Agricultural land typically lacks such shelter-providing leaf litter. In turn, lotic species may be sensitive because deforestation drastically alters tropical streams, changing the flow of water and stream chemistry and leading to increased erosion, sedimentation and water temperature (Ramírez *et al.*, 2008). Experimental studies have shown that increasing sediment load in streams can negatively impact growth rate and development of tadpoles (Gillespie, 2002). Further, altered prey availability may be responsible for the declines of stream breeding species in agriculture, as macroinvertebrates in deforested streams in Madagascar decline as a result of shift in prey availability (Benstead & Pringle, 2004).Finally, we examined how the environmental context of habitat conversion influences species response, particularly whether the effect of vertical niche position and reproductive mode are consistent in different climates. We find that interactions between traits and the environment are both important and common, as the majority of climate variables we tested improved model fit and were retained in our final set of models (Table 1, Table S1). We find that overall lentic breeding frogs are the "winners" in converted habitats, however the context of climate influences responses of lotic breeders and direct developers. For example, in colder climates within the tropics, the impact of habitat conversion is reduced for lotic breeding species, and direct developers become most abundant in complex agriculture. Some direct developing species, shift their preferred habitats with elevation, often at high elevation, colder sites, preferring the warmer human converted habitat to natural vegetation (Frishkoff *et al.*, 2015). However, in warmer areas lotic and direct developing frogs decline in both forms of agriculture, while lentic species maintain their abundance in modified habitats. Direct developers often have lower thermal tolerances than lentic-breeding species (Nowakowski et al. 2018c, von May et al. 2019), which likely contributes to their increased sensitivity to habitat conversion in regions with greater maximum temperatures (indicated by greater abundance changes from forest to agriculture, Fig 4c). Lotic breeding species may be especially prone to declines due to habitat conversion in warmer areas due to increased water temperatures in deforested streams, which may be up to 6 °C warmer than forested streams (Ilha *et al.*, 2018), or decreased levels of dissolved oxygen, which can accompany the warming water.

Influences of the environment potentially drive the geographic variation in species responses that has been apparent in previous studies. For example, diurnal dung beetles are generally less sensitive to habitat conversion than nocturnal species when considering all regions. However including geographic context reveals that trait-based responses may be context dependent; in the neotropics diurnal dung beetles species are more sensitive than nocturnal species, while in Afro-Eurasia activity period has no effect (Nichols *et al.*, 2013). While we focus on maximum temperature here, we find support for effects of multiple climate variables, as well as latitude, on trait mediated responses to conversion (Appendix S3; Fig S3.1-S3.5, Table S1).

Regional temperature gradients influence species and assemblage-level responses to habitat conversion (Mantyka-pringle *et al.*, 2012; Nowakowski *et al.*, 2018b; Frishkoff *et al.*, 2019). For example, species turnover and reduced abundances associated with habitat conversion are most pronounced in warm, tropical regions (Mantyka-pringle *et al.*, 2012; Nowakowski *et al.*, 2018b). High sensitivity to habitat conversion in the tropics may arise from the interaction between thermal niches and local microclimates; for example, greater temperature differences are expected between open and closed-canopy habitats in the lowland tropics (Nowakowski *et al.*, 2018c) and many lowland tropical ectotherms are living close to their upper thermal tolerances (Sunday *et al.*, 2014). Recent research has established that the winners and losers of habitat conversion are often dictated by thermal tolerances, with species with higher thermal tolerances more likely to persist in anthropogenic land uses (Frishkoff *et al.*, 2015; Frishkoff *et al.*, 2016; Nowakowski *et al.*, 2018c; Williams *et al.*, 2019). As a result, species responses to local habitat conversion differ throughout their ranges as well as across gradients in climate and landscape structure (Frishkoff *et al.*, 2016; Frishkoff *et al.*, 2019; Frishkoff & Karp, 2019; Orme *et al.*, 2019).

We find that arboreal amphibians are less sensitive to habitat conversion in warmer areas. Infact arboreal species are on average even more abundant in complex agriculture in warm climates than in primary forest. Arboreal amphibians from warmer climates might be more resistant to habitat conversion as a result of preadaption to climate extremes. Because they live above thermally buffered forest understory, arboreal species frequently are exposed to greater variation in temperature and relative humidity (Madigosky & Vatnick, 2000; Scheffers & Williams, 2018); this may render these species resistant to the harsh changes in the environment which accompany habitat conversion. Further, arboreal species are often more resistance to water loss than terrestrial species, which may in turn facilitate survival in agriculture with relatively harsh microclimates (Wygoda, 1984, 1988; Young *et al.*, 2005). Some arboreal frogs, such as *Phyllomedusa* sp. have adaptations such as waxy secretions which help prevent desiccation (Mc Clanahan *et al.*, 1978; Delfino *et al.*, 1998), while others, such as *Smilisca baudinii*, have evolved the ability to form cocoons which allow them to persist through periods of drought (McDiarmid & Foster, 1987). In addition to their ability to reduce cutaneous water loss, arboreal amphibians often have higher thermal tolerances than predominantly terrestrial or aquatic amphibians (Tracy & Christian, 2005; von May *et al.*, 2019).However, in simple agriculture arboreal species always decline regardless of climate, as the loss of their preferred vegetative structure seems to negate any potential benefits of higher thermal tolerances (Fig. 5). This finding highlights the complexity of species responses to habitat modification: species may be filtered out by multiple mechanisms. Some species may decline as habitat modification pushes them outside of their thermal tolerances despite an undisturbed microhabitat. Other species may decline because of the loss of their preferred vegetation stratum, despite microclimate conditions being within their tolerance limits.

Ultimately, species sensitivity to habitat conversion depends on multiple factors, both species-specific and context dependent. Our results highlight that caution is needed to understand how response to habitat conversion is mediated by traits, because the same trait (*e.g.* reproductive mode) may behave differently in alternative climate zones. However, by directly accounting for these climate interactions we demonstrate how it is possible to improve our understanding of species responses to environmental change. Not all forms of habitat conversion are equal in their impacts on biodiversity (Newbold *et al.*, 2015), with the most structurally simple human land uses being the most damaging. If we wish to preserve relatively diverse communities, when feasible we should prioritize crop types that maximize structural complexity, or add structural complexity to simplified crops (e.g. hedgerows or agroforestry). Preserving biodiversity hinges on our ability to identify the species which are most sensitive to specific anthropogenic changes, particularly habitat conversion and climate change. Future work should focus on identifying sensitive species through incorporating trait-by-environment interactions to more fully understand the mechanisms driving sensitivity. Improved predictability of species sensitivity will then allow us to implement efforts to identify and protect areas that effectively maintain these most sensitive species.

Acknowledgements

We would like to thank Jonathan Campbell who assisted with identifying natural history information for poorly known species. We also thank William Budnick for helpful discussions regarding this research. This study was made possible by the Herpetology Library at the University of Texas at Arlington Amphibian and Reptile Diversity and Research Center. Finally, we are grateful for those who take the time to record and disseminate detailed natural history information, making analyses such as ours possible.

Data availability statement

Abundance data used in this study came primarily from the PREDICTS database (Hudson et al., 2017); all additional sources of abundance data are found in Supporting Information Appendix S1. All code, trait and abundance data required to perform the analyses are available on Figshare: https://doi.org/10.6084/m9.figshare.13160399.v1

Chapter 2 Figures and tables

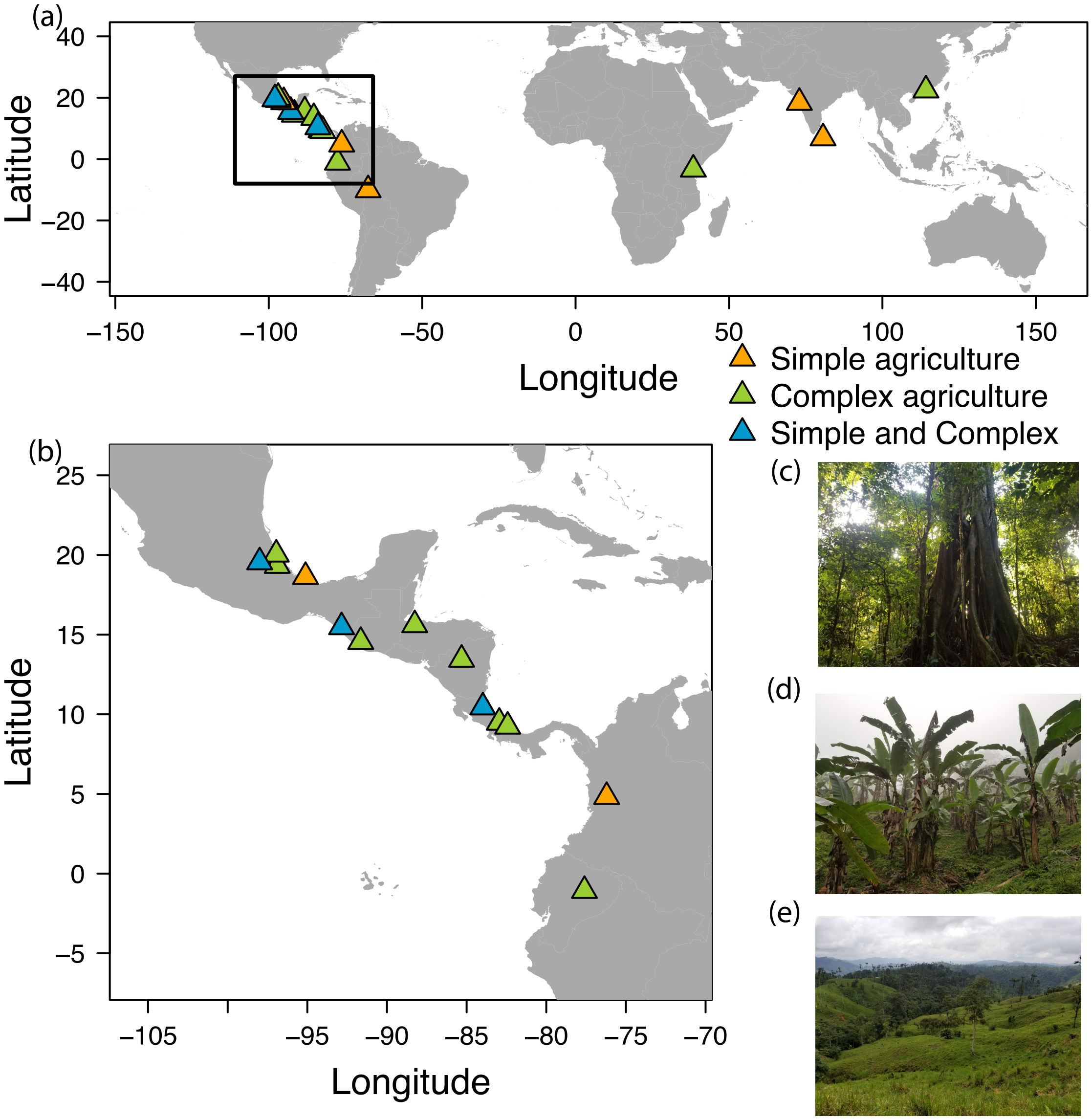


Figure 1 a) Distribution of 18 study locations included in our analysis. b) The greatest concentration of studies (N=14) is in Central America and northern South America. All studies contained c) primary forest, while 13 contained d) complex agriculture, and 8 studies contained e) simple agriculture.

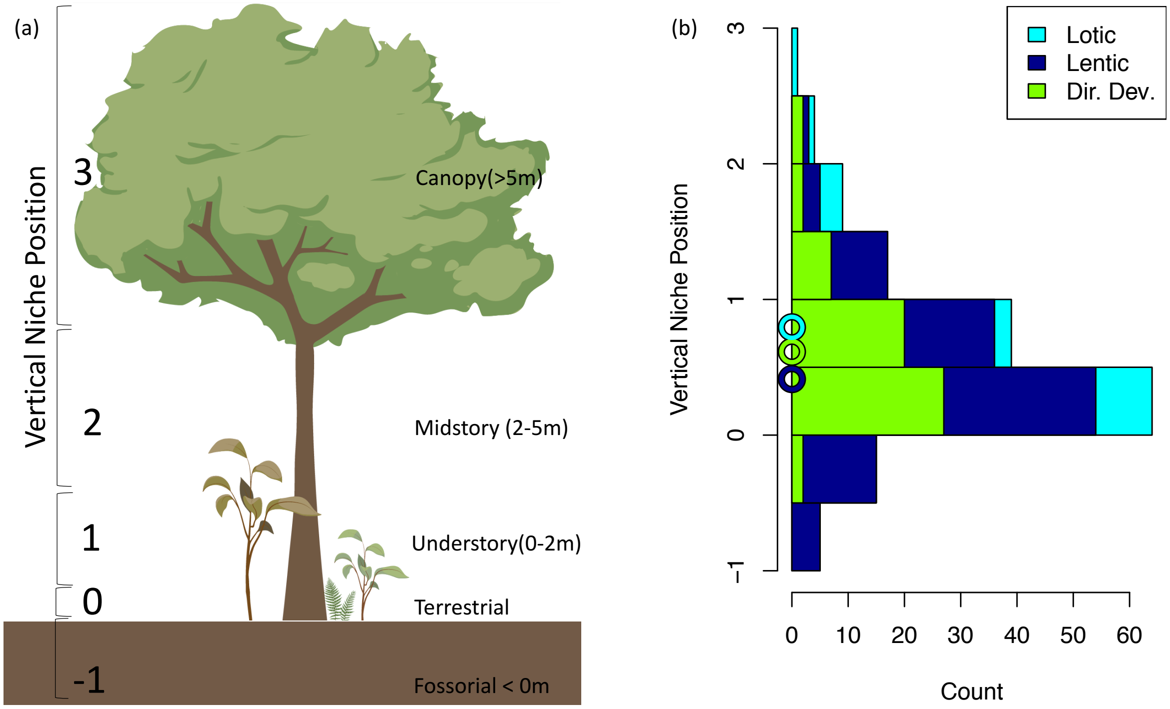


Figure 2 a) Schematic depicting how vertical niche position was scored numerically based on species accounts of the height and/or vegetative stratum where species occurred. b) Histogram of species' vertical niche position within each reproductive mode. There were a total of 75 species whose larvae developed in lentic (still) water, 19 lotic (stream) species, and 60 direct developing species included in the analysis. Means within each group are represented by a color-coded open circle.

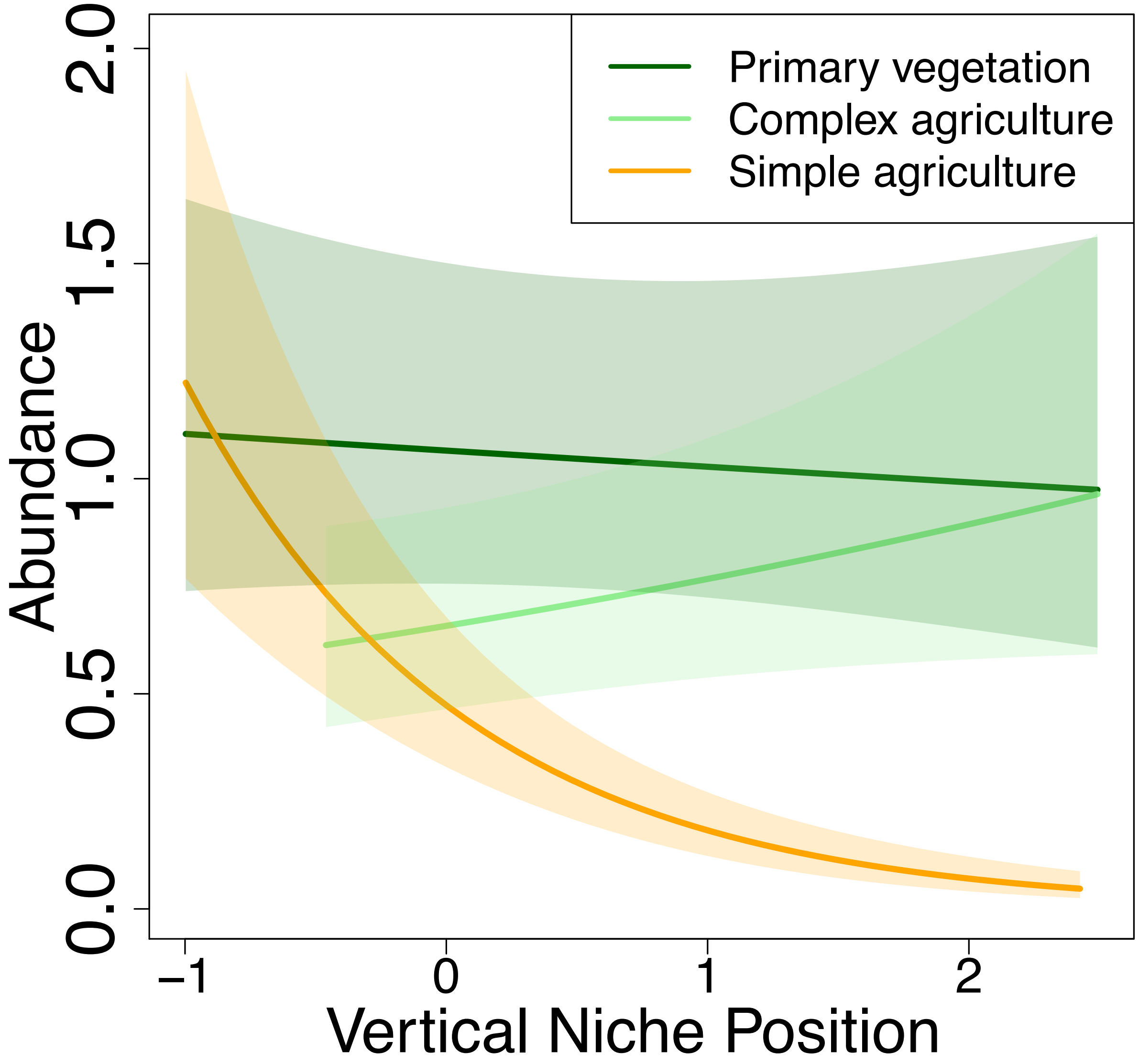
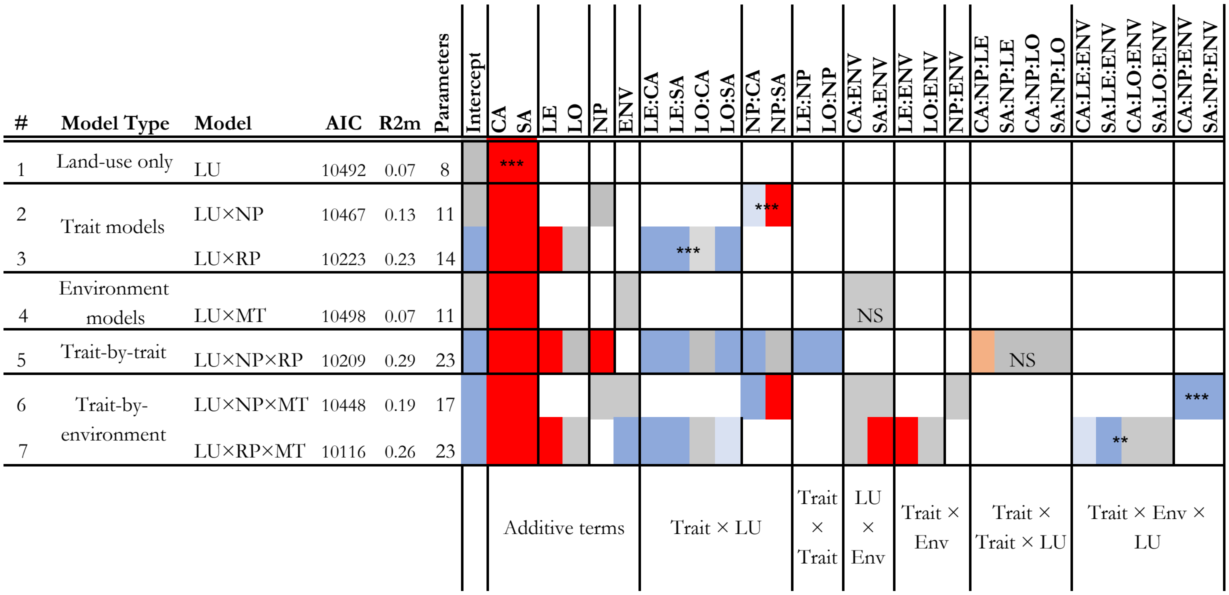


Figure 3 Model-predicted relationship between vertical niche position and abundance in three different land uses. Line segments span the range of niche position for which we had data within a given land use. Shaded regions represent standard error for model predictions, predictions shown here correspond to model 2 (Table 1.).

Table 1. All models predicting amphibian abundance. R^2m refers to marginal R^2. Terms (LO=lotic, LE=lentic, ENV=climate variable, NP=niche position, CA= complex agriculture, SA=simple agriculture, MT= Maximum Temperature; Bio5 from WorldClim) that were significant based on Wald tests are indicated by dark red or blue ($p < 0.05$), while lightly shaded colors $p < 0.1$. Blue represents a positive parameter estimate and red represents a negative parameter estimate. From each model, we denote whether the set of terms is significant p >0.1(NS), p<0.01(**), p<0.001(***), as evaluated by a likelihood ratio test of nested models. The model intercept was in reference to a species in primary vegetation, that is direct developing (when reproductive mode was included in the model). All models have the same sample size (total observations = 6,742), and contain the full set of species (N = 154).



#	Model Type	Model	AIC	R2m	Parameters	Intercept	CA	SA	LE	LO	NP	ENV	LE:CA	LE:SA	LO:CA	LO:SA	NP:CA	NP:SA	LE:NP	LO:NP	CA:ENV	SA:ENV	LE:ENV	LO:ENV	NP:ENV	CA:NP:LE	SA:NP:LE	CA:NP:LO	SA:NP:LO	CA:LE:ENV	SA:LE:ENV	CA:LO:ENV	SA:LO:ENV	CA:NP:ENV	SA:NP:ENV
1	Land-use only	LU	10492	0.07	8	▨	🟥 ***	🟥																											
2	Trait models	LU×NP	10467	0.13	11	▨	🟥	🟥			▨						▤	🟥 ***																	
3		LU×RP	10223	0.23	14	🟦	🟥	🟥	🟥	▨			🟦	🟦 ***	░	🟦																			
4	Environment models	LU×MT	10498	0.07	11	▨	🟥	🟥				▨									▨	▨ NS													
5	Trait-by-trait	LU×NP×RP	10209	0.29	23	🟦	🟥	🟥	🟥	▨	🟥		🟦	🟦	▨	🟦	🟦	▨	🟦	🟦						🟧	▨	▨ NS	▨						
6	Trait-by-environment	LU×NP×MT	10448	0.19	17	🟦	🟥	🟥			▨	▨					🟦	🟥			▨	▨			▨									🟦 ***	🟦
7		LU×RP×MT	10116	0.26	23	🟦	🟥	🟥	🟥	▨		🟦	🟦	🟦	▨	▤					▨	🟥	🟥	▨						▤	🟦 **	▨	▨		
							Additive terms						Trait × LU						Trait × Trait		LU × Env		Trait × Env			Trait × Trait × LU				Trait × Env × LU					

Table 2. Model summary for model 6 (Table 1.). We denote whether each parameter is significant p <0.1(.), p<0.05(*), p<0.01(**), p<0.001(***) based on Wald tests. Negative binomial dispersion parameter, phi= 5.85. Pagel's lambda = 0.23.

<table>
<tr><th colspan="4">Model 6 : LU * Max Temp * Niche Pos</th></tr>
<tr><th colspan="4">Fixed Effects</th></tr>
<tr><th>Parameters</th><th>Parameter Estimate</th><th>Standard error</th><th>p-value</th></tr>
<tr><td>Intercept</td><td>0.05</td><td>0.35</td><td></td></tr>
<tr><td>LU : Comp Ag</td><td>-0.40</td><td>0.13</td><td>**</td></tr>
<tr><td>LU : Simp Ag</td><td>-1.17</td><td>0.14</td><td>***</td></tr>
<tr><td>Max Temp</td><td>0.11</td><td>0.13</td><td></td></tr>
<tr><td>Niche Pos</td><td>-0.06</td><td>0.11</td><td></td></tr>
<tr><td>Comp Ag : Max Temp</td><td>0.01</td><td>0.14</td><td></td></tr>
<tr><td>Simp Ag : Max Temp</td><td>-0.07</td><td>0.10</td><td></td></tr>
<tr><td>Comp Ag : Niche Pos</td><td>0.23</td><td>0.08</td><td>**</td></tr>
<tr><td>Simp Ag : Niche Pos</td><td>-0.61</td><td>0.15</td><td>***</td></tr>
<tr><td>Max Temp : Niche Pos</td><td>-0.06</td><td>0.05</td><td></td></tr>
<tr><td>Comp Ag : Niche Pos : Max Temp</td><td>0.22</td><td>0.08</td><td>**</td></tr>
<tr><td>Simp Ag : Niche Pos : Max Temp</td><td>0.51</td><td>0.12</td><td>***</td></tr>
<tr><th colspan="4">Random Effects</th></tr>
<tr><th></th><th colspan="3">Standard Deviation</th></tr>
<tr><td>Phylogeny</td><td colspan="3">0.43</td></tr>
<tr><td>Species</td><td colspan="3">0.79</td></tr>
<tr><td>Study</td><td colspan="3">1.04</td></tr>
<tr><td>Site</td><td colspan="3">0.59</td></tr>
</table>

Table 3. Model summary for model 7(Table 1.) We denote whether each parameter is significant p <0.1 (.), p<0.05(*), p<0.01(**), p<0.001(***) based on Wald tests. Negative binomial dispersion parameter, phi= 3.86. Pagel’s lambda = 0.21.

Model 7: LU * Max Temp * RP			
Fixed effects			
Parameters	**Parameter Estimate**	**Standard error**	**p-value**
Intercept	1.05	0.39	**
Comp Ag	-0.75	0.14	***
Simp Ag	-3.30	0.23	***
Max Temp	0.61	0.14	***
Lentic	-1.95	0.29	***
Lotic	-0.58	0.40	
Comp Ag : Max Temp	-0.16	0.15	
Simp Ag : Max Temp	-0.45	0.15	**
Comp Ag : Lentic	1.18	0.17	***
Simp Ag : Lentic	3.86	0.24	***
Comp Ag : Lotic	-0.25	0.24	
Simp Ag : Lotic	1.18	0.66	.
Max Temp : Lentic	-1.04	0.11	***
Max Temp : Lotic	0.02	0.18	
Comp Ag : Max Temp : Lentic	0.30	0.17	.
Simp Ag : Max Temp : Lentic	0.46	0.18	*
Comp Ag : Max Temp : Lotic	-0.27	0.22	
Simp Ag : Max Temp : Lotic	-0.63	0.40	
Random Effects			
	Standard Deviation		
Phylogeny	0.48		
Species	0.94		
Study	1.07		
Site	0.48		

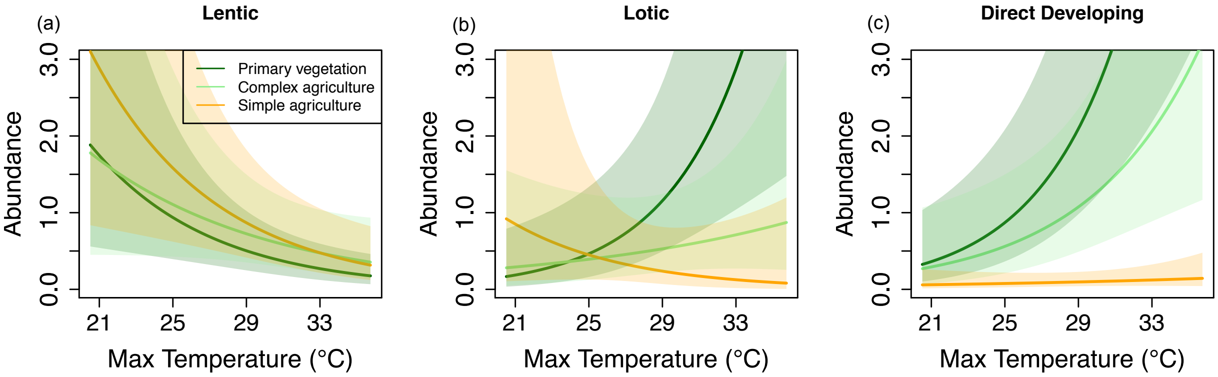


Figure 4 Model predicted relationship between reproductive mode and abundance in three different land uses for (a) lentic breeding species (pond breeders), (b) lotic breeding species (stream breeders), and (c) direct developing species (model 7, Table 3). Shaded regions represent standard error.

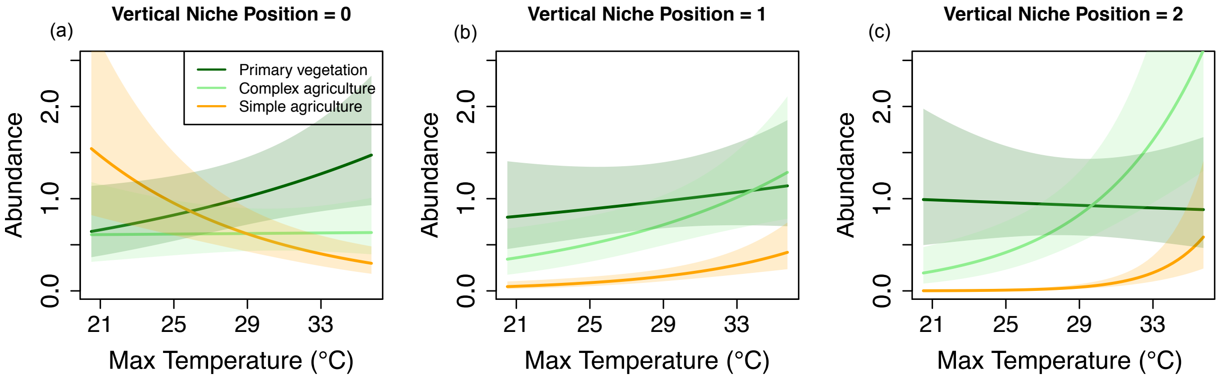


Figure 5 Model predicted relationship between vertical niche position and abundance across land uses for climate zones (model 6, Table 2). Vertical niche position 0 (a) represents a species which is terrestrial ;(b) vertical niche position 1 represents a species primarily found in the understory; (c) vertical niche position 2 represents a species primarily found in the midstory. Shaded regions represent standard error.

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Appendix 2.1. Data Sources

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Appendix 2.2. Amphibian scoring protocol:

To obtain natural history information we first searched for the species on *AmphibiaWeb* (AmphibiaWeb, 2019). Some regions we used other sources in addition to AmphibiaWeb, to supplement our initial search; Ecuador (Ron et al., 2019), Costa Rica (Savage, 2002; Leenders, 2016), Hylid frogs (Duellman, 1970), Peruvian direct developing frogs (Lehr & Duellman, 2009), and for Amazonian frogs (Duellman, 2005). We supplemented our information for all species by then searching on google scholar, web of science, and researchgate, with the species name and the terms: ‘habitat use’, ‘microhabitat’, ‘foraging’, ‘reproductive habitat’, ‘calling behavior’, ‘reproductive mode’, ‘niche’, ‘ecology’ and ‘behavior’. We exhausted all available sources based off of those search methods to obtain the information. When information was further unavailable we would consult *Amphibians of the World* (Frost, 2020), to find papers which include information on the frog. We used the extensive library at the University of Texas at Arlington Amphibian and Reptile Diversity Center to obtain hard copies of unavailable articles or books which contained natural history information. We were unable to obtain natural history information for a few species of Central American frogs, so we consulted Dr. Jonathan Campbell who then verbally described their habitat use from his field experience which we recorded and scored. Species which we were unable to fully score habitat uses or reproductive mode were removed from the study.

We classified species habitat use into the following categories initially: Canopy, Midstory, Understory, Terrestrial, Aquatic, and Fossorial. Our scoring of frog habitat use was based off of observations of the species, rather than where they may be, yet not be observed. To reflect this, we described the layers of the forest on a scale which 5m and up represents the canopy, as species that use the canopy may be observed down to this height in the forest, yet it is extremely difficult to observe species above about 15m in a forest. Very few descriptions of species describe species being observed greater than 15m, although some species may live over 60m above the ground in the canopy. We translated verbal descriptions referring to species occurring above 5m, or where the canopy is mentioned in the description as records of a species in the canopy, when species were mentioned to occur in arboreal bromeliads we would count that as half canopy and half midstory. Midstory for use referred to trunks of trees or large branches, and heights corresponding to 2-5m high. Understory consisted of all vegetation occurring from 0-2m high, as well as verbal descriptions mentioning species occurring in bushes, saplings, grassy vegetation or other low lying vegetation. When scoring the general habitat use of a given species we took into account all sources of information and gave most weight to sources with greater detail or volume of information of habitat use for a given species; when concrete data from a study assessing microhabitat use of a species was available we always used that data to directly be taken into account in the species score. For example, if an IUCN species account vaguely states: “a species is usually found in trees” we would give more weight to an account from *Hylids of Middle America* (Duellman, 1970) that states: “species is always found at least

10-15m above the ground". As all species were scored by Alex Murray we feel that consistency was achieved across all species included in our study.

We classified all habitat, including reproductive habitat initially as pseudocontinuous variables representing the proportion of time using a given habitat, this included reproductive habitat. We initially classified the reproductive habitat broken down into the area of deposition receiving half of the score and the area of egg development receiving half of the score. For species, which breed in more than one type of habitat, particularly for species which breed in water we reclassified from the initial score into one of two groups, lentic and lotic. Some species of frogs with aquatic tadpoles lay eggs in places other than bodies of water, such as on the surfaces of leaves, depressions on the ground or in the leaf litter; for such species we scored them based off of whether the tadpoles developed in moving(lotic) or still water(lentic). For example, a species which lays its eggs on leaves overhanging a stream, and has tadpoles which develop in the stream would be considered lotic breeding. While a frog which lays eggs in depressions next to rivers could be lentic or lotic breeding. If the species has tadpoles which live in pools outside of the current of the stream, say flooded forest in pools of water left from high water then it would be classified as lentic breeding, while a species which has eggs washed into the stream and tadpoles living in moving water of the stream would be classified as lotic breeding. As lentic breeding is generally more common in frogs and often associated with generalist species, we only classified species which breed in lotic water more than 80% of the time as lotic breeding, allowing us to isolate species which truly require moving water to breed in, rather than species which are just indifferent.

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Appendix 3 Supplemental Figures and Tables

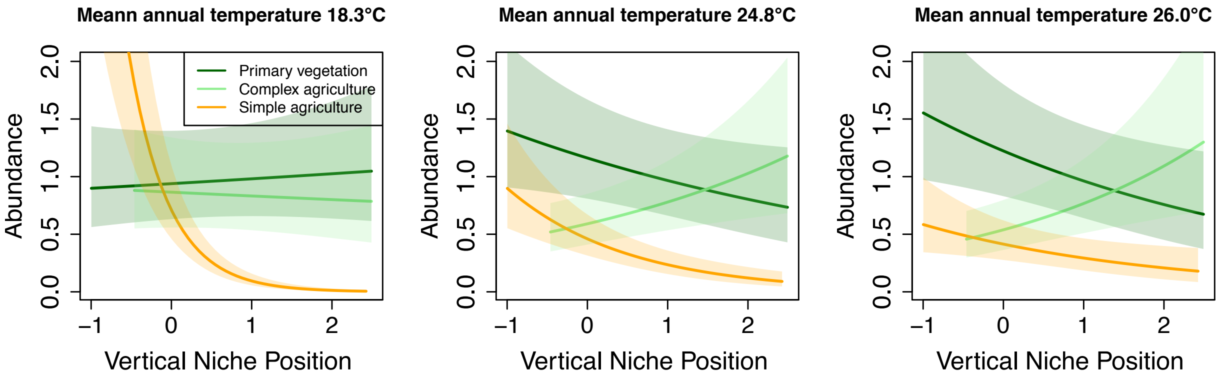

Figure S3.1 Model predicted relationship between vertical niche position and abundance in three different land uses for three different climate zones. Low (a) represents the 10th percentile of the range for mean annual temperature among sites, (b) mid represents the 50th percentile and (c) high is the 90th percentile. Shaded regions represent standard error.

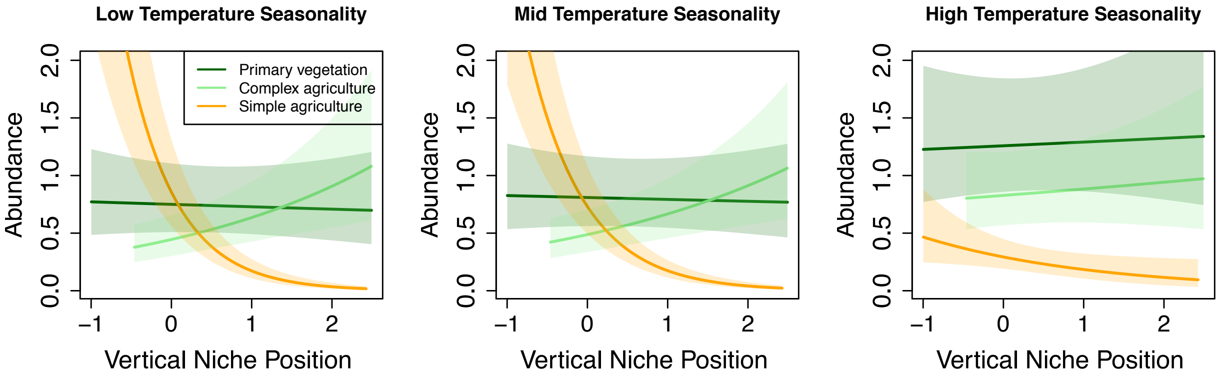

Figure S3.2 Model predicted relationship between vertical niche position and abundance across land uses for three different climate zones. Low (a) represents the 10th percentile of the range for temperature seasonality among sites, (b) mid represents the 50th percentile and (c) high is the 90th percentile. Shaded regions represent standard error.

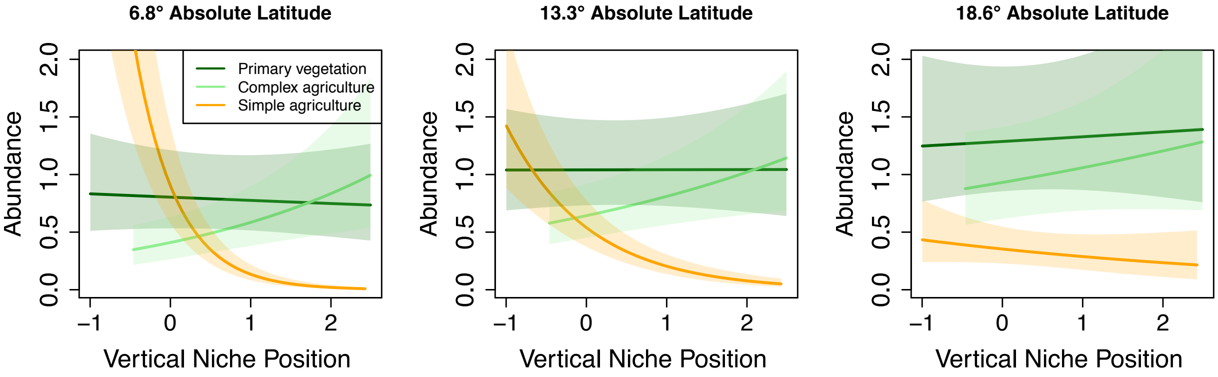

Figure S3.3 Model predicted relationship between vertical niche position and abundance across land uses for three latitudes. Low (a) represents the 10th percentile of the range for absolute latitude among sites, (b) mid represents the 50th percentile and (c) high is the 90th percentile. Shaded regions represent standard error.

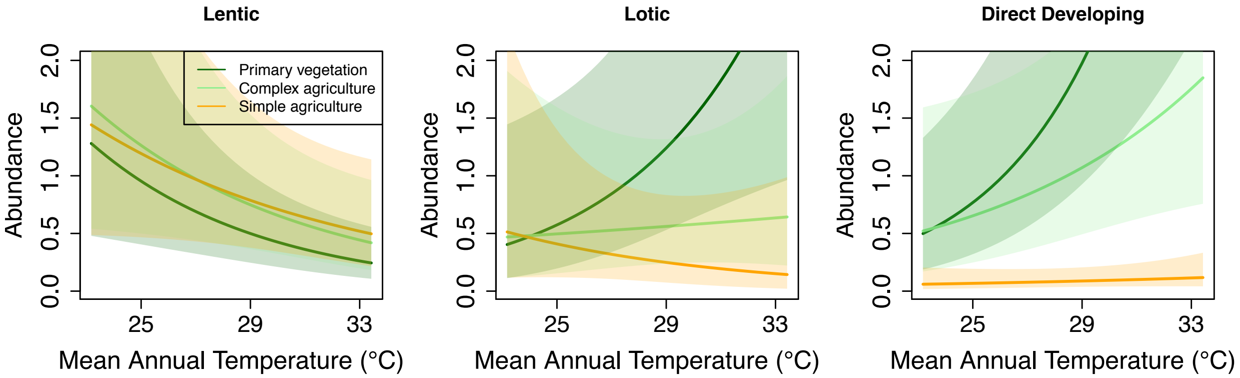

Figure S3.4 Model predicted relationship between reproductive mode and abundance across land uses for (a) lentic breeding species (pond breeders), (b) lotic breeding species (stream breeders), and (c) direct developing species. Shaded regions represent standard error.

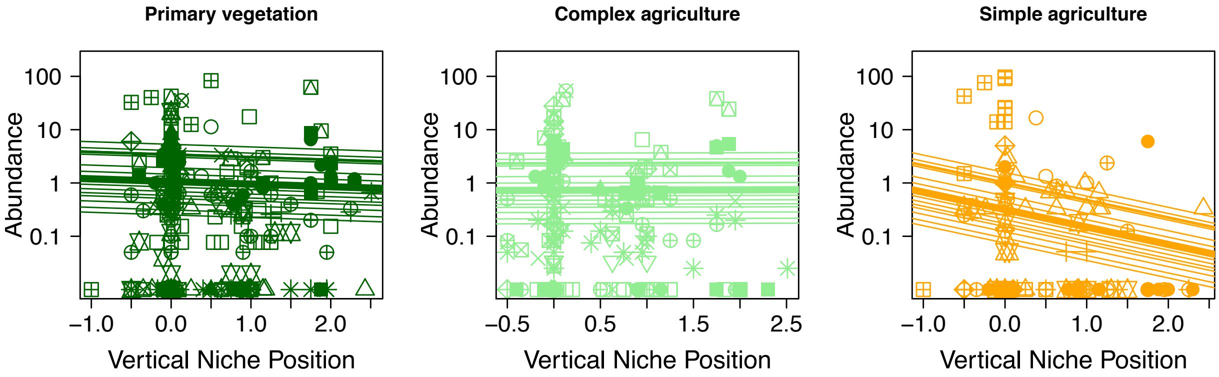

Figure S3.5 Mean abundance of species within land use for each study, shapes are consistent across studies. Lines represent model predicted relationship between vertical niche position and abundance by land use, intercepts are shifted based off of the effect of each individual study on abundance. Predicted relationship displayed based off of Model 2.

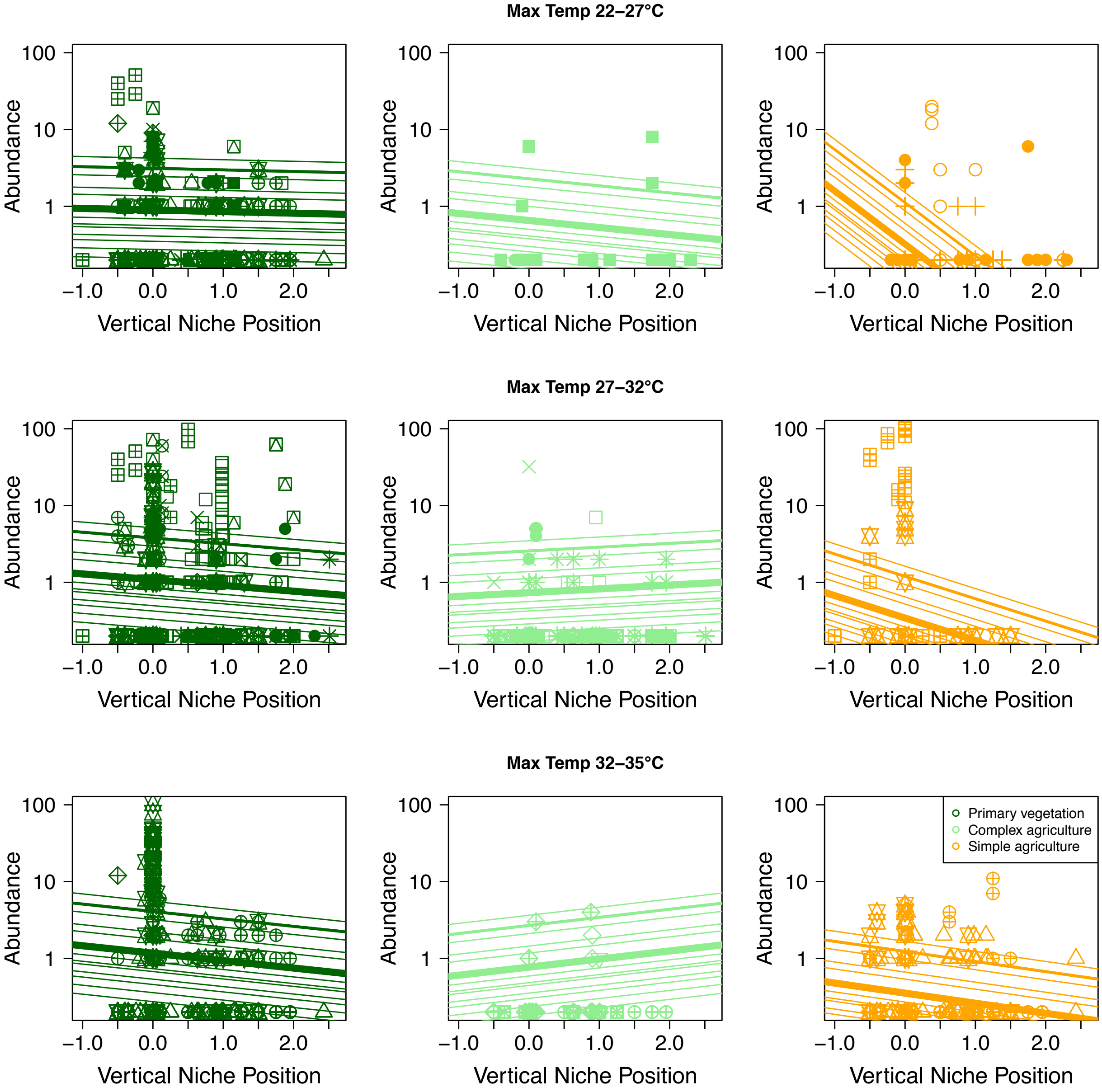

Figure S3.6 Raw abundance data for each of the 6,742 data points included in study. Lines represent model predicted relationship between vertical niche position, maximum temperature, land use and abundance. Intercepts are shifted based off of the effect of each individual study on abundance. Predicted relationship displayed based off of Model 6.

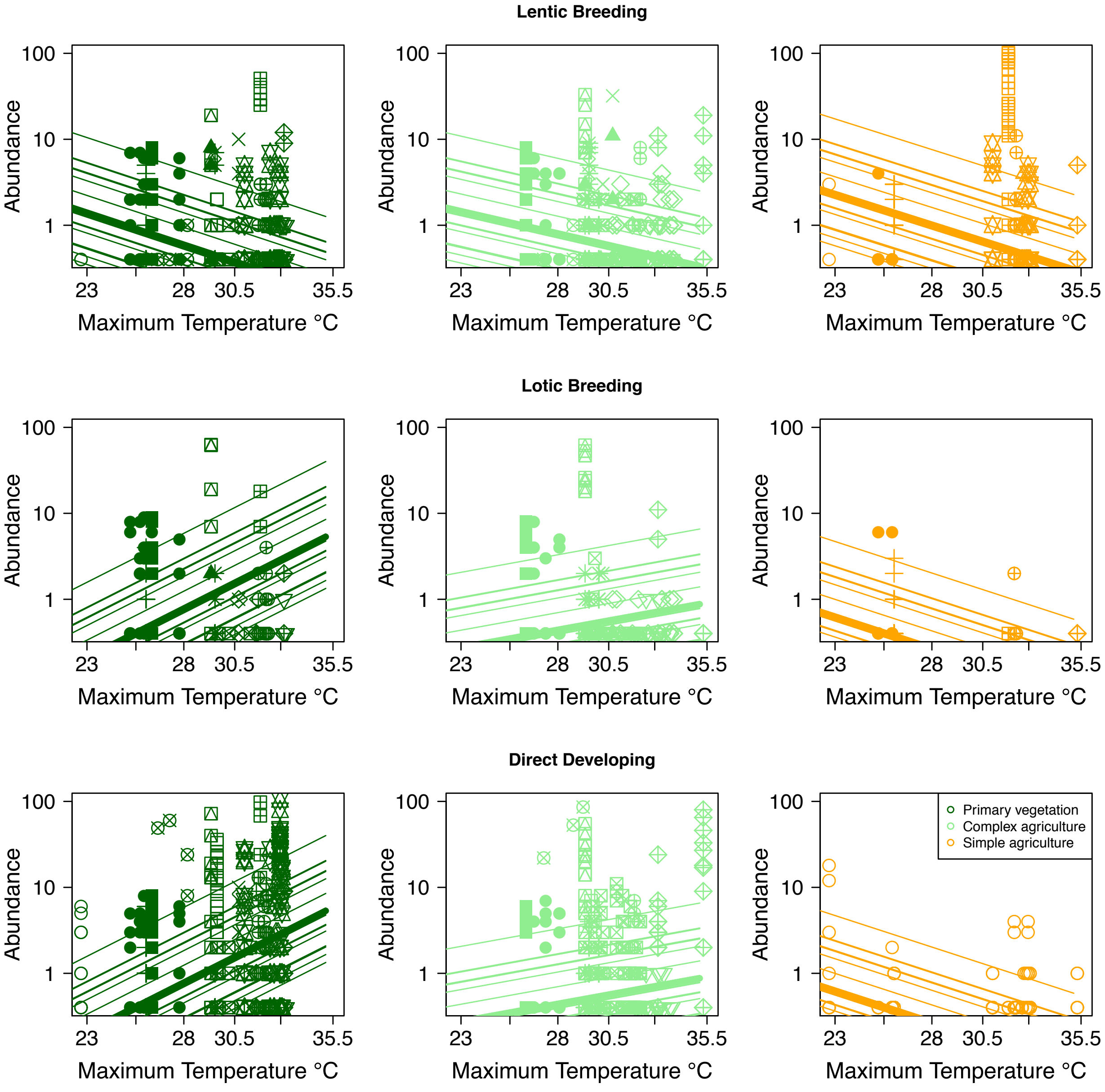

Figure S3.7 Raw abundance data for each of the 6,742 data points included in study. Lines represent model predicted relationship between maximum temperature, reproductive mode, land use and abundance. Intercepts are shifted based off of the effect of each individual study on abundance. Predicted relationship displayed based off of Model 7.

Table S1. Top models including AIC and marginal R^2 values. Dark colors, red and blue represent terms (LO=lotic, LE=lentic, ENV=climate variable, NP=niche position, CA= complex agriculture, SA=simple agriculture, MT= Max Temperature, MAT= Mean Annual Temperature, ST=Temperature Seasonality, AP= Annual Precipitation, SP=Precipitation seasonality, AL=Absolute Latitude) that were significant in the models with $p < 0.05$, while lightly shaded colors $p < 0.1$. Blue represents a positive parameter estimate and red represents a negative parameter estimate. From each model, we denote whether the set of terms is significant p >0.1(NS), p<0.01(**), p<0.001(***). The model intercept was in reference to a species in primary vegetation, that is direct developing (when reproductive mode was included in the model).

Model Type	Model	AIC	R2m	Parameters	LU	LU:RP	LU:NP	LU:ENV	LU:RP:NP	LU:ENV:NP	LU:ENV:RP
Land-use only	LU	10492	0.07	2	***						
Trait models	LU×NP	10467	0.13	5			***				
	LU×RP	10223	0.23	8		***					
Environment models	LU×MT	10498	0.07	5				NS			
	LU×MAT	10497	0.07	5				NS			
	LU×ST	10488	0.08	5				*			
	LU×MAP	10493	0.09	5				NS			
	LU×SP	10467	0.16	5				***			
	LU×AL	10494	0.08	5				NS			
Trait-by-trait	LU×NP×RP	10209	0.29	17					NS		
Trait-by-environment	LU×NP×MT	10448	0.19	11						***	
	LU×NP×MAT	10453	0.19	11						***	
	LU×NP×ST	10449	0.15	11						*	
	LU×NP×MAP	10463	0.15	11						NS	
	LU×NP×SP	10440	0.23	11						NS	
	LU×NP×AL	10449	0.16	11						***	
	LU×RP×MT	10116	0.26	17							**
	LU×RP×MAT	10118	0.26	17							***
	LU×RP×ST	10212	0.23	17							NS
	LU×RP×MAP	10182	0.23	17							NS
	LU×RP×SP	10148	0.28	17							***
	LU×RP×AL	10206	0.22	17							.

Table S2. Model comparison of phylogenetic and non-phylogenetic models for models discussed in main text. Values for ΔAIC represent difference in AIC from non phylo model and phylo model. Non-phylo models include a random effect of species, phylo have an added a random effect structure corresponding to evolution along the phylogeny. As such each model contains both a phylogenetic independent source of random variation (the 'species' random effect), and a phylogenetically dependent source of random variation (the 'phylo' random effect). Partitioning the amount of variance explained by the model between these two sources of random variation yields the pagel's lambda value, or heritability value .

#	Model Type	Model	AIC(non-phylo)	AIC(phylo)	ΔAIC	R2m(non-phylo)	R2m(phylo)	Pagel's lambda
1	Land-use only	LU	10515	10492	23	0.07	0.07	0.20
2	Trait models	LU×NP	10486	10467	19	0.16	0.13	0.22
3		LU×RP	10226	10223	4	0.25	0.23	0.22
4	Environment models	LU×MT	10521	10498	23	0.07	0.07	0.19
5	Trait-by-trait	LU×NP×RP	10211	10209	3	0.32	0.29	0.25
6	Trait-by-environment	LU×NP×MT	10467	10448	19	0.22	0.19	0.23
7		LU×RP×MT	10119	10116	3	0.28	0.26	0.21

Chapter 3

Ancient occupation by humans leads to missing bird diversity in otherwise natural habitats

Alexander H. Murray[1], Luke O. Frishkoff[1]

[1]Department of Quantitative Biology, University of Texas at Arlington, Arlington, Texas, USA

Abstract

Habitat modification is responsible for great amounts of biodiversity loss. However, variation exists in how communities respond to land-use change. One interesting option is that historical factors have played a role in determining the sensitivity of contemporary communities. We use bird community data from 54 studies across the world to test our primary hypothesis, that historical human presence reduces community sensitivity to land-use change. We find humans have reduced the sensitivity of communities, as primary vegetation in areas with larger human populations contain fewer species, and fewer species sensitive to land-use change, meanwhile species richness in simple agriculture is unimpacted. The greatest impact of humans date back to 12,000 YBP suggesting that early humans may have caused even more widespread extinctions (local/global) than previously appreciated.

Main Text:

Biodiversity is declining, and an imperative for the 21st century is to understand why. Anthropogenic influences such as habitat modification, climate change and invasive species contribute to many declines (Pereira *et al.*, 2012). Amongst these, habitat modification is responsible for threatening the greatest number of species but the degree to which habitat modification results in declines varies substantially between studies and species. Modern day conditions account for some of this variation, as both the severity of land use change (Newbold *et al.*, 2015; Murray *et al.*, 2021; Etard *et al.*, 2022) and climatological context alter outcomes of land-use change (Murray *et al.*, 2021).For example, the effects of habitat loss and fragmentation are most negative in areas with warm maximum temperatures (Mantyka-pringle *et al.*, 2012). But an intriguing possibility is that historical factors also play a key role in explaining modern variation in biodiversity loss due to habitat conversion. The extinction filter hypothesis (Balmford, 1996) proposes such a phenomena, by which the ability to deal with future disturbance is determined by prior exposure to similar disturbances. Perhaps areas with long histories of human disturbance have modern day communities that are more resistant to biodiversity loss due to land-use change. If so, the underlying mechanism could take two alternative routes. First, communities may have already faced a similar threat and lost species which are unable to deal with the threat, leaving only resilient species behind. Alternatively, species exposed to a long history of threats may have adapted (either evolutionarily or through behavioral plasticity) to cope, allowing them to be less sensitive to future threats.

Support for the extinction filter hypothesis exists for some forms of habitat change. Communities which have been subjected to less frequent natural disturbances tend to contain species that are more sensitive to human-caused forest loss (Drapeau *et al.*, 2016). Regions impacted by historical disturbance(Fire, storms and deforestation) have fewer forest dependent species remaining today (Betts *et al.*, 2019), and in the most intact landscapes habitat modification has the most damaging impacts on biodiversity (Betts *et al.*, 2017). Archeological evidence supports the idea that historical human impacts may have had large biodiversity consequences. Wherever humans appeared as they spread out of Africa, extinctions followed in short time (Diamond, 1989). In Australia human-induced extinctions may date back 40-50,000 YBP (years before present) when large mammals were lost shortly after human arrival on the continent (Miller *et al.*, 2005; Rule *et al.*, 2012). Similar declines occurred in in the Americas, approximately 12,000 years ago when extinctions of megafauna coincided with human arrival and spread (Stuart, 2015; Prates & Perez, 2021). While the megafauna extinctions are most prominently documented, prehistoric extinctions caused by humans are widespread across the tree of life. Following human arrival, many reptile and amphibian species went extinct in New Zealand (Towns & Daugherty, 1994). At least 581 prehistoric extinctions have been documented in birds (Sayol *et al.*, 2020) with many of these extinctions occurring on islands, however, mainland areas have been impacted as well. Yet these numbers are likely much lower than the true number (Duncan *et al.*, 2013), as poorly documented "dark extinctions" (Boehm & Cronk, 2021) or "dark extirpations" could be widespread. Early humans contributed to extinctions in a variety of ways including: hunting (Duncan *et al.*, 2002), introductions of non-native species, and alteration of natural habitats (forested areas often became heavily degraded and more open) (Haberle, 2007; Summerhayes *et al.*, 2010; Yerkes *et al.*, 2012; Zheng *et al.*, 2021). Given the many ways in which humans have historically impacted species, human population size may best represent the totality of human impacts at a location.

Here, we test the hypothesis that early humans caused sensitive species to be lost leading to communities which are less sensitive to habitat modification. To accomplish this we use estimates of human populations dating back >12,000 YBP and pair this with modern-day bird community data. We aim to differentiate between two competing hypotheses, the dark extinction hypothesis and the adaptive resilience hypothesis. The dark extinction hypothesis predicts that species richness should be lower in primary habitat in regions with large historical human presences when compared to areas with lower historical human presence, due to the loss of the most sensitive species from the ecosystem. Because species in human-modified habitats are by definition less sensitive to human presence, these habitats would not suffer the same declines. Alternatively, the adaptive resilience hypothesis predicts that sustained human presence should generate an increase in resilient species (either through adaptation, acclimation, or selective immigration). As such, this hypothesis predicts an increase in human-associated species in areas with sustained human presence. Such a scenario may be possible as a wide variety of animals have been shown to adapt to human influences (Winchell *et al.*, 2016; Sullivan *et al.*, 2017; Mascarenhas *et al.*, 2022), and human commensals are frequently among the most successful invasive species, demonstrating an ability to colonize human impacted areas through time (Ravinet *et al.*, 2018; Puckett *et al.*, 2020).

We used the PREDICTS Database (Hudson *et al.*, 2017) to obtain bird community data in different land uses across the globe. We classified land use into 5 different categories based off authors descriptions. Three of these are forms of natural land: Primary vegetation representing the undisturbed habitat for the ecoregion in question, mature secondary vegetation and young secondary vegetation. We represent human-dominated land in two alternative forms: structurally “complex” and “simple” agriculture. Complex agriculture contains large bushy or tree like crops that are generally more than 2 meter tall and may offer more vegetative structure for organisms to use as habitat, in some ways partially mimicking some forms of primary vegetation—such forms of agriculture include coffee, nut, and tree plantations or orchards. In contrast simple agriculture has lower stature crops that grow less than 2m tall such that they have relatively little useable habitat structure and includes pasture lands as well as low stature row crops. To best exploit the paired nature of the data, we removed all studies which did not contain primary vegetation, and at least one other land use category (young secondary vegetation, complex agriculture, simple agriculture). Within studies we eliminated sites which had unequal sampling effort. After cleaning records, we retained 54 different studies, with 3,975 unique sites, 55,267 species-by- site pairings, and 2,645 total bird species (roughly one fourth of all named species). We matched these biodiversity surveys with human population density data and land use estimates obtained from (Klein Goldewijk *et al.*, 2017) at a 5 arc minute resolution for multiple time periods between 12,000 YBP to 2000 CE. In our analyses we controlled for mean annual temperature and precipitation at 1km resolution (Fick & Hijmans, 2017), to ensure that climate related differences across the globe were not spuriously driving observed trends. To determine if differences in species richness between land covers is altered by the history of human presence we tested the influence of human dominated land uses on species richness by including an interaction between land use type and human population density as measured in different time periods. We controlled for the effects of climate as a fixed effect and study as a random effect using generalized linear mixed effects models with a negative binomial distribution.

Overall bird species richness was greatest in primary vegetation and lowest in simple agriculture, however human population density had great influences over species richness. Human population density has increased greatly in the last 12,000 years, population densities during the oldest time period 12,000 YBP (0-2.1 humans per km^2 at sites) were very low compared to the most recent time period 2000 CE (0-1,8000 humans per km^2). Of all time periods considered, the oldest time period, 12,000 YBP was the best at describing the data (Table 1.), suggesting that extremely early human impacts have compounded to structure modern day bird communities (human density by land use interaction effect: $Chi^2 = 47.7$, $p < 0.001$). Historical human population density is negatively correlated with sensitivity of communities, areas with greater historical human population sizes have less sensitive communities (Figure 2). We find support for the dark extinction hypothesis, that ancient humans have increased the perceived resilience of communities by eliminating species that would otherwise occur in primary vegetation. Specifically, on average fewer species persist in today's primary vegetation in areas where human populations were high 12,000 year ago, while the number of species occurring in structurally simple agriculture is unimpacted by human populations (Figure 2). Within primary vegetation, predicted species richness declines by 20% when comparing areas with no humans 12,000 YBP to areas with relatively high human populations (0.67 humans per km^2, the 95% quantile of surveyed bird communities analyzed). This level of species richness loss within primary vegetation is similar to the amount of change between primary vegetation and agriculture in areas which lacked humans 12,000 YBP, where average bird species richness declines by 22% from primary vegetation to short vegetation, and 19% from primary vegetation to complex agriculture. In contrast, in areas with relatively high human populations (0.67 humans per km^2), species richness loss was sufficiently high in primary vegetation that species richness is not significantly different between landcovers, with predicted declines of only 2% in simple agriculture, and 11% in complex agriculture.

In order to understand the mechanism behind species loss in primary vegetation we assessed whether this variation in loss of species richness across habitat type reflects a loss of primary vegetation specialists, as opposed to a loss of species which are capable of inhabiting both disturbed and natural habitats. We classified species as primary vegetation specialists if they were only ever found within primary vegetation within the study in question. We then tested whether primary vegetation communities, with larger human populations 12,000 YBP, had fewer primary vegetation specialists, as opposed to multi-habitat generalists. There was only modest support for this hypothesis: primary vegetation specialists tended to account for a smaller number of species occurring in primary vegetation where human populations were large 12,000 YBP, however this result is only marginally significant (p-value = 0.07). This suggests that ancient human impacts extend beyond only the most specialized species, affecting habitat generalists as well.

Past research has suggested that sensitivity to habitat modification and extinctions are not randomly distributed throughout the tree of life (Nowakowski *et al.*, 2018), for example species from rapidly speciating lineages may be most prone to extinctions (Greenberg & Mooers, 2017; Greenberg *et al.*, 2021). Evolutionary distinct species, those with few extant close relatives, are believed to amongst those most frequently lost when natural habitats are converted to those for human use (Frishkoff *et al.*, 2014; Greenberg *et al.*, 2018). We assessed the phylogenetic diversity, phylogenetic clustering, and median (and mean) evolutionary distinctiveness of communities to assess whether historical human occupancy has disproportionately reduced phylogenetic diversity by eliminating evolutionarily unique species. We obtained a tree of all birds from (Jetz *et al.*, 2012). We first tested if phylogenetic diversity decreases as species richness does in areas with higher human populations 12,000 YBP, while controlling for the effects of climate and study. Similar to trends with species richness, phylogenetic diversity decreases in primary vegetation and complex agriculture while in simple agriculture remains relatively unchanged by human population size (human density by land use interaction effect: $Chi^2 = 15.5$, p =0.004; Figure 3a). Since phylogenetic diversity is tightly correlated with species richness, we next assessed phylogenetic clustering within communities, to determine if clustering increases in communities with long histories of human occupation, as would be expected if evolutionarily distinct species are disproportionately eliminated. In areas with minimal human influence in the deep past, communities across land use types showed roughly equivalent degrees of phylogenetic clustering. However, contrary to our expectation, as historical human influence increased, communities in primary vegetation and complex agriculture both became less clustered suggesting that the species that remain are more broadly sampling the avian tree of life (human density by land use interaction effect: $Chi^2 = 15.6$, p =0.004; Figure 3b). Assessments of global evolutionary distinctiveness (ED) (Jetz *et al.*, 2014) support this result. Median (and mean; human density by land use interaction effect: $Chi^2 = 13.3$, p =0.008) ED values were similar across habitats with low human populations in ancient times. However, in areas with high human populations 12,000 YBP, the mean evolutionary distinctiveness of today’s communities is higher in primary vegetation, whereas in simple agriculture it is relatively unchanged (human density by land use interaction effect: $Chi^2 = 21.3$, p <0.001; Figure 3c). Together these results suggest that the species lost from primary vegetation in areas long occupied by humans represent species that were closely related to other species that still occur at the sites and may come primarily from recently radiating clades.

Our results suggest that impacts from early humans may extend far beyond megafaunal extinction. We use birds as a study system, primarily because they have the greatest amount of data out of vertebrate groups within the PREDICTS database and are widely studied, however we believe this to be a phenomena which is widespread across other taxonomic groups as well. In particular less mobile groups of plants and animals may bear even stronger signals of direct human presence (DAMBRINE *et al.*, 2007; Ockinger *et al.*, 2010), and their ability to recolonize areas may be hindered by their immobility (Lawes *et al.*, 2007; Cunillera-Montcusí *et al.*, 2021). For example plant diversity in areas previously occupied by humans often still reflects this history of use even thousands years later (DAMBRINE *et al.*, 2007). Alternatively, the mobility of birds, and in particular migratory birds may make them more sensitive to such impacts, as they may require a lack of disturbance in multiple areas for success, including breeding grounds, over wintering areas, and suitable habitat connecting between (Norris *et al.*, 2004; Martin *et al.*, 2007; Iwamura *et al.*, 2013; Runge *et al.*, 2014; Xu *et al.*, 2019).The data suggest that humans have acted as an extinction filter, and that even early human populations are linked to declines in bird species richness in primary vegetation. While we find a negative relationship between human population density and avian biodiversity, both today and in the past, historical patterns of human occupancy up to 12,000 years ago better predict modern day patterns of bird diversity across land uses than do more recent population trends. The greater predictive power of the earliest populations distributions occurs despite the low population densities at this time. We hypothesize that even at relatively low absolute densities, human impacts on landcover and through hunting, compounded over hundreds to thousands of years, resulted in sustained species losses in the landscapes involved.

The declines in species richness we document in primary vegetation could manifest as a result of either merely local or global extinction of the species at hand. Evolutionary distinctiveness hints that we have perhaps underestimated the extent to which global extinctions occurred dating back in time, and thus have pruned back bushier branches of the tree of life, while counter intuitively leaving longer branches relatively less affected. The exact mechanism by which the extirpations we infer in primary vegetation occurred is not certain, as hunting, human-driven fire regimes, and land use change often all occurred together. However, habitat modification may have been the primary way in which species were impacted by early humans, as communities in primary vegetation and complex agriculture show similar patterns of decreasing species richness and phylogenetic diversity, meanwhile in simple agriculture the community is largely unimpacted by historical human presence. Complex agriculture and primary vegetation have structural similarities, particularly in forested regions, in that they tend to be closed canopy and have vegetative structure, meanwhile simple agriculture has little to no canopy cover, and lacks the same level of vegetative structure. If prehistoric humans were primarily impacting birds through habitat modification, and this led forest to be converted to more open and less structurally complex habitat then species which were dependent on forest/closed canopy might decline, while species which exist in more open areas may have been left relatively unimpacted or increased due to an increase in suitable habitat. If hunting were the primary mechanism by which species were being impacted by humans, then we might expect to see equal differences across land use types. Regardless of mechanism, communities in primary vegetation bear the brunt of the impacts, which is counter to modern thinking of intact primary vegetation as areas which are most untouched by human influence, however the possibility of widespread influences of humans in otherwise intact habitats has recently been hinted at (Ellis *et* *al.*, 2021). If these differences in species richness do not represent global extinctions, but rather that these communities were affected by local extirpations of species, then it suggests that these species have not been able to recolonize primary vegetation since. A potential mechanism may result from remnant patches of primary vegetation being too small or too isolated for successful colonization, such that in areas of long human habitation have more fully paid the extinction debt incurred by initial human impacts (Tilman *et al.*, 1994; Hanski & Ovaskainen, 2002) . Without sub-fossils or fortuitously preserved specimens, determining whether these less diverse areas are a result of true extinctions is difficult. The alternative hypothesis, that adaptation is responsible for a reduced sensitivity of communities to disturbance is not supported by our study, although the two hypotheses are not necessarily mutually exclusive. If this were occurring a positive relationship between species richness in disturbed habitats and human population would be expected, which we did not find.

The severity of human impacts on the environment has led to the naming of this recent time period as the Anthropocene, the start of such time period has been debated, with most suggesting a relatively recent start date between 1610 and 1964 (Lewis & Maslin, 2015). Regardless of the date of start of the Anthropocene, our results highlight that human impacts dating back to 12,000 YBP are widespread and pervasive, altering diversity of communities and sensitivity to contemporary habitat loss, underplaying the value of such early impacts may hamper our understanding of biodiversity patterns and conservation needs. Contemporary patterns of biodiversity and community structure are considered to be a product of historical factors and contemporary conditions(Hagen *et al.*, 2021), however outside of a few select systems (mammals and islands), historical human presence is rarely considered as a potential driver of differences in diversity. Including influences of early humans in studies of biodiversity patterns may help improve our understanding of what drives different levels of biodiversity in regions with similar climates. Further, we find sensitivity to habitat modification is dependent on prior human inhabitation of regions, adding to the growing number of factors which are known to account for variation in communities' sensitivity. With emerging evidence of multiple factors influencing community/species/population sensitivity a great need exists to integrate these multiple factors in a unified framework. This will allow us to understand their relative importance and combined effects and will be critical enabling most efficient use of the limited resources available for conservation, as it will enhance our ability to identify areas most in need of preservation based off sensitivity and importance of communities within, allowing for sustained biodiversity in the future.

Figures and Tables:

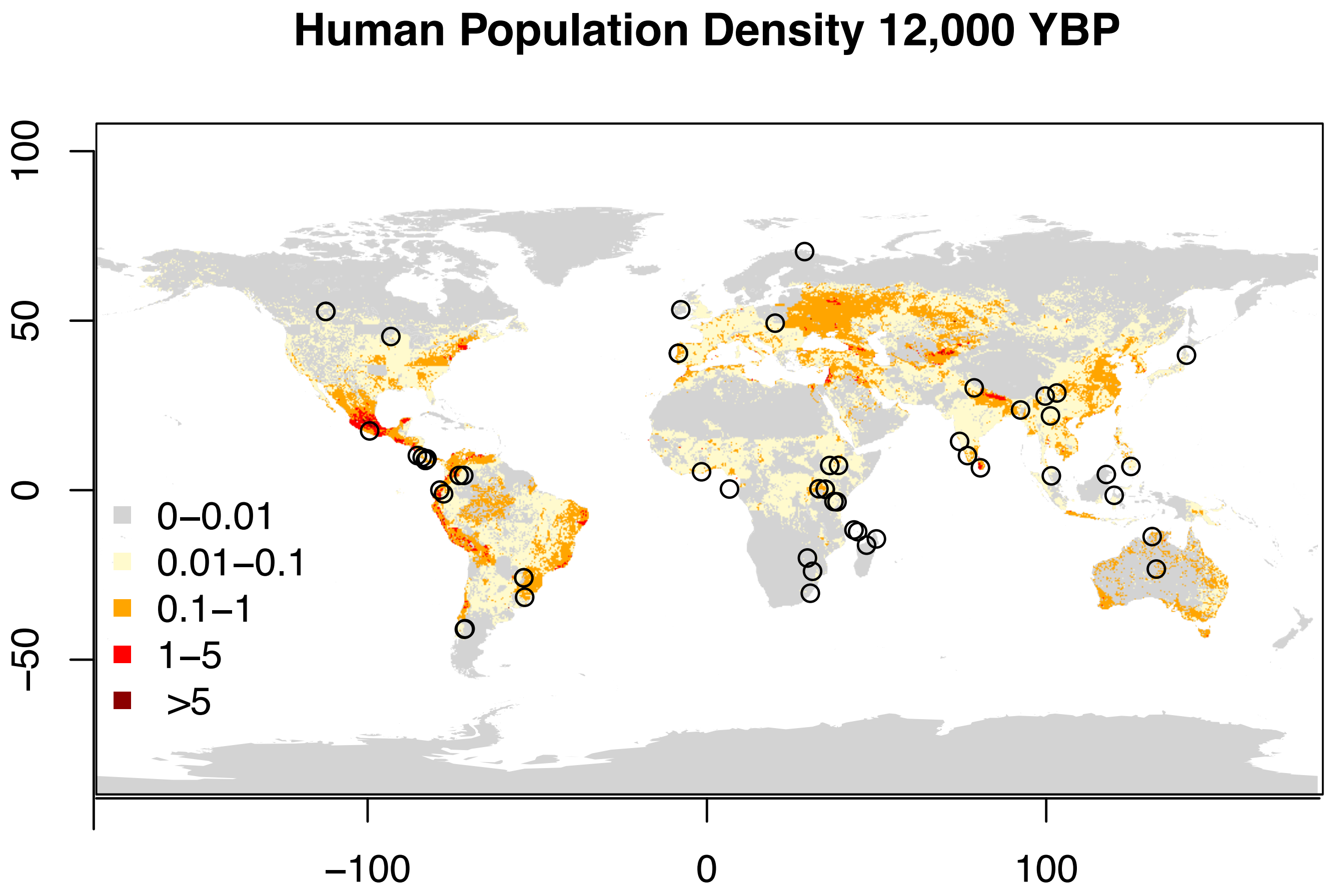

Figure 1. Map displays human population density (humans per km^2) estimates from Hyde 3.2 for ~ 12,000 YBP (Years Before Present). Points represent the central location of each of the 54 studies included in our analysis.

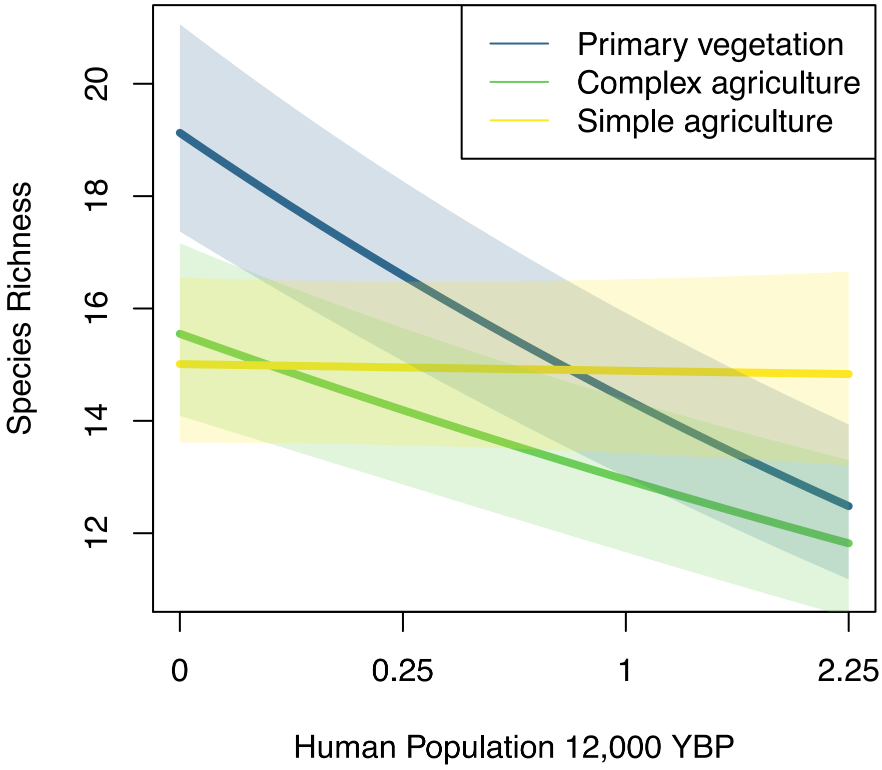

Figure 2. Model predicted relationships between human population density ~12,000 YBP (humans per km^2) and species richness, shaded areas represent standard error.

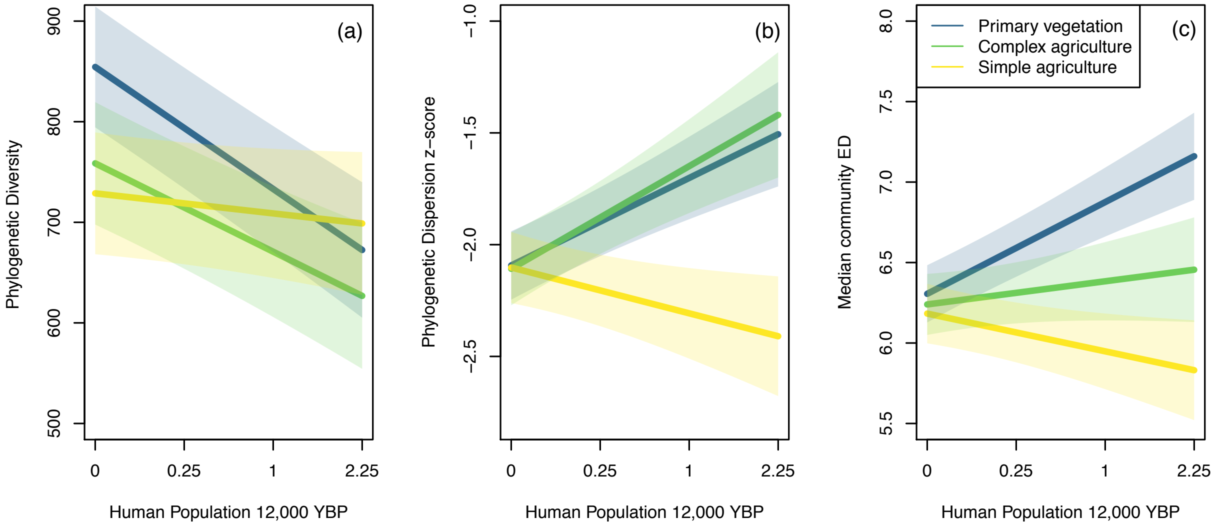

Figure 3. a) Model predicted phylogenetic diversity (Faith's PD). B) Model predicted mean phylogenetic distance (MPD) Z-score with human population density 12,000 YBP (humans per km^2) C) Model predicted median evolutionary distinctiveness (ED) relationship with human population density 12,000YBP.

Table 1. Results from models testing the impacts of human population density on species richness at different time periods, all models contain the full set of data from 54 studies. _P-value <0.05 *, <0.01**, <0.001***._

Model #	Time period	AIC	ΔAIC	Human population * PLU	bio1 * PLU	bio12
1	12,000 YBP	23341.3	0	***	***	
2	4,000 YBP	23382	40.7	**	***	
3	2,000 YBP	23390.7	49.4	*	***	
4	500 CE	23388.2	46.9	*	***	
5	1000 CE	23379.9	38.6	**	***	
6	1500 CE	23384.9	43.6	*	***	
7	1700 CE	23386.3	45	*	***	
8	1800 CE	23389	47.7	*	***	
9	1900 CE	23381.4	40.1	***	***	
10	2000 CE	23382.4	41.1	***	***	

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Appendix 3.1. Supplemental Methods

Trends in species richness

We obtained community data from the PREDICTS database and combined the original data release with the 2022 additional data release. We filtered our dataset to only contain birds, as they have the largest dataset amongst vertebrate species with the most widespread distribution of sites. A total of 69,7801 of species by site pairings existed before we cleaned the dataset. We removed studies which contain small taxonomic scope such as single species studies, single land uses, or no primary vegetation. After cleaning records, we retained 54 different studies, with 3,975 unique sites, 55,267 species-by- site pairings, and 2,645 total bird species. We classified land use into 5 different categories based off authors descriptions. Three of these are forms of natural land: Primary vegetation representing the undisturbed habitat for the ecoregion in question, mature secondary vegetation (generally representing vegetation that has regrown for at least 50 years since clearing) and young secondary vegetation (less than 50 years since clearing). We represent human-dominated land in two alternative forms: structurally "complex" and "simple" agriculture. The greatest number of sites were primary vegetation 1,559, followed by complex agriculture 894, simple agriculture 860, young secondary vegetation 649, and mature secondary vegetation 13. We present results in main text for primary vegetation, complex agriculture, and simple agriculture as the interest is in how species richness is impacted by land-use change, however patterns found in simple agriculture and young vegetation are similar (Figure S1). We tested the influence of human dominated land uses on species richness by including an interaction between land use type and human population density as measured in different time periods (10 total time periods from 12,000 YBP to 2000CE), to determine if differences in species richness between land covers is altered by the history of human presence. Because human population densities are bounded by zero, a large proportion of the data were small values, and relatively few had large values. To reduce the leverage of large values we therefore applied a square root transformation of human population density before analysis, though results are broadly concordant regardless of whether square root or raw data are used (Table S1). We controlled for the effects of climate by including mean annual precipitation, and an interaction between land use and mean annual temperature (because effects of habitat modification can be stronger in warmer areas) as fixed effects, and study as a random effect using generalized linear mixed effects models with a negative binomial distribution in the *glmmTMB* in R (Magnusson *et al.*, 2017).

Specialization

We classified species as primary vegetation specialists if they were only ever found within primary vegetation within the study in question, in this way species could be classified as primary vegetation specialists in one study and not in another, as habitat use can vary across species ranges. We tested whether primary vegetation communities where there were larger human populations 12,000 YBP had fewer primary vegetation specialists, as opposed to multi-habitat generalists (everything that is not a primary vegetation specialist). We filtered our dataset down to only include primary vegetation sites, a total of 1,559 sites from 54 studies. We used generalized linear mixed effects models with a binomial distribution in the *glmmTMB* in R (Magnusson *et al.*, 2017) with the number of primary specialists observed at a site compared to generalist species at a site as the response variable. We included human population size 12,000 YBP, mean annual temperature, and mean annual precipitation as fixed effects, and controlled for study as a random effect.

Phylogenetic diversity

We obtained a tree of all birds (Jetz *et al.*, 2012)(Ericson tree), and calculated Faith's phylogenetic diversity for each site using the *pd* function in Picante (Kembel *et al.*, 2010). We tested if phylogenetic diversity decreases in areas with higher human populations 12,000 YBP, by using phylogenetic diversity as our response variable and including interactions between human population size 12,000 YBP and land use, mean annual precipitation, and an interaction between land use and mean annual temperature as fixed effects, while controlling for the effect of study as a random effect using generalized linear mixed effects models with a gaussian distribution in the *glmmTMB* in R (Magnusson *et al.*, 2017).

We tested how clustered our communities were by calculating phylogenetic dispersion. To do so we calculated mean pairwise distance within sites and z-scores from comparisons to a tip-swap null distribution (1,000 simulations) using the *ses.mpd* function in Picante (Kembel *et al.*, 2010). We extracted the z-scores and then asked what controlled whether a community was phylogenetically more clustered, or more over dispersed in areas with large prehistoric populations. We used z-scores as our response variable and including interactions between human population size 12,000 YBP and land use, mean annual precipitation, and an interaction between land use and mean annual temperature as fixed effects, while controlling for the effect of study as a random effect using generalized linear mixed effects models with a gaussian distribution in the *glmmTMB* in R (Magnusson *et al.*, 2017).

We assessed mean and median evolutionary distinctiveness (ED) of bird species within sites by obtaining values of ED from (Jetz *et al.*, 2014). We used median ED (and mean in separate models) as response variables and including interactions between human population size 12,000 YBP and land use, mean annual precipitation, and an interaction between land use and mean annual temperature as fixed effects, while controlling for the effect of study as a random effect using generalized linear mixed effects models with a gaussian distribution in the *glmmTMB* in R (Magnusson *et al.*, 2017).

Appendix 3.2. Supplemental Figures and Tables

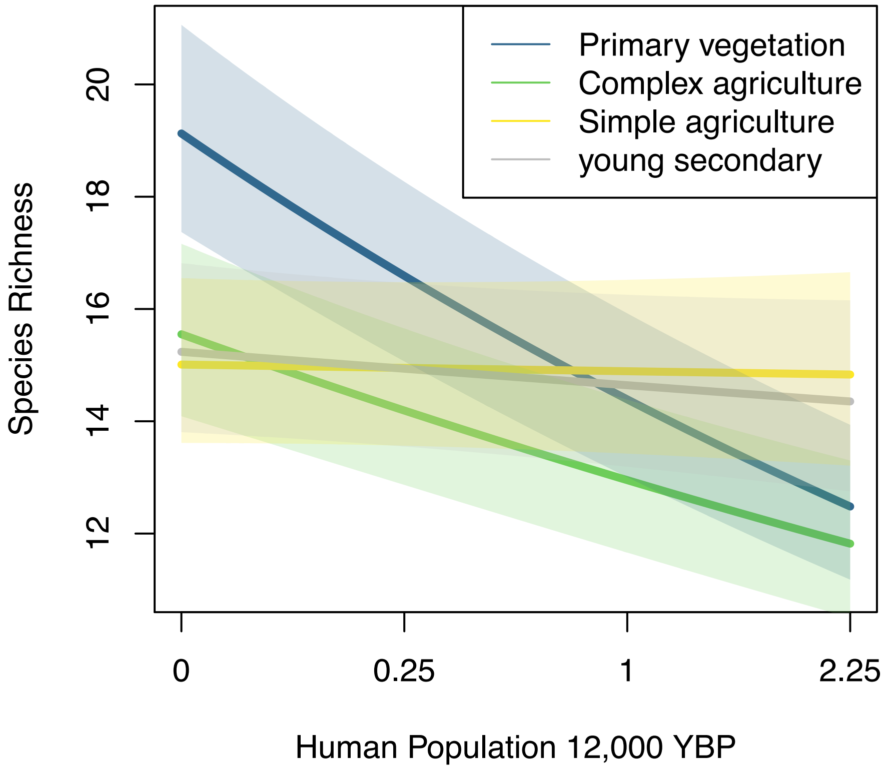


Figure S1. Model predicted relationships between human population density ~12,000 YBP (humans per km^2) and species richness, shaded areas represent standard error.

Table S1. Results from models testing the impacts of human population density on species richness at different time periods, all models contain the full set of data from 54 studies. This set of models is based off raw values of Human population density, not the square root as presented in the main text. *P-value <0.05 *, <0.01**, <0.001****.

Model #	Time period	AIC	ΔAIC	Time period * PLU	bio1 * PLU	bio12
1	12,000 YBP	23331	0	***	***	
2	4,000 YBP	23388.7	57.7	.	***	
3	2,000 YBP	23392.4	61.4	*	***	
4	500 CE	23391.4	60.4	*	***	
5	1000 CE	23390.8	59.8	*	***	
6	1500 CE	23393.2	62.2		***	
7	1700 CE	23392.4	61.4	*	***	
8	1800 CE	23393.5	62.5	*	***	
9	1900 CE	23389.4	58.4	**	***	
10	2000 CE	23386.4	55.4	**	***	

Chapter 4

Competition intensification drives century long declines in a common lizard species, *Sceloporus consobrinus*.

Alexander H. Murray[1], Edita Folfas[1], Morgan A. Page[2], Zachary K. Lange[1], Joseph L. Mruzek[1,3],
Luke O. Frishkoff[1]

[1]Department of Quantitative Biology, University of Texas at Arlington, Arlington, Texas, USA
[2]Department of Biology, Marshall University,350 Science Building, 1 John Marshall Drive,
Huntington, West Virginia25755, USA
[3]Forestry and Environmental Conservation Department, Clemson University, 261 Lehotsky Hall,
Clemson, SC 29634, USA

Abstract:

Habitat modification and climate change have been identified as primary mechanisms responsible for historical and ongoing population declines. However, species interactions, though difficult to study, may be of similar importance. Here we use a combination of historical species records, standardized transect surveys, and staged competition trials to assess the role of competition in recent population trends and distributions of two closely related lizard species: the prairie lizard (*Sceloporus consobrinus*) and the Texas Spiny lizard (*S. olivaceus*). Occurrence data reveals divergent population trends. *S. consobrinus* has decreased while *S. olivaceus* has increased in relative frequency over the last 100 years. We spatially aggregated records of all lizards within the range of *S. consobrinus* to determine the role of climate suitability, climate change, landcover, and species interactions in shaping the occurrence patterns of *S. consobrinus*. In contrast to other lizard species, presence of *S. olivaceus* greatly reduces occurrence of *S. consobrinus* and explains occurrence better than either climate suitability or landcover variables. To test whether patterns of co-occurrence detected using occurrence data are indicative of competition we conducted transects surveys to assess local lizard communities and paired this with behavioral trials to determine specific species interactions. Despite occurring in similar habitats, and across similar regions, transect surveys revealed lower abundance of *S. consobrinus* on transects containing *S. olivaceus*, with both species only co-occurring on 2 of 176 transects. Shifts in habitat use implicate competitive displacement, with *S. consobrinus* occupying areas with three times less canopy cover at sites with *S. olivaceus* compared to those without. Behavioral trials revealed the competitive dominance of *S. olivaceus*, which controlled the prime basking position, and initiated more interactions that led to the retreat or hiding by *S. consobrinus*. Our study highlights how impacts of competition can fluctuate through time and

demonstrates the ability of competition to alter species distributions when interactions between species intensify.

Introduction

The last century has been marked by incredible changes in biodiversity writ large, emerging from shifts in community assemblages, population declines, changes in species distributions and species extinctions (Pereira *et al.*, 2012; Dornelas *et al.*, 2014; McGill *et al.*, 2015; Dornelas *et al.*, 2019). Explaining and ultimately predicting when and why some species decline is essential to both understand the ecology of the contemporary world, and combat severe biodiversity loss. Habitat modification and climate change in particular are linked to many species' declines (Pereira *et al.*, 2012), yet substantial variation exists between species in how they respond to these global change drivers. While many species are "losers", and suffer as a result of anthropogenic change, a few "winners" benefit and expand their population sizes and distributions (McKinney & Lockwood, 1999; Daily *et al.*, 2001; Mendenhall *et al.*, 2016). However, being a "winner" versus a "loser" is not necessarily a static trait, and treating it as such risks overlooking the complexity of the natural world. Across a given species' range responses to the same type of anthropogenic induced change often varies (Frishkoff *et al.*, 2015; Orme *et al.*, 2019; Williams *et al.*, 2021; Williams *et al.*, 2022) . Some of this variation within species can be accounted for by proximity to physiological limits—for example deforestation, and the resulting local habitat warming due to increased solar warming, can result in extirpation at the warm-edge of a species' range, while the same deforestation may benefit the species towards the cold end (Frishkoff *et al.*, 2015). Yet other cases of varying tolerance to global changes are not well understood, as changes in communities are often not well explained by changing climate alone (Miller *et al.*, 2018). Perhaps our inability to explain variation within species is hampered by our failure to consider the role that species interactions are playing, and how anthropogenic influence may be rewriting their strength and outcomes (Suttle *et al.*, 2007; Blois *et al.*, 2013; Alexander *et al.*, 2016; Urban *et al.*, 2016).

Climate plays a key role in determining species range limits (Angert & Schemske, 2005; Stanton-Geddes *et al.*, 2012; Hargreaves *et al.*, 2014; Lee-Yaw *et al.*, 2016), community structure (Jackson *et al.*, 2001), and species richness (Qian *et al.*, 2007; Grace *et al.*, 2016). Meanwhile, ecologists have vehemently disputed the role of competition in setting range limits, structuring communities and determining species richness (Connell, 1961; Wiens, 1977; Connell, 1980; Schoener, 1982; Connell, 1983; Roughgarden, 1983; Simberloff, 1983). Disagreement may stem in part from studies seeking to find an effect of competition but failing to do so, particularly in vertebrates (Tinkle, 1982; M'Closkey & Baia, 1987; Paterson *et al.*, 2018). Failure to find strong competition amongst currently co-existing species should not be surprising, as species tend to minimize such interactions through niche partitioning, and so reduce the strength of competition between them, allowing them to persist in the presence of competitors. Evidence for niche partitioning is widespread, and multidimensional, with species evolving or changing behavior to minimize overlap in diet (Huey *et al.*, 1974), microhabitat use (Jenssen, 1973; Salzburg, 1984), thermal preferences (Watson & Gough, 2012) and morphology (Huey & Pianka, 1977). Communities of today, have been constructed by abiotic factors and biotic interactions over time, and species within them may bear the potential mark of competition, a "ghost of competition past" (Connell, 1980) meanwhile not showing effects of competition, that is present species interactions do not appear to be strong. This may make it difficult to detect competition and may in part account for the doubt amongst some for their importance, because the interactions which are proposed to be so important can be so difficult to observe and quantify in the present. Expectations that interactions shaping community structure through time should persist until the present is problematic as it fails to consider that conditions (here referring to all aspects both abiotic and biotic under which two species interact) dictate strength and outcomes of interactions, and these conditions change through time. Competitive interactions may depend on abiotic factors, such that temperature determines competitive dominance between species (Taniguchi & Nakano, 2000; Jiang & Morin, 2004; Oyugi *et al.*, 2011), and habitat structure can also be important (Petren & Case, 1998). The strength of interactions often depends on resource availability, which tends to fluctuate in time, and so effects of competition vary temporally. Finally, coexistence between competing species may only be possible when habitat heterogeneity allows for efficient niche partitioning to minimize interactions between competing species, reductions in habitat diversity can decrease co-occurrence between competing species (J. Harmon *et al.*, 2007). As human impacts across the globe continue to increase, we are altering the conditions under which species interact, making it exceedingly likely that many species interactions are changing, yet we currently know little of their extent or consequences (Blois *et al.*, 2013; Alexander *et al.*, 2016).

If species interactions are changing, they may lead to changes in local abundance and/or alter species' distributions. However, such changes may go largely unnoticed if looking at broad scales, as it has been suggested that competitive exclusion can take a long time to scale from local to regional levels (Yackulic, 2017). One of the challenges is that the long-term community datasets that could be used to assess potential competitive interactions are largely lacking, and so assessing changes in strength of competition through time, its causes and impacts is difficult. Here we test our hypothesis that competitive interactions are both important for structuring communities and geographic distributions through time, using two species of closely related lizard species, the prairie lizard (*Sceloporus consobrinus*) and the Texas Spiny Lizard (*S. olivaceus*). Anecdotes, personal communications, and isolated reports all suggest that *S. olivaceus* abundance has been increasing, while *S. consobrinus* has been declining (Mora, 1991). Some of this trend is likely due to urbanization and other development—*S. olivaceus* appears more tolerant of urban areas than *S. consobrinus* (AHM personal observation). However, even in preserved localities with no history of land-use change, *S. consobrinus* has disappeared, and *S. olivaceus* remains (Mora, 1991). This anecdotal pattern conforms to expectations if interspecific competition were responsible. Such an interpretation is further supported by the size and shape of these species' ranges. *S. consobrinus* (along with phenotypically similar allospecies that are distinguishable primarily by genetics) is widespread between the Mississippi river and the Rocky mountains. However, occurrence records suggest much lower occurrence frequency or even absence in an internal portion of their range in central Texas—a geographic region very similar to the U.S. portion of *S. olivaceus*' range (which runs in a narrow band from Central Texas south into Mexico).

We combine occurrence data, transect surveys and behavioral trials to work from macro- to micro-scale, testing our core hypothesis that *S. consobrinus* and *S. olivaceus* compete and that such competition is structuring range limits and contributing to the decline of *S. consobrinus*. First, we use historical occurrence data to test our hypothesis that relative rates of occurrence of *S. consobrinus* are decreasing through time (and *S. olivaceus* increasing) to confirm anecdotal reports. Second, we use these records to assess broad-scale co-occurrence, asking whether *S. consobrinus* occurrence is lower than expected in areas which are otherwise suitable for it if *S. olivaceus* is also present. Third, we use standardized transect surveys to test whether broad-scale species co-occurrences are representative of fine scale community structure, and test our hypothesis that abundance of *S. consobrinus* will be lower on transects which contain *S. olivaceus*. Finally, we test whether species associations detected using occurrence and transect data are indicative of competition using behavioral trials to test that *S. olivaceus* and *S. consobrinus* compete via behavioral interference, and specifically, that *S. olivaceus* is the superior competitor.

Methods

Study system

We focus our study within Texas, which spans a large precipitation gradient with extreme variation in habitat across the state and possesses diverse lizard communities. Lizards have been a focal group for the study of competition (Pacala & Roughgarden, 1982), vary greatly in how they respond to land use change (Doherty *et al.*, 2020),and can be highly sensitive to changing environmental conditions (Sinervo *et al.*, 2010; Walker *et al.*, 2015). Their sensitivity to anthropogenic change is likely amplified by their relatively low mobility, leaving them unable to rapidly track changing availability of resources in space, in contrast to groups like birds (Blake & Hoppes, 1986; Kasper Thorup, 2017). This limitation is crucial with regards to competition, because resource availability often determines lizard abundance and strength of competition (Dunham, 1980; Guyer, 1988). Texas presents an interesting case study area, because species living near their climatic limits, and those living in communities containing many closely related species, may be especially susceptible to being ‘pushed over the edge’ by competitive interactions. Our focal region of Texas represents such an area of transition from the mesic eastern portion of the North American continent to the xeric west. All species of lizards in Texas having a range limit within the state and experiencing total community turnover from east to west across the state.

In the last century the Texas landscape has seen an incredible amount of change, from major human population increases and urban sprawl, to shifts in precipitation patterns, forest cover and introduction of non-native species such as feral hogs and fire ants. Many lizard species are likely to be declining, however little is known on the population trends of most species outside a few charismatic species such as the Texas horned lizard (*Phrynosoma cornutum,* Harlan 1825).

We focus on one such ecologically less-studied species, the so-called Prairie lizard (*Sceloporus consobrinus,* Baird and Girard 1854) whose population trends are unknown and was once common throughout the state in habitats ranging xeric scrub, to prairies, to closed-canopy broadleaf and pine forests. In conjunction with its wide distribution, *Sceloporus consobrinus* exhibits incredible beauty and phenotypic diversity. They are small (max SVL= 68mm) (Lawrence LC Jones & Lovich, 2009), semi-arboreal lizards which in many parts of their range are heavily arboreal but in more sparsely vegetated areas can be heavily terrestrial. They belong to the *Sceloporus undulatus* group (Leache, 2009), which is distributed throughout the US and in most places contains a single small to medium sized lizard. In central Texas, *S. consobrinus'*s range overlaps with a much larger closely related species, the Texas Spiny Lizard (*Sceloporus olivaceus*, Smith 1934; max SVL= 124mm) (Kennedy, 1973),which is endemic to wooded habitats of central Texas and Northern Mexico. Both species are diurnal insectivores, and in Texas can be found active year-round, with less activity in the cooler winter months. Little is known about how territorial or aggressive these species are, but they are likely to defend territories similar to other *Sceloporus sp.* (Ruby, 1978). The local distributions of *S. olivaceus* suggests this may be the case, as single trees tend to not possess multiple male *S. olivaceus*

(Blair, 1960) , however territories of lizards may overlap heavily as in other *Sceloporus sp*. (Sheldahl & Martins, 2000).

Trends in occurrence

Data

In order to document divergent trends in occurrence in lizard fauna over the course of the 20th and 21st centuries we assessed time- and geo-referenced occurrence data from GBIF. First, we assessed whether the general trends in records of *Sceloporus consobrinus* are decreasing through time and whether the trends in records for *S. consobrinus* differ from *S. olivaceus*. Lizard occurrence data was downloaded on December 3rd, 2021, from GBIF, and records which lacked coordinates or year were dropped. We constrained the area of study to the distribution of *S. consobrinus* and dropped records which fell outside of this distribution, we retained 91,660 records of lizards between 1920 and 2021. Records of *S. undulatus* falling within the distribution of *S. consobrinus* were reclassified as *S. consobrinus* to reflect updated taxonomy (Figure S1). To assess the trends in observations over time we grouped the data into ten-year periods from 1920-2021, except for one two-year period, 2020-2021. The time period with the fewest records was 1920-1929 with 1,902 records and the time period with the most records was 2010-2019 with 29,499 records.

Analysis

To test if the number of records of *S. consobrinus* and *S. olivaceus* relative to the total number of lizard observations within the range of *S. consobrinus* is changing through time we used a linear model, with a gaussian distribution, using the *glm()* function (Team, 2016). We used log(relative abundance) as our response variable, model structure was: *log(count/total) ~ year * species*. These and all subsequent analyses were performed in R version 3.6.2.

Current Distribution

Pseudo-sites

To understand what explains the current distribution of *Sceloporus consobrinus*, we spatially and temporally aggregated records (records were grouped into ten-year periods) into pseudo-sites, allowing us to assess the influence of land-use, climate and species interactions on the current distribution of *S. consobrinus*. To aggregate our data spatially we generated pseudo-sites, by creating 100,000 random points within the distribution of *S. consobrinus* using the *randomPoints()* function (Hijmans *et al.*, 2017). We buffered our points by a 2km radius to allow for the grouping of records spatially. We further cleaned the GBIF dataset by dropping all records with a coordinate uncertainty greater than 2km and restricted the time period to only the most recent records, 2020-2021. For the two focal species, outlier records were assessed visually to confirm ID, records with incorrect ID were dropped or changed (for a full description of data cleaning see code in supplement). We then intersected the occurrence records with them using the *intersect()* function (Hijmans RJ, 2015). For each pseudo-site, we summed observations and dropped pseudo-sites containing fewer than 5 records. To ensure each pseudo-site represented a unique community, with no duplicate records we spatially thinned out the data set by 4km using the *thin()* function (Aiello-Lammens *et al.*, 2015), we retained a total of 396 pseudo-sites.

Climate Suitability and Land-use data

We used Maxent (Phillips *et al.*, 2006) to predict the climatic suitability for *S. consobrinus* and *S. olivaceus*. We downloaded occurrence records from GBIF as outlined above, and refined records further by removing all records with greater than 1km coordinate uncertainty, and outliers. Initial queries returned 8,132 records for *S. consobrinus*; however many records are incorrectly listed as *S. undulatus*, and following inclusion of these records, and following cleaning up a total of 3,953 records remained, after thinning (thinned by 1km), we retained a total of 2,527 (Figure S3). *S. olivaceus* began with 11,725 records, after cleaning up records a total of 7,323 remained, after thinning we retained a total of 2,817 (Figure S4). Climate data were obtained at 1km resolution from WorldClim (Fick & Hijmans, 2017). We selected climate variables based off stepwise exclusion using *vifstep* function from the package *usdm* (Naimi *et al.*, 2014). The final set of variables included in the model of *S. consobrinus* contained (bioclim15, bioclim18, bioclim2, bioclim4, bioclim5, bioclim8, bioclim9) and for *S. olivaceus* (bioclim15, bioclim18, bioclim2, bioclim4, bioclim5, bioclim8, bioclim9). Calibration area was determined based off a minimum convex polygon which includes all occurrence points and a 200km buffer around the area. Occurrence records were grouped into 5 groups using a *kfold* function from the *dismo* package (Hijmans *et al.*, 2017),and 80% of records were used for model training, 20% was used to evaluate the models. Models were run using the *maxent()* function, output was formatted as a logistic output as it represents an attempt to determine probability that a species is in a location given the environmental conditions (Elith *et al.*, 2011). We evaluated model performance with 10,000 background points and 20% of occurrence records for each species using the *evaluate()* function (Hijmans *et al.*, 2017). Values for AUC value for *S. consobrinus*= 0.749, AUC for *S. olivaceus* =0.909. Model predictions were made for both species in the calibration area (Supplement Figure S5, S6).

We obtained land-use data for urban area, pasture, crop and forest at 1km for the year 2020 (Li et al 2022). Maxent predicted habitat suitability and land-use data were extracted to the pseudo-sites as the mean value for the pseudo-site. For each time period we extracted mean annual temperature (MAT) and mean annual precipitation (MAP) to the sites, as the mean over the time period from which the pseudo-site community was sampled. Historical climate data was obtained at 1km resolution (Group, 2011). Changing climatic conditions may favor one species over another, and so we accounted for recent climate change by creating rasters representing changes in MAP and MAT by subtracting the mean for 1920-1929 from the mean value for 2010-2019 and extracted these values to our pseudo-sites.

Analysis

Generalized linear models were used to assess the factors responsible for the current distribution of *Sceloporus consobrinus*. We used presence/absence of *S. consobrinus* in the 396 pseudo-sites as the response variable. First, we tested whether climate suitability is a good predictor of the current distribution of *S. consobrinus*. Second, we tested whether land-cover type influences occurrence of *S. consobrinus*. Third, assessed the potential for competitive interactions influencing *S. consobrinus*, by including presence/absence of 11 of the most frequently observed lizard species on transect in the model. Finally, we tested whether climate change has influenced *S. consobrinus* by including the change in MAT and change in MAP in models.

In all models we included number of records at the site to control for the influence of sample size. We evaluated model performance based of off AIC values, and pseudo-R^2 values generated the *pR2()* function (Jackman, 2015). Final models included climate suitability, land-cover and species interactions.

Mechanisms driving trends

To better understand the factors driving general trends in relative records of species through time we generated spatially and temporally aggregated records into pseudo-sites. This allowed us to assess the influence of land-use, climate and species interactions on occurrence of

S. consobrinus, particularly the effect of *S. olivaceus* on *S. consobrinus,* and infer whether the strength of interactions between the two species has changed through time.

Pseudo-sites

Pseudo-sites were generated based off the same 100,000 points used in the current distribution analysis, and data from all years between 1920-2021 was included and cleaned following the protocol described above. Sites were dropped which contained fewer than 5 records during a given time period and thinned based on a 4km radius. For each pseudo-site we extracted land cover data corresponding to the first year of the ten-year time period of the site (Li et al 2022). Maxent predicted habitat suitability for *S. consobrinus* and *S. olivaceus*, as well as land-use data were extracted to the pseudo-sites as the mean value for the pseudo-site. We retained a total of 1340 pseudo-site year combinations between 1920-2021. The average number of records per site was 16 and the range was 5 to 450.

Analysis

To test if occurrence of *S. consobrinus* is changing through time we used generalized linear models with presence/absence of *S. consobrinus* in the 1340 pseudo-sites as the response variable. First, we tested whether the general trend of decline in observations of *S. consobrinus* through time is supported by a reduction in occupancy at suitable locations by *S. consobrinus*, while including year, habitat suitability, sampling and landcover as predictors of the occurrence of *S. consobrinus*. Next, we assessed whether the effect size of *S. olivaceus* on *S. consobrinus* has changed through time, through including an interaction between *S. olivaceus* presence and time in the model. Such an increase in realized competitive force may be caused by a variety of factors including an increase in population size of *S. olivaceus*, changing environmental conditions that cause them to come into contract more frequently, or changing environmental conditions that enhance the per-individual competitive ability of *S. olivaceus*. One likely avenue that this could take is through urbanization, because suitable habitats for these species may be especially limiting, rendering competition for territory a plausible mechanism for restricting population size (whereas predation or food resource limitation may be more limiting in natural habitats). We tested whether changing landcover is contributing to changing trends between *S. olivaceus* and *S. consobrinus*, including an interaction between *S. olivaceus* presence and amount of urbanization, to test if urban areas have a more negative impact on *S. consobrinus* when *S. olivaceus* is present. Finally, we tested whether climate conditions altered the rate of exclusion by *S. olivaceus*, including interactions with climate and *S. olivaceus* presence, to determine if co-occurrence is more likely in some climates compared to others. We evaluated model performance based of off AIC values. Final models included climate suitability for *S. consobrinus,* land-cover and interactions between urbanization and *S. olivaceus* presence as well as interactions of climate and *S. olivaceus* presence.

Lizard Community Surveys

Transect

Occurrence record data can offer a glimpse into communities at coarse geographic and time scales yet lacks the ability to display the nuance of habitat partitioning within communities at finer scales. To better understand the associations between species, their microhabitat use, and partitioning within the landscape at the spatial and temporal scales over which individual lizards actually interact with one another we used transect surveys between March 2020-June 2022 to document lizard communities across Texas.

Transects consisted of 200m surveys, broken into four, 50m sub-transects. Sub-transects occurred in consistent habitat throughout their length and allowed finer resolution data on species co-occurrence. Individual lizard surveys were conducted by a single individual walking slowly and scanning all substrates within line of sight. All cover objects of suitable sizes (>$500cm^2$) within 2m of the transect line were flipped to check for lizards. When a lizard was observed, it was photographed to serve as a long-term record and for species confirmation, and microhabitat data was taken (Substrate, Perch Height, Perch Diameter, and Perch Temperature). Surveys average about 120 minutes to complete and were only performed in habitat representative of the natural vegetation in a region. A total of 37 sites(1-36 transects per site) were visited for surveys spanning most of the range of *S. consobrinus* in Texas. In locations which are large, many surveys would take place, with multiple types of habitats (canyons, riparian forest, prairie etc.), covering all natural habitat types at the site. To maximize detection probability on transects, surveys were only performed during the months of the year when our focal species are most active (March-October), and under suitable climate conditions (ambient temperature > 20 degrees C°, and no rain). Surveys were also performed at night, however very few *Sceloporus* were observed during night surveys as they are difficult to observe sleeping, and here we present results exclusively from day-time surveys. A total of 176 surveys are included here. We recorded vegetation data to understand how vegetative structure influences the lizard community, measurements were taken at the midpoint of each sub-transect. We recorded canopy height and canopy cover, with canopy cover being the primary vegetative measurement of interest. Canopy cover was measured using a Spherical Crown Densiometer, taking a total of 16 measurements per transect, 4 measurements every 50m along the transect (1 in each cardinal direction).

Analysis

Data were analyzed using generalized additive mixed models using the *gamm()* function (wood, 2015) ,and Poisson distribution to determine the influence of *Sceloporus olivaceus* on the abundance of *S. consobrinus*, while controlling for the canopy cover, and climatic suitability, and location. We accounted for the influence of climate on species abundance by including mean annual temperature and mean annual precipitation of the transect in the model. The vast majority of our sites were non-disturbed primary vegetation, but we controlled for the effect of landscape level urbanization by extracting the amount of urbanization within 2km surrounding our sites, in the same method done for pseudo-sites. To test if at local scales *S. consobrinus* are being excluded from otherwise suitable habitat we included presence/absence of *S. olivaceus* at the transect level as a predictor variable. In addition to the influence of *S. olivaceus* on *S. consobrinus* we tested for species associations with the other 10 most common species.

Additionally, we compared habitat use between *S. olivaceus* and *S. consobrinus* to determine if they have shared preference based off perch height, substrate temperatures when active and canopy cover on transects where they are found. To do this we used t-tests to compare the means between the two species. Since competition can alter habitat use, we tested whether habitat use of *S. consobrinus* differs in areas which lack *S. olivaceus* compared to those where it is present. To do this we grouped observations of *S. consobrinus* into sites which contain olivaceus (those where we observed *S. olivaceus*) and those where *S. olivaceus* is absent and compared canopy cover between the two.

Competition Trials

We conducted competition trials between *S. olivaceus* and *S. consobrinus* to assess which species is dominant based off rates of aggression, rates of retreat, and changes in habitat use when in the presence of individuals of a competitor vs when alone.

Data

Competition trials took place inside of a 100x45x45cm enclosure containing a variety of substrates, including leaf litter, dirt, rock, and branches of 3 different sizes (Supplemental Figure S7). Each enclosure had a heat lamp placed directly on top of the cage as *Sceloporus sp.* have high thermal needs compared to the ambient room temperature. Trials lasted 120 minutes and were recorded using a set of security cameras so lizard habitat-use and interactions could be scored later. Lizards were only used in one trial per treatment. A total of 21 trials were performed with adult male *S. olivaceus* paired with adult male *S. consobrinus*, 9 trials were run with only *S. consobrinus*.

Analysis

Competition trials were scored in 1-minute increments every 10 minutes, starting with the first minute of the trial. During each scoring period substrate use was recorded as well as any interactions between individuals. Interactions were recorded to include which lizard initiated the interaction, as well as what the initial behavior was and how the other lizard reacted. Behaviors by lizards initiating interactions were scored based off level of aggression, 1 (approaching the other lizard, pushups, and headbobs), 2 (approaching while head bobbing or pushuping, or approaching and touching), 3 (biting). Responses to the initial behavior was recorded as 0 (no response), -1 (retreat but maintain substrate), -2 (retreat and change substrate), -3 (retreat and hide). Lizard responses to behavior of other individuals was scored in the same manner, allowing for negative and positive values. We tested the hypothesis that *S. olivaceus* is the dominant competitor by using paired t-tests to compare mean levels of aggression, response to aggression within trials, and habitat use withing trials. T-tests were used to determine if the behavior in 2 species trials differs from single species trials as it pertains to habitat use.

Results

Trends in occurrence

As a proportion of all lizards, *Sceloporus consobrinus* has declined in frequency of observations over the last century (p-value < 0.001, Figure 1a), making up more than 20% of lizard records in the early decades of the 20th century, but only ~ 5% in the 2010s.

Distribution of *S. consobrinus*

Alternative hypotheses related to changes in landcover, climate, or species interactions may all potentially explain the observed declines of *S. consobrinus.* We first examined how each of these classes of predictors explained the current distribution of occurrences. Surprisingly, climate alone does a very poor job of explaining *S. consobrinus* presence at our 396, 2km radius "pseudo-sites" ($R^2 = 0.008$; $p > 0.05$, Table 1.). We then tested if landcover could help explain why *S. consobrinus* is absent from climatically suitable areas. Urbanization has a strong negative influence on *S. consobrinus* (p-value <0.001, $R^2= 0.14$). Other forms of land use appeared to have little influence on this habitat generalist: none of forest cover, pasture, and crop had significant influence (Table 1.) While present day climate suitability had limited predictive capacity, the degree of climate change over the last century was a strong predictor of their current distribution. Areas which had warmed recently (p-value<0.001, $R^2 = 0.11$), and those which had gotten wetter recently (p-value<0.001, $R^2 = 0.08$) were less likely to be occupied by *S. consobrinus* (Table 1).

On top of effects of climate and landcover, species interactions may also limit species distributions. We therefore tested for associations between species within pseudo-sites, while controlling for climate suitability, sampling amount, and urbanization in all assessments. Of the 11 common Texas lizard species analyzed, four had significant associations with *S. consobrinus* presence. The strongest correlation was with *S. olivaceus* (p-value <0.001, $R^2=0.24$) for which occurrence of *S. olivaceus* was associated with diminished occurrence of *S. consobrinus*. Green anoles (*Anolis carolinensis)* also had a strong negative correlation in occurrence with *S. consobrinus* (p-value<0.001, R^2=0.21). In contrast both the little brown skink (*Scincella lateralis*, p-value<0.05, R^2= 0.16) and the five lined Skink (*Plestiodon fasciatus;* p-value<0.05, R^2= 0.16) had positive association with *S. consobrinus*. Including multiple species within one model suggested a strong negative effects of *S. olivaceus* and *A. carolinensis*, and a weak positive influence of *S. lateralis*, R^2=0.33 (Table 1). Our best model included landcover, species associations and climate change, R^2= 0.34, with climate change no longer having a significant influence on *S. consobrinus* occurrence once species associations were incorporated (Table 1).

Presence-absence within pseudo-sites predicts a strong negative correlation between *S. olivaceus* presence and *S. consobrinus* presence, suggesting perhaps the two species could be competing. Presence alone however may not be enough to exclude species from otherwise suitable habitat if the competing species occurs at low densities or is not distributed consistently across the landscape, as this may allow for species to avoid the negative effects of competition if they can occupy the portions of the habitat where the superior competitor does not exist. Maxent predicted climate suitability may represent a metric of consistency of the distribution of a species in a location, thus areas with high measures of climate suitability may represent areas where the species is more ubiquitous across the landscape and therefore better able to exert competitive effects. Using predicted climate suitability as a proxy for consistency of distribution in a landscape, we tested if climatically suitable areas for *S. olivaceus*, are less likely to contain *S. consobrinus*, while controlling for the effects of climate and land cover. Climate suitability of *S. olivaceus* does a better job of predicting *S. consobrinus* at the pseudo-site level than does presence of *S. olivaceus* within the pseudo-site, with areas of high climate suitability for *S.*

olivaceus unlikely to contain *S. consobrinus* ((p-value <0.00, R^2=0.37). This is the case despite the fact that in Texas, *S. olivaceus'* range is contained within the range of *S. consobrinus* both geographically, and environmentally. This apparent tight connection between the success of *S. olivaceus* and absence *S. consobrinus* raises the hypothesis that *S. olivaceus* may be playing a role in the decline of *S. consobrinus*.

Potential mechanisms driving declines

Having observed a decline in *S. consobrinus* through time (p-value<0.001, R^2=0.09; Table 2), we sought to understand which factors could explain declining trends. The average amount of urban cover for sites in 1920 (6% of land urban) was far less than today (56% of land urban) suggesting that urbanization may be in part responsible for the decline of *S. consobrinus*. Likewise, relative records of *S. consobrinus* versus *S. olivaceus* as a fraction of total lizard records move in opposite directions, with *S. olivaceus* increasing over the last 100 years, as *S. consobrinus* declines (Interaction between year and species identity predicting relative frequency, R^2=0.57, p-value <0.001, Figure 1a)--as would be expected if *S. consobrinus* were being impacted by a competitor. Interestingly, when examining these historical records, instances of co-occurrence between *S. consobrinus* and *S. olivaceus* in 2km radius "pseudo sites" were more common during the early 20th century than they are today (Interaction effect between year and *S. olivaceus* presence on predicting occurrence of *S. consobrinus*, p-value <0.001, R^2=0.25, Figure 1c).

One possibility is that changing landcover and climate over the last century have been favorable for *S. olivaceus* allowing for it to exclude *S. consobrinus* in areas which have experienced changes. We tested whether urbanization impacts the frequency of co-occurrence, and we found that in urban areas the effect of *S. olivaceus* is amplified, further decreasing the already low capacity for *S. consobrinus* to occur (p-value<0.001, R^2= 0.25, Figure 2). We further tested for interactions between climate and *S. olivaceus* occurrence to determine if certain climatic conditions allow for co-occurrence while others do not. Warmer areas overall were less likely to possess *S. consobrinus* (Figure 3), however no interaction between *S. olivaceus* presence and mean annual temperature was detected (p-value> 0.05, R^2=0.28) (Table 2). Wetter areas were more likely to possess *S. consobrinus*, but wetter areas where *S. olivaceus* occurred were highly unlikely to contain *S. consobrinus* (p-value<0.001, R^2=0.30) (Table 2, Figure 3). Urbanization and precipitation alter the strength of *S. olivaceus* presence on *S. consobrinus* occurrence and suggest that the outcome competition between the two species may depend on climate and habitat structure. While negative co-occurrence of observation records at broad spatial scales seems to implicate competition between *S. olivaceus* and *S. consobrinus*, proper evaluation of this hypothesis requires standardized surveys to evaluate co-occurrence at fine scales.

Lizard Communities

We analyzed data from 176 transect surveys to assess if the trends of exclusion of *S. consobrinus* by *S. olivaceus* is supported by patterns of co-occurrence at smaller spatial scales, in the same 200m transects during the same day (Figure 4).

We tested if microhabitat use between the two species was different based off perch height and substrate temperatures of individuals observed on transects. Average perch height was not significantly different, *S. consobrinus* mean= 107cm, *S. olivaceus* mean = 135cm, p-value= 0.12, and overlapped substantially. Likewise, both species were most frequently observed on woody substrates, often on tree trunks, fallen logs or branches. (Figure 5a). Substrate temperatures of field active individuals were also not significantly different between the two species (*S. consobrinus* mean= 33.7, *S. olivaceus* mean = 33.0, p-value=0.18). Based on microhabitat use, niche similarity between *S. consobrinus* and *S. olivaceus* is greater than between any other common co-occurring species in the Texas lizard fauna, lending plausibility to competition between this species pair. In contrast, A. *carolinensis,* which was implicated as a potential competitor in broadscale analyses above, has substantially different thermal preferences (Figure 5a), even though structural habitat use is not dissimilar.

We tested if the two species generally overlap in the habitats which they use based off canopy cover, we found *S. olivaceus* generally occurs in more closed canopy habitat than *S. consobrinus*.

If competition between *S. consobrinus* and *S. olivaceus* is occurring, we might expect to see character displacement, where *S. consobrinus* alters its habitat use when in the presence of *S. olivaceus*. Perch height is unaffected in this way, meanwhile the average canopy cover where *S. consobrinus* is found depends on whether *S. olivaceus* is present in the region. Both *S. olivaceus*, and *S. consobrinus* at sites where *S. olivaceus* does not occur, occupy transects with similar canopy cover (mean *S. olivaceus* 47.7%, mean *S. consobrinus* when olivaceus is not present 49.5%). In this circumstance canopy covered used by these species is statistically indistinguishable. But in areas where *S. olivaceus* is present, *S. consobrinus* associates with much more open areas, occurring on transects with approximately one third the amount of canopy cover (16.8 %). As a result, in areas where both species occur, *S. olivaceus* uses more closed canopy environments (the same environments *S. consobrinus* would use in the absence of *S. olivaceus*), while *S. consobrinus* becomes restricted to more open habitats (p-value <0.001, Figure 5b).

At the local level then, there is a signature of potential competition leading to habitat displacement. Is there similarly a signature of competition in raw abundance values?

Overall, *S. consobrinus* was observed on 40 transects, whereas *S. olivaceus* was observed on 58. Frequency of *S. consobrinus* occurrence was lower in regions possessing *S. olivaceus* (22/144, 15%), compared with transects outside of the range of *S. olivaceus* (18/32, 56%). Co-occurrence between *S. olivaceus* and *S. consobrinus* was only observed on 2 of 176 transects, much less than expected by chance. If competition were responsible for *S. consobrinus*' declines through time, then we would expect present day transects with *S. olivaceus*, to have lower than expected *S. consobrinus* abundance than expected based on their climate suitability for *S. consobrinus*, their canopy cover, and their degree of urbanization. Indeed, abundance of *S. consobrinus* was significantly lower on transects where *S. olivaceus* was present (p-value 0.024, full model R^2=0.57). Urbanization at landscape scales (within 2km of the transect) negatively impacted *S. consobrinus* (p-value=0.016). However, corresponding to results of occurrence records presented above, the predicted climate suitability from Maxent models did not have a significant impact on abundance of *S. consobrinus* (p-value >0.05). Finally, canopy cover did not have a significant influence over abundance of *S. consobrinus* (p-value >0.05), *S. consobrinus* was found on transects ranging from 0 to 89.3% Canopy Cover.

Competition Trials

Patterns of co-occurrence, when controlling for the environment, can flag potential cases of negative species interactions, but the nature of these interactions are tentative. Specifically, we hypothesize that competition between *S. consobrinus* and *S. olivaceus* is asymmetric, such that historical increases in *S. olivaceus* could cause the declines in *S. consobrinus* (rather than vice versa). We staged competition trials to confirm this asymmetry and establish if *S. olivaceus* is indeed the dominant competitor.

When placed together in the same enclosure *S. olivaceus* initiated more than twice as many antagonistic interactions by doing push-ups, head bobbing, or approaching *S. consobrinus* than vice versa (mean number of interactions initiated: *S. olivaceus* = 3.8, *S. consobrinus* = 1.75, Figure 6a). As expected, when responding to these interactions *S. consobrinus* was much more likely to retreat and hide, rather than either not responding, or responding with a counter-interaction (average interaction response scores: *S. olivaceus* mean = 0.15, *S. consobrinus* = -1.1, p-value =0.001, Figure 6b. The negative value for *S. consobrinus* indicates that retreat is frequent, whereas the slightly positive value for *S. olivaceus* is driven largely by their tendency to not respond to antagonistic displays from *S. consobrinus* and their occasional counter-displays).

Beyond the types of interactions engaged in, competition trials also revealed that *S. olivaceus* dominated the single available basking location when in the presence of *S. consobrinus* (p-value= <0.001, mean proportion of time on basking log for *S. olivaceus* = 0.58, *S. consobrinus* = 0.25, Figure 6c). In contrast, the amount of time that *S. consobrinus* spent hiding (either under cover or by burying itself under soil/leaf litter) increased greatly when *S. olivaceus* was present compared to when *S. consobrinus* was alone (p-value= 0.004, mean proportion of time spent hiding alone =0.008, with *S. olivaceus* present = 0.17, Figure 6d).

Discussion

We uncovered a dramatic decline of *S. consobrinus* over the last 100 years (Figure1a,c) and evaluated major hypotheses to explain this decline. Land use change, particularly urbanization appears to negatively impact *S. consobrinus*, leading to absence in heavily urbanized areas. However, declines of *S. consobrinus* are not confined to urban areas, with reductions in occurrence taking place in areas far from cities (Figure 2). In such instances, multifaceted evidence across scales points towards interspecific competition with *S. olivaceus* playing a role in excluding *S. consobrinus* from otherwise suitable habitat (Figure 1b). The strength of competition appears to be strong enough to completely override the measurable influence of climate: occurrence in areas with the lowest climate suitability (0) which lack *S. olivaceus* and those with highest climate suitability (1) which possess *S. olivaceus* do not differ in predicted occurrence of *S. consobrinus* (Figure 1b). The negative association with *S. olivaceus* largely drives trends of decreasing *S. consobrinus* in natural areas, co-occurrence with *S. olivaceus* at the pseudo-site level becoming increasingly rare with time (Figure 1c, 2). The conclusions stemming from these broad scale historical records were borne out in transect surveys assessing differences in lizard communities across Texas (Figure 4). Field observations demonstrated a high level of overlap in habitat use between the two species, as *S. olivaceus* uses more similar microhabitat to *S. consobrinus* than any of the other frequently observed species (Figure 5a). In the absence of *S. olivaceus*, the two species are found in habitats with similar canopy cover, but in regions where S. *olivaceus* occurs, *S. consobrinus* occupies far more open areas, effectively partitioning the local habitat (Figure 5b). At the transect level *S. consobrinus* abundance is lower on transects possessing *S. olivaceus* compared with those where it is absent. Despite having similar habitat requirements and the range of *S. consobrinus* subsuming nearly all of *S. olivaceus*'s Texas range, the two species only co-occurred on 2 of 176 transects. Finally, experimental competition trials revealed *S. olivaceus* as a superior competitor to *S. consobrinus*. *Sceloporus olivaceus* were more aggressive, initiating more interactions between individuals, and were almost exclusively the winner of interactions (Figure 6a,b). Matching data from transects, we find that the presence of *S. olivaceus* lead *S. consobrinus* to shift their habitat usage in the presence of *S. olivaceus,* spending over 15% of the time hiding, compared to less than 1% when alone (Figure 6d). These results when taken together suggest that *S. olivaceus* is competitively dominant, capable of excluding *S. consobrinus* via behavioral interference from areas it would otherwise occupy in the absence of *S. olivaceus*, and that the frequency of such competitive exclusion has been increasing over the last century, to the detriment of *S. consobrinus*.

Present day occurrence of *S. consobrinus* is poorly explained by climate alone (Table 1), suggesting that other factors are playing a disproportionately large role in determining their range. Habitat modification, specifically urbanization, is in part responsible for excluding them from otherwise suitable areas (Table 1), and while *S. consobrinus* are largely absent in cities other lizards such as *Anolis* sp. can tolerate urbanization well (Winchell *et al.*, 2020). Declines associated with urbanization may stem from many different factors (Shochat *et al.*, 2006), as conversion from natural habitats to urban ones can increase temperatures, push species past their thermal limits, reduce resource availability, alter availability of microhabitat and alter species interactions (Shochat *et al.*, 2010). However, absences in areas unimpacted by direct urbanization points to other possibilities such as climate change as a potential driver of population declines. We found that *S. consobrinus* occurrence was less likely in areas that have experienced warming or had increased in precipitation over the last century (Table 1). Yet, warming seems an unlikely cause as much of the area in which they are absent from today have not experienced a great amount of warming. Indeed, once presence of *S. olivaceus* is added in the model the effect of climate change is no longer significant (Table 1). Previous studies have not predicted a decline based off climate alone for *S. consobrinus* (Buckley, 2008). If warming or precipitation changes are playing a role in the current distribution of *S. consobrinus* it may be in the form of altering biotic factors influencing *S. consobrinus*, such as altering strength of competition, reducing prey availability, or altering habitat structure.

Ultimately, the presence of *S. olivaceus* better explains *S. consobrinus* occurrence than any other variable we assessed, including urbanization (Table 1). These results were mirrored at a fine scale by our transect data, showing decreased abundance of *S. consobrinus* on transects containing *S. olivaceus*. Competition may be responsible for absence of *S. consobrinus* in natural areas which are climatically suitable. Previous studies have demonstrated that competition can lead to exclusion from otherwise suitable areas, as one study found urban adapted bird species were less likely to breed in cities if a superior competitor is present, suggesting competition is responsible for their absence (Martin & Bonier, 2018). Meanwhile other studies suggest that species interactions are responsible for species not maximizing their abundance in accordance with measures of climate suitability (Braz *et al.*, 2020). Certainly, other species interactions may be important outside of *S. olivaceus*. *Anolis carolinensis* presence was also negatively associated with *S. consobrinus* based off pseudo-site analysis. At the transect level the two species were not significantly associated with each other, suggesting that caution should be used in scenarios of inferring species interactions from occurrence data. Signals detected at coarse scales may simply indicate preferences for alternative environments not included in the analysis. For example, *S. consobrinus* and *A. carolinensis* have greatly different preferences in body temperature, and *A. carolinensis* is more heavily arboreal (Figure 5a), and prefers different habitat types, occupying areas with more closed canopy than *S. consobrinus*. Additionally, *Scincella lateralis*, a small and terrestrial lizard, was significantly positively associated with *S. consobrinus* in the pseudo-sites, yet no relationship was found on transects. Our results suggest that if attempting to assess species interactions based off occurrence data alone, caution must be used in selecting species pairs being assessed and must be replicated at fine spatial scales at which species interactions might actually occur.

Competitive interactions have been suggested to be more likely between closely related species (Darwin, 1859), particularly as closely related species tend to have high levels of niche overlap, which itself promotes the likelihood of competition. Our species pair is extremely closely related, possibly capable of hybridization (Smith *et al.*, 1991), and have high levels of niche overlap, as both species were found primarily on woody substrates (tree trunks, logs, branches) between 1-1.5m high and 33-34 °C (Figure 5). Behavioral trials between *S. consobrinus* and *S. olivaceus* revealed strong competition interference, with the much larger *S. olivaceus* clearly dominant (Figure 6). Actual attacks, rather than merely aggressive displays were rare. In only one instance did *S. olivaceus* engage physically with *S. consobrinus*, an interaction that resulted in the *S. consobrinus* autotomizing its tail. Fear of such consequences, even when attacks are extremely uncommon, may lead to behavioral changes in *S. consobrinus*. The dominance of *S. olivaceus* is likely due to their larger size, previous studies have found size to be key in determining dominance (Munday *et al.*, 2001; Price & Sheilds, 2002). Lizards have been shown to avoid each other in the wild because they are afraid of each other, and this can lead to population and community level consequences (Pringle *et al.*, 2019). Interference competition resulting from aggressive behavior has been shown to shift habitat use in other species of lizards (Culbertson & Herrmann, 2019). While shifting habitat use may allow for coexistence of species, shifting habitat use can have negative consequences such as altering thermoregulation success or foraging ability. Yet it may not always be possible to partition habitat use, and in such instances the possibility for exclusion of the inferior species exists. While our data suggests behavioral interference as a factor in excluding *S. consobrinus* from otherwise suitable areas, it is not exclusive from exploitative competition. Both species are primarily insectivorous, and likely share prey, however in our study we did not assess the influence of prey availability on the rate of co-existence between the two species.

Interestingly, co-occurrence between *S. olivaceus* on *S. consobrinus* was historically much more common than it presently is. Urbanization seems to contribute to this trend, as in more urban areas *S. olivaceus* is favored over *S. consobrinus*. As a result, the general increase of *S. olivaceus* and the decrease of *S. consobrinus* through the last century (Figure 1) may in part be due to increasing urbanization benefitting *S. olivaceus* (Figure 2). However, urbanization, cannot explain the declines which have occurred in areas lacking any obvious direct changes in land-use, which have occurred at different times across Texas. The decline of *S. consobrinus* was first mentioned 30 years ago in an unpublished dissertation from the Welder Wildlife Refuge in Southern Texas (Mora, 1991). This study found that between 1959 and 1988 *S. consobrinus* went from being the most common lizard found in all habitat types on the refuge, accounting for 17% percent of all lizard observations, to only one individual being observed over a two-year period (out of 1,706 lizards observed, i.e. 0.059% of observations). During this time *S. olivaceus* increased greatly, becoming the most widespread lizard in the refuge, and accounting for 38% of all lizard observations in 1988. Other *S. consobrinus* declines are not well documented, however some North Texas populations of *S. consobrinus*, which were extant throughout 1975-2000, (Jones & Ferguson, 1980; Ryberg *et al.*, 2005) are now absent (AHM personal observation). In central Texas hill country, a population of *S. consobrinus* which was abundant until 1990 has since been lost, even in the absence of land-use change (David G. Barker personal communication). In all three of these regions *S. olivaceus* remains abundant today.

We propose that increasing competition from *S. olivaceus* is largely behind these declines. The exact mechanism behind such increased competition is uncertain, and in the absence of long-term data sets is difficult to test, however three potential scenarios present themselves: (1) Habitat modification across the landscape has reduced habitat heterogeneity, and in a less patchy environment the superior competitor is able to dominate. (2) Changes in resource availability may be responsible for increasing the strength of competition (3) Increasing abundance of *S. olivaceus* resulting in heightened total competitive pressure on *S. consobrinus*.

Habitat heterogeneity is crucial for the coexistence between competing species, allowing them to partition themselves and avoid negative consequences of competition (Pianka, 1967) (Ben-Hur & Kadmon, 2020). In the absence of competitor free space species are susceptible to competitive exclusion. This may be the case between *S. consobrinus* and *S. olivaceus*. While they have similar habitat use, *S. olivaceus* is more of a habitat specialist than *S. consobrinus*. *S. olivaceus* prefers wooded or forested areas with a preference for mature oak, hackberry and mesquite trees (Blair, 1960). They are rarely encountered in areas lacking trees. In the drier western portions of its range *S. olivaceus* is patchily distributed across the landscape, largely confined to forested areas near water bodies (Milstead, 1950). *S. consobrinus* is more of a generalist, as it readily occupies forested areas in locations without *S. olivaceus*, but is also capable of occupying open habitats, and exhibits incredible variation in habitat use (as well as habitat-matching coloration) throughout its range (Leache & Reeder, 2002). The need for S. *olivaceus* to have trees may explain why climate suitability for *S. olivaceus* is such a strong predictor of *S. consobrinus* occurrence. Areas where climate suitability is high for *S. olivaceus* may also be regions where *S. olivaceus* is more widespread across the landscape, and thus able to more directly impact *S. consobrinus,* compared to regions where it has a more limited local distribution.

Likewise, land use change may play a role in reducing habitat heterogeneity that once supported co-existence. Over the last century land cover has changed greatly across Texas. Urban areas have increased, land which was previously prairie and forest has been converted to pasture or agriculture, and elsewhere forest cover appears to be increasing; in general at a landscape scale habitat heterogeneity of natural landscapes is being reduced. In the absence of patches of unsuitable habitat for *S. olivaceus*, areas with too few trees, *S. consobrinus* may be more susceptible to local extinctions resulting from competition with *S. olivaceus*, as habitat where it can escape competition with *S. olivaceus* are lacking. This scenario is consistent with our finding that co-occurrence between the two species is especially unlikely in wetter areas, as compared to dry areas (Figure 3), as such areas usually are more heavily forested and suitable for *S. olivaceus*. This finding is further in line with the decline of *S. consobrinus* at Welder Wildlife Refuge, which occurred over a time with increasing precipitation, and likewise increased density of vegetation across the landscape (Mora 1991). If *S. consobrinus* is experiencing a decrease in competitor-free habitat as a result of landscape processes, declines at regional scales may be sped up by the dual negative effects of competition and urbanization working together, as even in patches of natural habitats of cities *S. consobrinus* is absent in central Texas.

Beyond habitat heterogeneity, resource availability may be dictating the strength of competition between *S. consobrinus* and *S. olivaceus*. This could come directly via environmental conditions leading to a reduction in prey availability. The effect could also be indirect, where land use change leaves some areas deprived of insects, causing more mobile insectivores such as birds or bats to redistribute themselves to undisturbed areas with more resources, which in turn exerts a higher pressure on the local resources that the competing *Sceloporus* sp. are bound to. This scenario could occur in central Texas, as it is a major migratory route for insectivorous birds (Dokter *et al.*, 2018), and contains large and apparently stable/growing bat population in central Texas (Stepanian & Wainwright, 2018). In times of low resource availability such as drought, *S. olivaceus* appears able to persist, while other lizards such as *Anolis carolinensis* may be locally extirpated (Blair, 1957). Perhaps enhancing *S. olivaceus* ability to deal with such fluctuation in resource availability is their ability to switch prey items during periods of low resource availability, even on rare occasions consuming small vertebrate prey such as rough green snakes (Blair, 1960), and have been observed eating *Hemidactylus turcicus* (AHM Personal Observation). Although not well documented, others have suggested that *S. olivaceus* may consume other lizards (Lawrence LC Jones & Lovich, 2009), and juvenile *S. consobrinus* are certainly small enough to be consumed by large *S. olivaceus*, so intra-guild predation may occur during periods of low resources, further impacting *S. consobrinus*.

Sceloporus olivaceus appears to be increasing in relative abundance over the last 100 years based off occurrence data (Figure 1a), and areas resurveyed over that time period show large increases of *S. olivaceus* (Mora, 1991). The increased abundance of *S. olivaceus* may explain decreased rates of co-occurrence with *S. consobrinus* as impacts of competition, and rates of co-occurrence can depend on density of competing species. When superior competitors are at high density, niche breadth of the inferior species can be reduced (Tarjuelo *et al.*, 2017), and successful foraging may be possible between competing species when the superior competitor is at low densities, but when density increases foraging success can be reduced (Hasegawa, 2016). The mechanism behind the apparent increase in abundance of *S. olivaceus* may be related to changing precipitation or vegetation patterns, however more research is required to say with any certainty.

Species interactions are believed to contribute to range limits and vary in their importance at warm versus cold range edge, with cool range limits often asserted to be controlled by climate, and species interactions playing a more important role at the warm range limit (Louthan *et al.*, 2015). Such claims are often supported by finding more suitable but unoccupied areas in the warm parts of species range when compared to the cool edge (Cunningham *et al.*, 2016). However, many instances of studies seeking to find biotic interactions responsible for warm range limits fail to do so and climate often receives more support for climate in setting warm edge of species ranges (Monasterio *et al.*, 2010; Cahill *et al.*, 2014; Grant *et al.*, 2018). Levels of support vary greatly across taxonomic groups, and in terrestrial vertebrates limited support exists and studies often rely on distributions of species to infer competition (Gross & Price, 2000; Freeman *et al.*, 2022), but studies combining distributional data and experimental measures of competition are rare. How competition can impact range limits varies, however it is commonly suggested to be important in maintaining boundaries between closely related parapatric species (Cunningham *et al.*, 2009), or in the case of range expansion leading to decline of the native species (Downes & Bauwens, 2002). Our study differs from past research in that we demonstrate how range retractions can result from increased competition between species with largely overlapping ranges, rather than as a result of a non-native invasion. Thus, our study highlights the fluctuating nature of both species interactions and species ranges in a novel way.

Conclusions

Here we find evidence that *Sceloporus consobrinus* has declined over the last 100 years, and that asymmetric interference competition with *S. olivaceus* is responsible. These declines lead to a reduction in the distribution of *S. consobrinus*, with many parts of central Texas and south Texas no longer harboring *S. consobrinus* populations. We demonstrate that broadscale associations between species occurrence patterns from historical records correspond to fine scale ecological data from transect surveys, which also match individual-level behavioral responses recorded from stage competition trials. Across all these scales the data support *S. olivaceus* as playing a role in limiting the distribution and abundance of *S. consobrinus.* We offer insight into the potential mechanisms responsible for an increase in their competition, with the acknowledgement that likely multiple factors may be important, and suggest future studies should focus on identifying the mechanisms by which species interactions are changing. The role of competition in setting range limits is widely studied, often in the context of invasive species or maintaining boundaries between closely related parapatric species. Our study suggests that the strength of competition can fluctuate through time, and increasing competition between native species with large areas of range overlap, can lead to range loss in the inferior species.

Figures and Tables

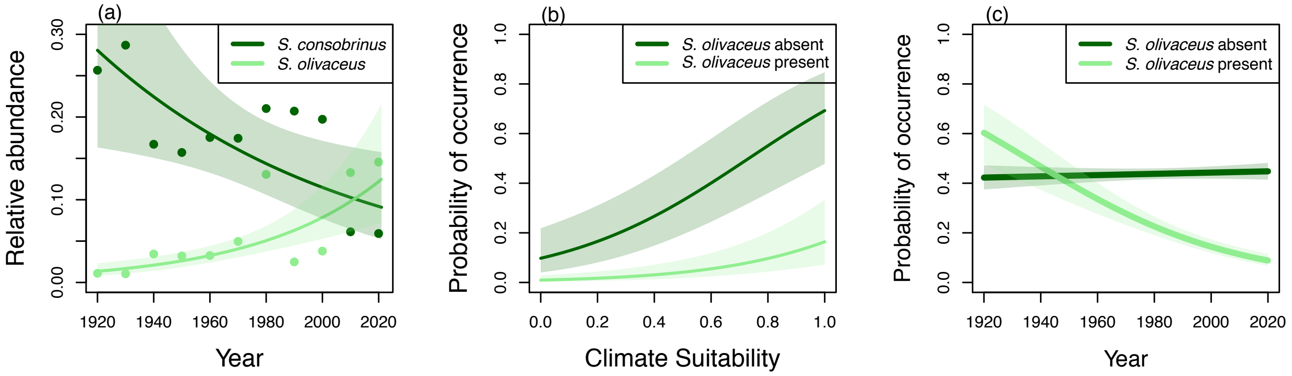


Figure 1. a) Trends in records of *Sceloporus consobrinus* and *S. olivaceus* over the last 100 years relative to all lizard records within the distribution of *S. consobrinus*. Lines represent model-based predictions of relative abundance for each species based off decadal values of relative frequency, shaded areas represent 95% confidence intervals from model predictions. Points are the raw values for relative frequency of each species for each ten-year period. b) Model-based predictions of the probability of occurrence of *S. consobrinus* in areas without urbanization based off Maxent predicted values for climate suitability (range in pseudo-sites 0.12-0.92, mean=0.61) while controlling for effects of sampling effort. Shaded areas represent standard error. c) Change in strength of competitive exclusion of *S. consobrinus* by *S. olivaceus* in natural areas(urban=0) through time, while controlling for the effect of climate suitability, and sampling.

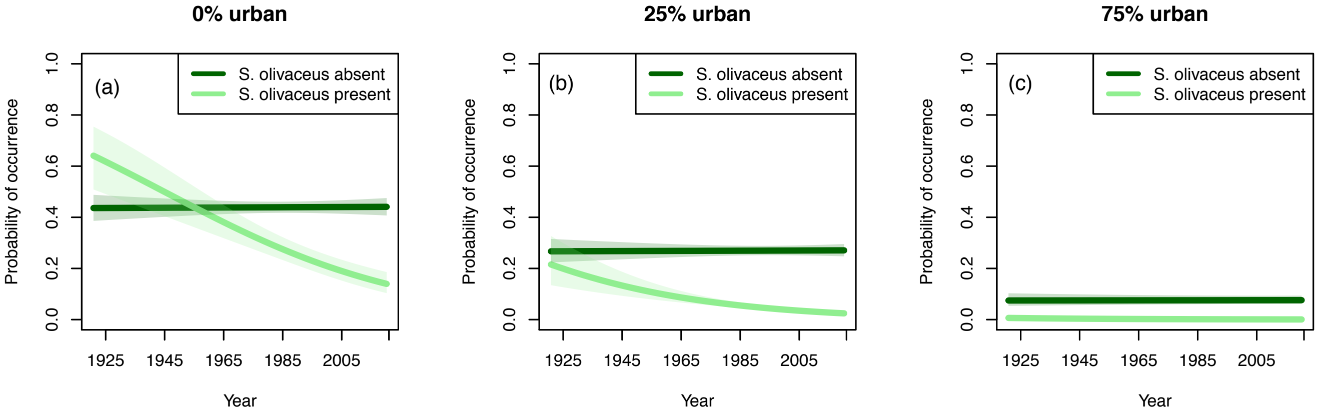
Table 1. Results from models testing the current distribution of *S. consobrinus*, 2020-2021.

Number of pseudo-sites=396. *P-value <0.05 *, <0.01**, <0.001****.

Model #	Type	AIC	R2	ΔAIC	1	2	3	4	5	6	7
1	*climate suitability*	271.5	0.008	86.1	hbs	sampling					
2	*climate suitability +landcover*	238.5	0.14	53.1	hbs	sampling	-urban***				
3	*climate suitability+ climate change*	246.9	0.11	61.5	hbs	sampling	-MAT change***				
4		255.4	0.08	70	hbs	sampling	-MAP change***				
5		229.6	0.18	44.2	hbs	sampling	-MAT change***	-MAP change ***			
6	*climate suitability+landcover+ climate change*	221.9	0.22	36.5	hbs	sampling	-urban**	-MAT change***	-MAP change**		
7	*climate suitability+ landcover+ species associations*	212.4	0.24	27	+hbs**	sampling	-urban***	-*S. olivaceus* ***			
8		221.6	0.21	36.2	hbs	sampling	-urban**	-*A. carolinensis* ***			
9		236.2	0.16	50.8	hbs	sampling	-urban***	+*P. fasctiatus* *			
10		236.1	0.16	50.7	hbs	sampling	-urban***	+*Scincella lateralis* *			
11		194.8	0.33	9.4	+hbs*	sampling	-urban**	-*S. olivaceus* ***	-*A. carolinensis* ***	+*Scincella lateralis* *	
12	*climaye suitability + species associations*	236.8	0.15	51.4	+hbs**	sampling	-*S. olivaceus* ***				
13	*climate suitability + climates suitability of S. olivaceus*	217	0.22	31.6	+hbs***	sampling	-hbs *S. olivaceus* ***				
14	*climate suitability+landcover+climate change+species associations*	193.5	0.34	8.1	+hbs*	sampling	-urban**	-*S. olivaceus* ***	-*A. carolinensis* ***	*Scincella lateralis*	MAT change
15	*climate suitability + climates suitability S. olivaceus +landcover+ species interactions +climate change*	185.4	0.37	0	+hbs*	sampling	-hbs *S. olivaceus* ***	-urban**	-*A. carolinensis* **	*Scincella lateralis*	MAT change

Table 2. Results from models testing the occurrence of *S. consobrinus* through time, 1920-2021. Number of pseudo-sites=1340. *P-value <0.05* *, *<0.01***, *<0.001****.

Model #	Type	AIC	R2	ΔAIC	1	2	3	4	5	6	7	8	9
1	*climate suitability + time*	1343.6	0.08	300.6	+hbs***	sampling	-year***						
2	*climate suitability +time+ landcover*	1171	0.2	128	+hbs***	sampling	-year*	-urban***					
3		1309	0.11	266	+hbs***	sampling	-year***	+forest***					
4	*climate suitability+time*species+ landcover*	1109	0.25	66	+hbs***	sampling	year	-year: S. olivaceus***	- S. olivaceus***	-urban***			
5	*climate suitability+time*species+ landcover*species*	1104	0.25	61	+hbs***	sampling	year	-year: S. olivaceus**	- S. olivaceus***	-urban***	-S. olivaceus:urban*		
6	*climate suitability+time*species+ climate*species +landcover*	1097	0.26	54	+hbs***	sampling	year	year: S. olivcaeus	- S. olivaceus**	MAP	-S. olivaceus:MAP***	-urban***	
7		1062	0.28	19	+hbs***	sampling	year	-year: S. olivaceus***	- S. olivaceus*	-MAT***	S. olivaceus:MAT	-urban***	
8	*climate suitability+time*species+ climate*species +landcover+climate*	1043	0.3	0	+hbs***	sampling	year	year: S. olivcaeus	- S. olivaceus***	+MAP*	-S. olivaceus:MAP***	-urban***	-MAT***


0% urban

25% urban

75% urban

Figure 2. a) Predicted probability of *S. consobrinus* occurrence over time in areas that have no urbanization based off presence or absence of *S. olivaceus* while controlling for effects of climate suitability and sampling. Shaded areas represent standard error. b) Predictions made for areas which are 25% urban. c) Predictions for areas where 75% is urban. Pseudo-sites ranged from 0-100% urban, with a median of 9.8%, 25% of pseudo-sites were below 1% while 75% of the pseudo-sites were above 76%.

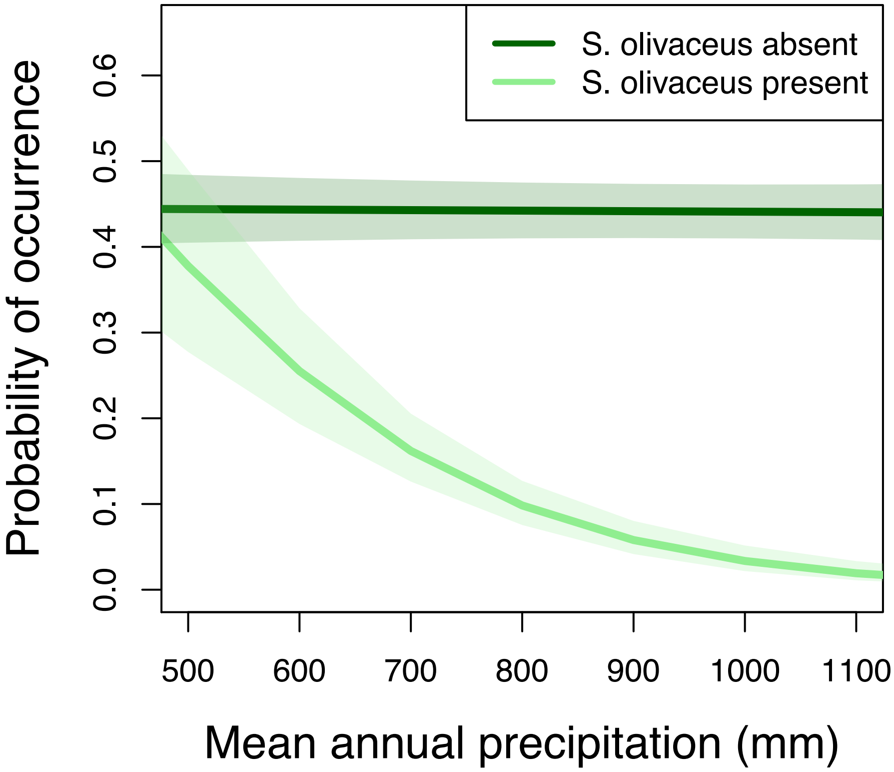


Figure 3. Model-based predictions of the probability of occurrence of *S. consobrinus* in areas without urbanization based off presence or absence of *S. olivaceus* and mean annual precipitation (range confined to the 5% and 95% for MAP at pseudo-sites where *S. olivaceus* is present). Shaded areas represent standard error.

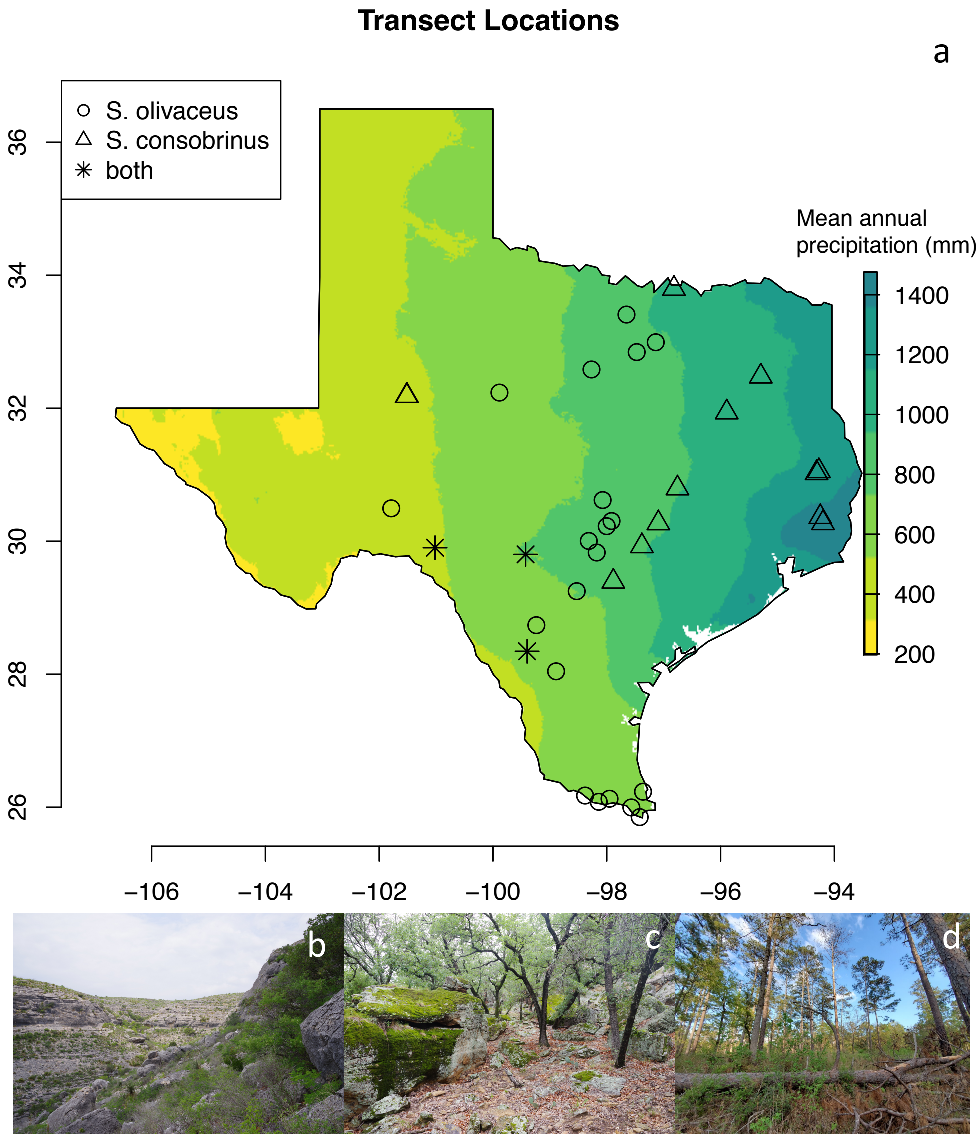


Figure 4. a). Distribution of sites where either *S. olivaceus* or *S. consobrinus* was observed. b). The Dolan Falls Preserve, habitat representative of the canyons in the western portion of the Edwards Plateau, forested base of canyon contains *S. olivaceus* open plateaus on top have *S. consobrinus*. c) Roger Fawcett WMA, central Texas cross timbers, habitat from a transect where *S. olivaceus* were observed. d) Angelina National Forest, *S. consobrinus* are abundant in the Longleaf Pine Forest of deep East Texas, often observed on trunks of trees, stumps and fallen logs.

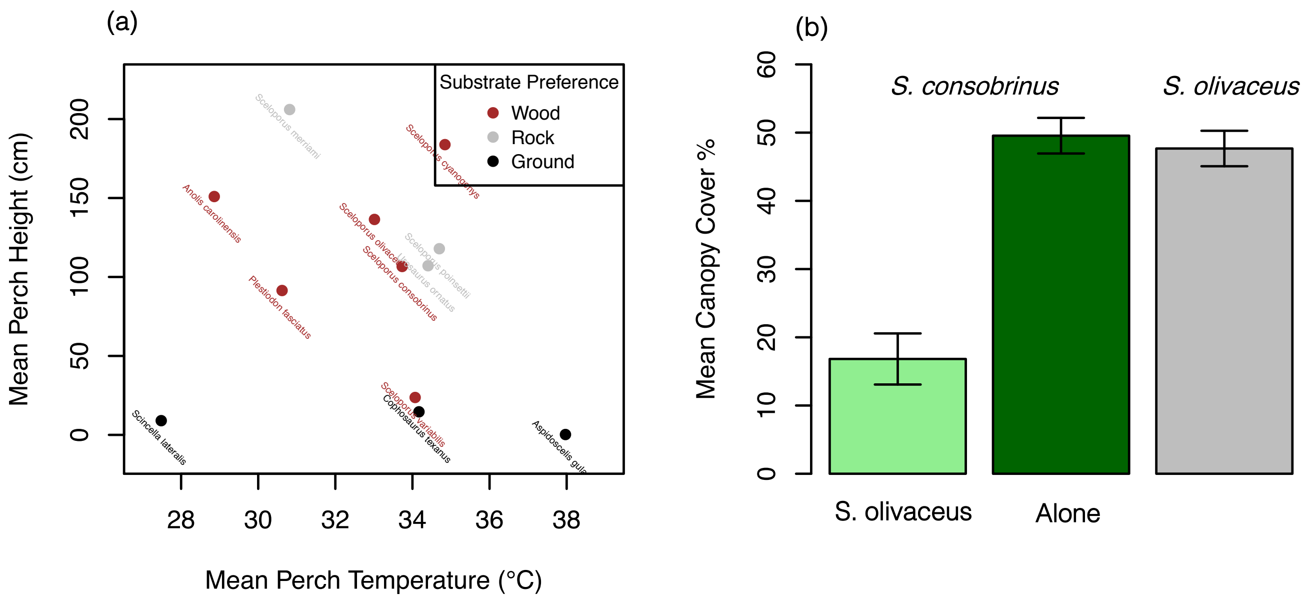


Figure 5. a) Microhabitat use amongst the 12 most common species recorded on transects. Point color represents the substrate which they are most frequently found on, for all species these colors represent greater than 50% of on transect observations). The species mean perch height and temperature values are only from active individuals observed during the day. b). Mean canopy cover of *S. consobrinus* from sites with and without *S. olivaceus*, compared to mean canopy cover for *S. olivaceus*, bars represent standard error.

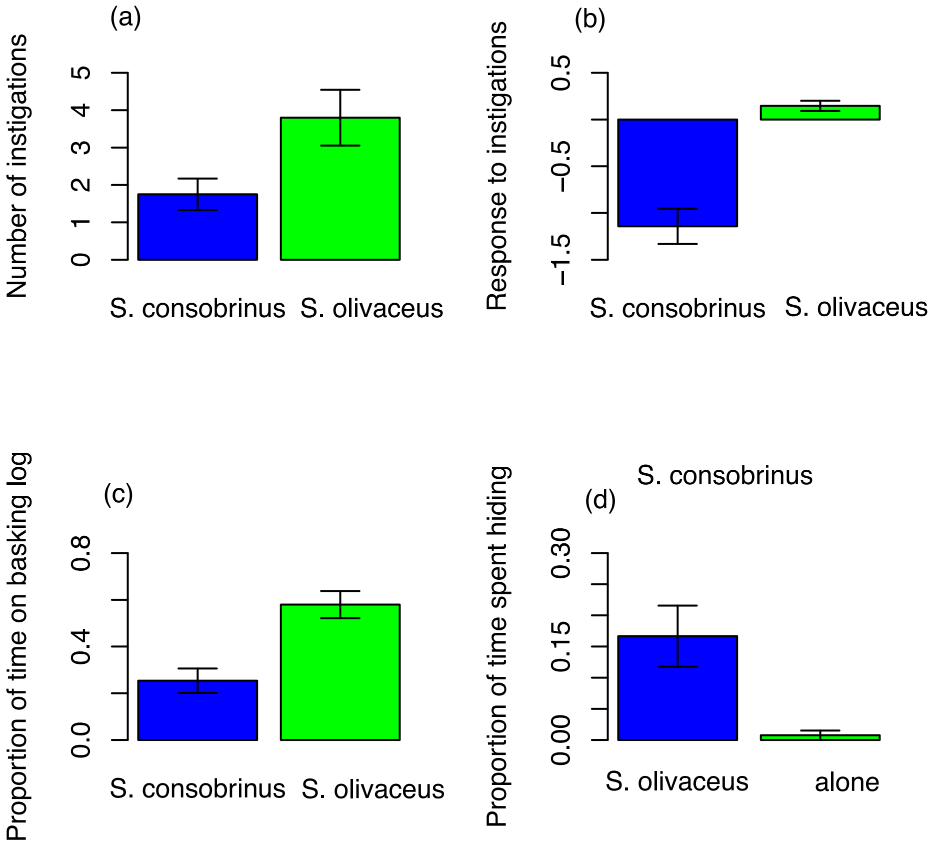


Figure 6. a) Mean number of instigations initiated by each species during behavioral trials, bars represent standard error. b) Mean response to interactions by each species. c) Proportion of time on the basking log during trials. d) Proportion of time spent hiding by *S. consobrinus* in trials with *S. olivaceus* compared to when *S. consobrinus* are alone.

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Appendix 4.1. Supplemental Figures

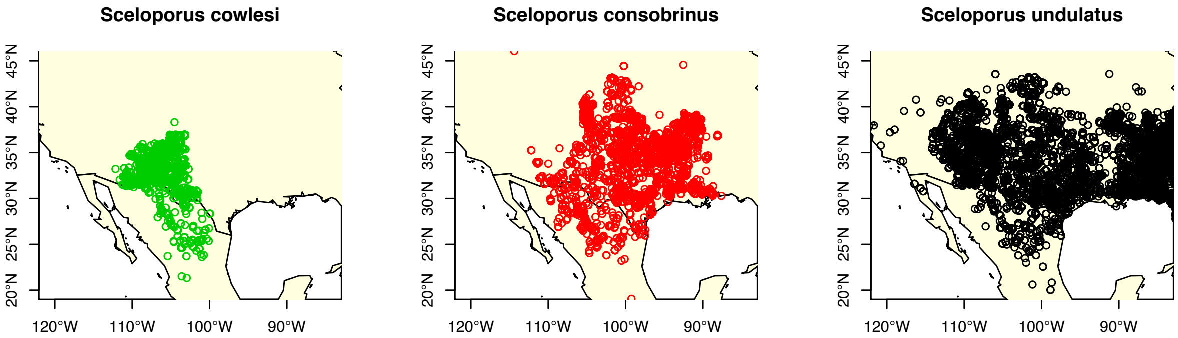

Figure S1 Occurrences of the *S. undulatus* group on gbif before data was cleaned and taxonomy updated.

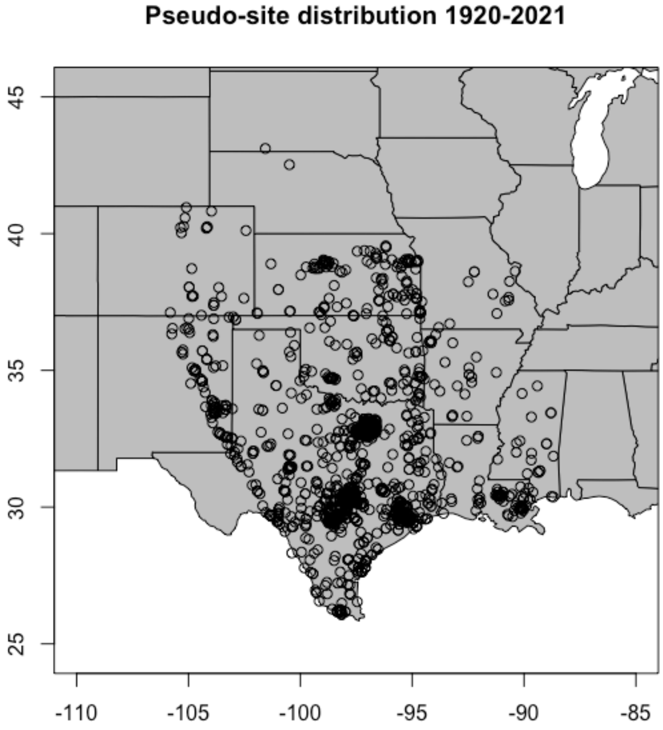

Figure S2. Pseudo site distribution at 2km sites, 1340 total records between 1920-2021 with a minimum of 5 observations per location.

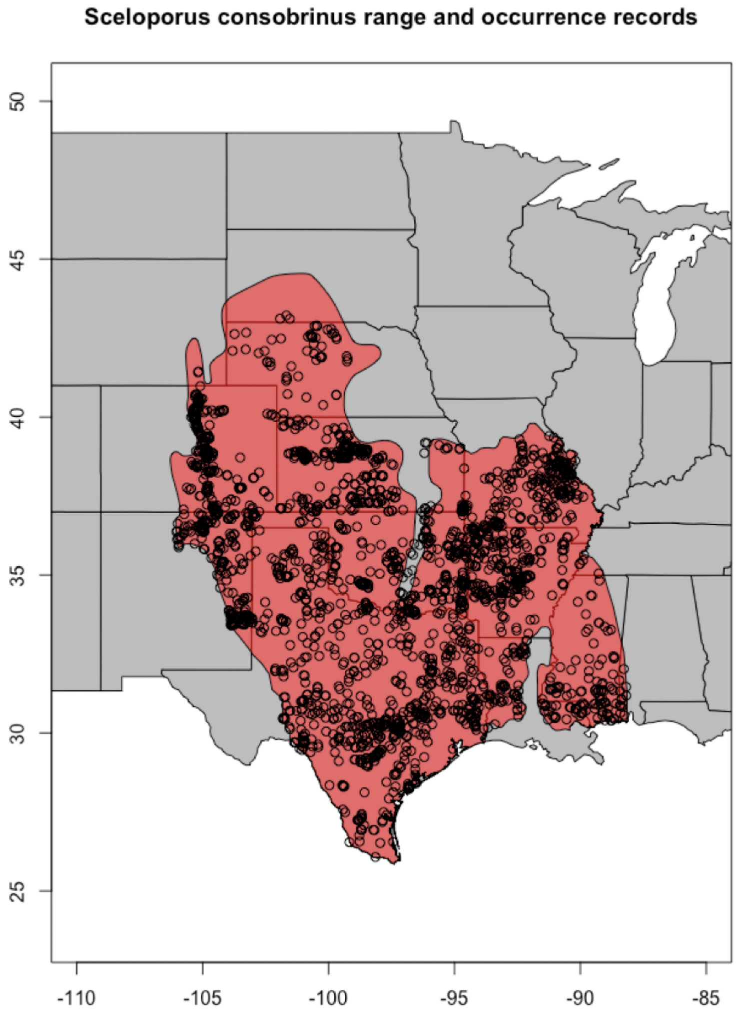

Figure S3 Cleaned up occurrence records post thinning used for Maxent models for *Sceloporus consobrinus*, 2527 records

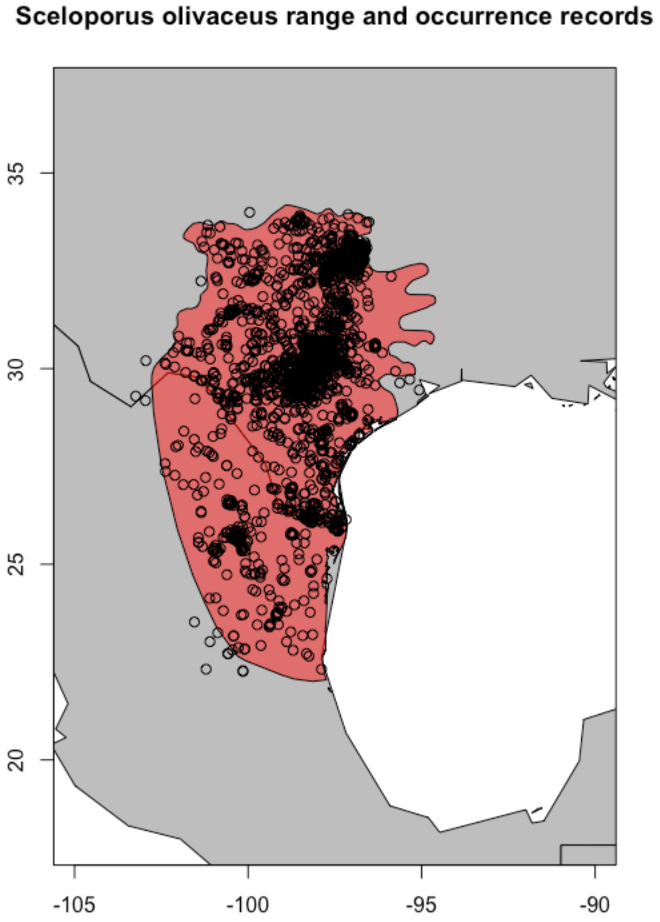

Figure S4 Cleaned up occurrence records post thinning used for Maxent models for *Sceloporus olivaceus*, 2817 records.

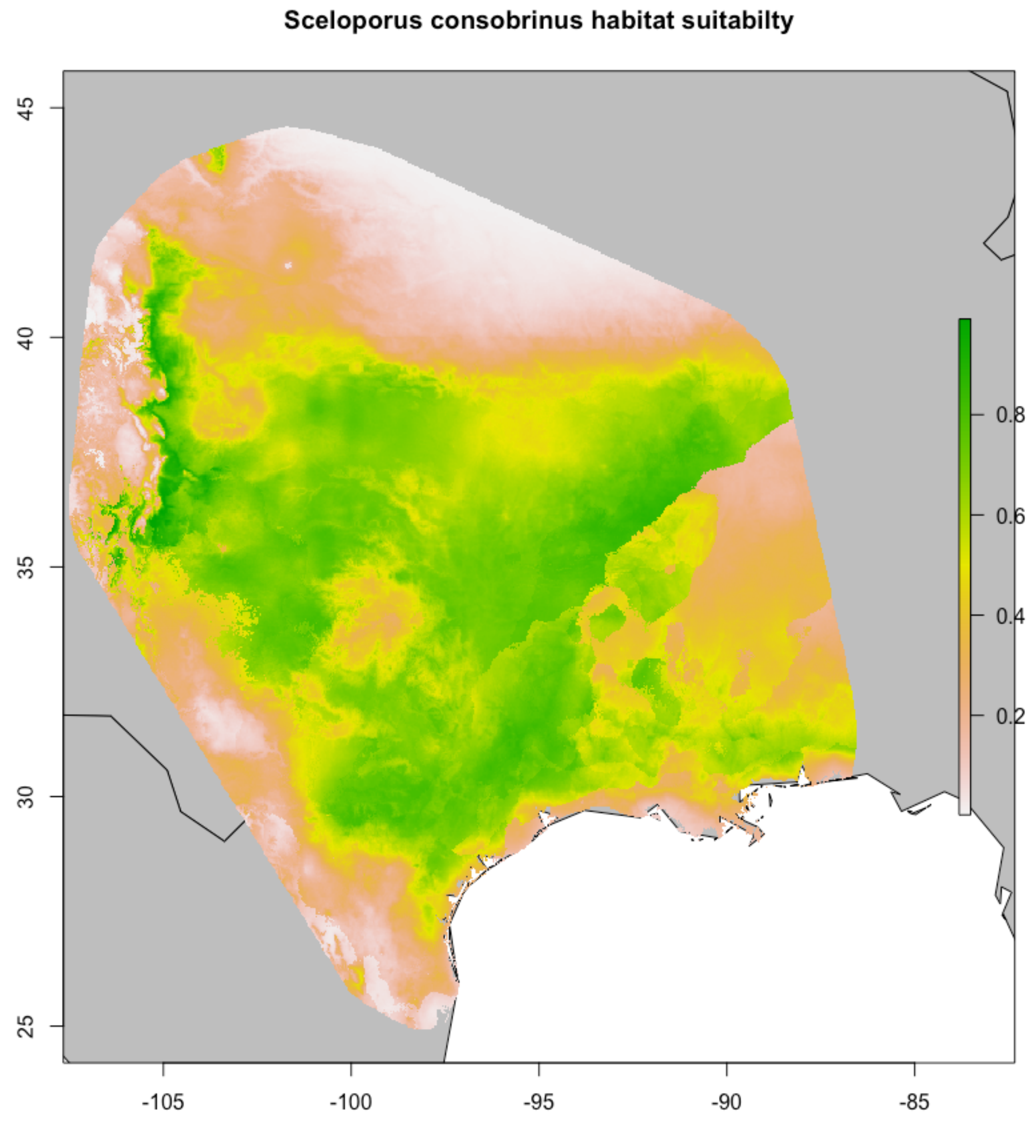

Figure S5. Maxent predicted climate suitability for *Sceloporus consobrinus*, AUC value=0.749.

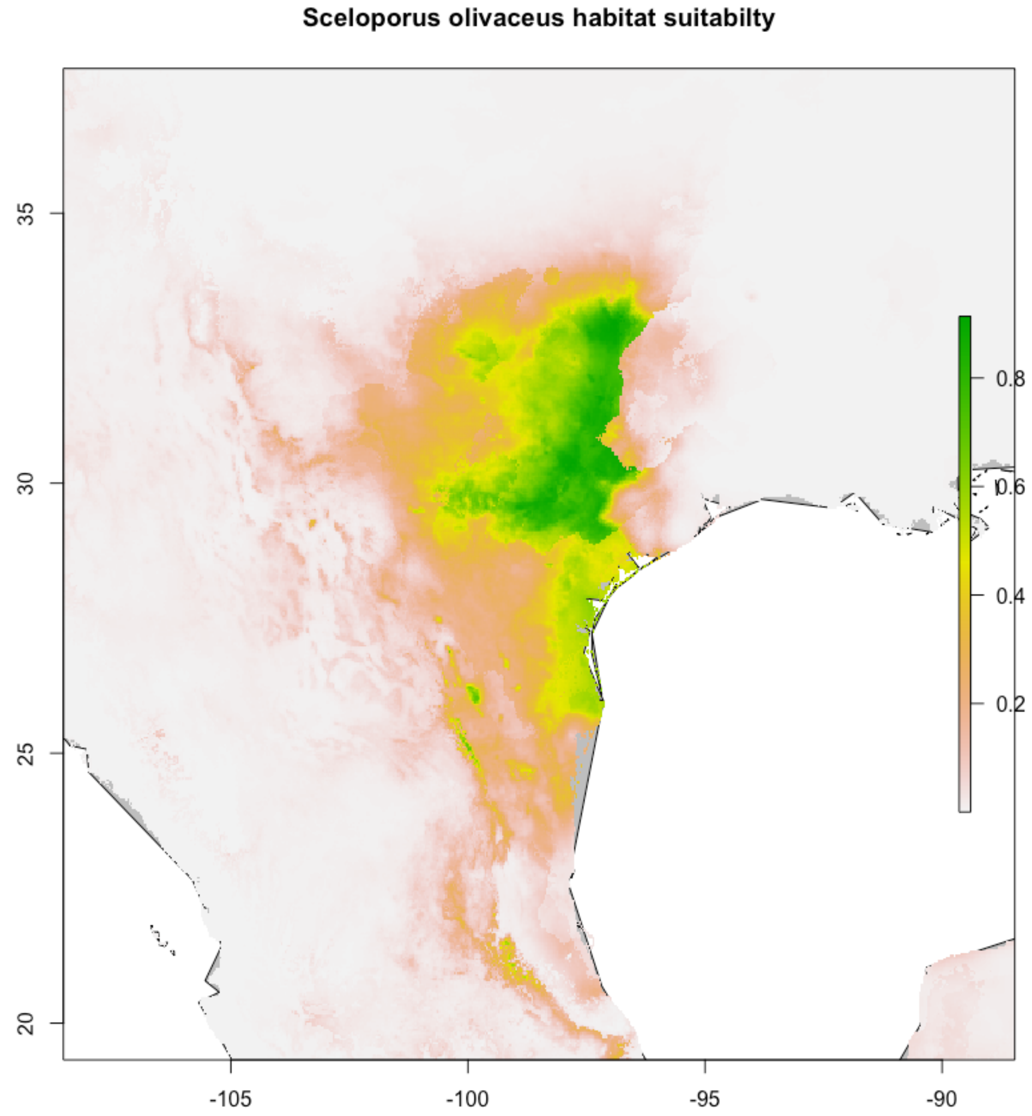

Figure S6. Maxent predicted climate suitability for *Sceloporus olivaceus* , AUC value=0.909.

Figure S7. Screenshot from a competition trial to display the setup. This image displays a *S. consobrinus* fleeing a large *S. olivaceus* after confrontation.

Chapter 5

General Conclusions

The goal of my research was to better understand how species and communities are changing as a result of human influences. To achieve this, I studied how amphibians' response to habitat modification is dependent on the severity of habitat modification, microhabitat use and climate. I next investigated how early human populations have altered communities, revealing a lasting effect of decreased species richness in areas inhabited by early humans, accounted for by the loss of the species most sensitive to habitat modification. Finally, I moved away from global studies, and combined fieldwork, with occurrence data and behavioral experiments to understand the role of species interactions on population trends and species occurrences. Combined my research highlights the ways in which communities and populations are changing, resulting either directly or indirectly from humans.

In chapter 2, I assessed the utility of trait-based studies for determining species' sensitivity to habitat modification. One of the of the goals of study was to address a simple hypothesis that lacked support in the literature, that being that arboreal amphibians are more sensitive to habitat modification than terrestrial amphibians, on account that they tend to lose the microhabitat in which they depend on during the process of habitat modification. I found support for this simple hypothesis, that arboreality does predispose species to be sensitive to habitat modification, yet the degree to which species decline is modulated by the degree of habitat modification and the climatic conditions.

In chapter 3, I tested the extinction filter hypothesis (Balmford, 1996), using bird communities across the world, to determine if prehistoric humans have contributed to variation amongst communities in their sensitivity to habitat modification. I found prehistoric humans have impacted how present-day communities respond to habitat modification, and that areas inhabited by humans long ago may be perceived as being less sensitive to habitat modification. However positive this may sound, it is not, as this lack of sensitivity may be accounted for by unknown extinctions which drive a loss of species richness in primary vegetation and relatively little change in species richness in heavily disturbed habitats. So rather than adapting to the influence of humans and becoming less sensitive as a whole, the communities simply have lost the most sensitive species already and are left less diverse than before. This leaves a phylogenetic signal with, increased phylogenetic dispersion in primary vegetation in areas with large human populations 12,000 YBP, and an increase in evolutionary distinctiveness within the communities. This highlights how lasting the impacts of humans are, in that early humans impacts are still seen in areas considered to be intact or pristine habitats today. This study informs conservation efforts as it suggests that we may want to focus our efforts on ensuring that areas which have had low human populations through time are spared from habitat modification, as they are most likely to possess sensitive species unable to cope with the land use changes.

In chapter 4, I shifted away from global analyses and dug into a more fine scale study to understand how species' are being impacted by climate, species interactions, and human habitat modification. My goal was to test if *S. consobrinus* is declining through time, and if so does competition with *S. olivaceus* play a role in this decline. I found that a once common lizard, *Sceloporus consobrinus* has experienced declines in relative abundance over the last century. These declines appear to stem from both urbanization and competition, with urban areas and those where *S. olivaceus* is present lacking *S. consobrinus*. Co-occurrence between *S.*

consobrinus and *S. olivaceus* has become increasingly rare in recent times. Co-occurrence is exceedingly unlikely in urbanized areas and areas with high precipitation where *S. olivaceus* is present. Results at transect level matched the results from occurrence data suggesting that competitive exclusion may be responsible for absences in otherwise suitable areas. Finally, behavioral trials revealed the competitive dominance of *S. olivaceus*, which controlled the prime basking position, and initiated more interactions that led to the retreat or hiding by *S. consobrinus*. I believe this to be the first study to combine occurrence data, community surveys and behavioral trials and find agreement amongst all data sources for competition between two lizard species. Further this sheds light on both the temporal changes in competition, and the context dependent nature of competitive outcomes, as species may be able to co-occur under some conditions and not elsewhere. It is my hope that this project will lead to more research on both *S. consobrinus* and *S. olivaceus*, as well as communities in transitional regions.

Through my research I addressed key gaps in our understanding of how biodiversity is changing and our impacts on it, advancing our ability for successful conservation. My second and third chapter focus on understanding how habitat modification impacts species, each revealing novel findings. My second chapter was the first study to reveal the importance of interactions between climate and traits in determining sensitivity to habitat modification. My third chapter demonstrates that early human impacts on modern communities may be greater than we currently appreciate, as it suggests that humans have influenced diversity in areas otherwise considered to be intact primary vegetation, potentially being responsible for "dark extinctions" (Boehm & Cronk, 2021). These results have important implications both for understanding patterns of biodiversity, and for conservation. In terms of biodiversity, it suggests that when considering historical factors which influence contemporary patterns of biodiversity we may want need to include some measur e of human influence, something which to this point is not incorporated in models of global biodiversity. In terms of conservation, it highlights the need to protect areas most untouched by human presence, as they are most likely to contain species that can only exist in primary vegetation and may be lost if the habitat is not protected. My fourth chapter presents an example of how species interactions can change through time, contributing to range loss, and population declines. This scenario is relatively undocumented in vertebrate species as most studies considering the role of competition in setting range limits focus on competition maintaining range limits between closely related parapatric species, or between invasive species and native species. That interactions between species with largely overlapping ranges can change through time and lead to range loss in the weaker competitor is not well documented and anthropogenic factors may be responsible for such a change, however more work is needed to test this.

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