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

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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
Anura, biodiversity, community change, conservation, countryside biogeography, global change, habitat loss, microhabitat, niche, traits

1 | 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 (Barnosky et al., 2011; Wake & Vredenburg, 2008). 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 (Daily et al., 2001; Elsen et al., 2017; McKinney & Lockwood, 1999; Mendenhall et al., 2016). 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; Nowakowski, Frishkoff, Thompson, et al., 2018; Sol et al., 2017). 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 (Cardillo et al., 2005; Fritz et al., 2009; Purvis et al., 2000), birds (Owens & Bennett, 2000), amphibians (Cooper et al., 2008), reptiles (Böhm et al., 2016) and butterflies (Kotiaho et al., 2005). Results of comparative analyses generally point to small geographic range size and habitat specialization as the primary causes of high extinction risk [usually measured as International Union for Conservation of Nature (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 understorey birds are particularly dependent on that strata's availability—because mango plantations lack understorey 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 that lay eggs in vegetation (Trimble & van Aarde, 2014). Traits that tie directly into the parts of the habitat that are being converted are likely to be strong links for identifying species that 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 that 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, Watling, et al., 2018). However, measuring thermal tolerances is time intensive, and therefore is not available for most species observed in community data sets. 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 (a) tolerance to habitat conversion is often treated as a property of a species and invariant between populations and (b) 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 data set 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 metre 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 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, Watling, et al., 2018). 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 pre-adapted to deal with the hot and dry conditions of human-modified habitats. In contrast, in cooler environments understorey 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.

2 | METHODS

2.1 | Community composition data

We compiled a database of 18 studies of amphibian abundance across land-use types, which includes 154 species (see Supporting Information 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 (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) database (Hudson

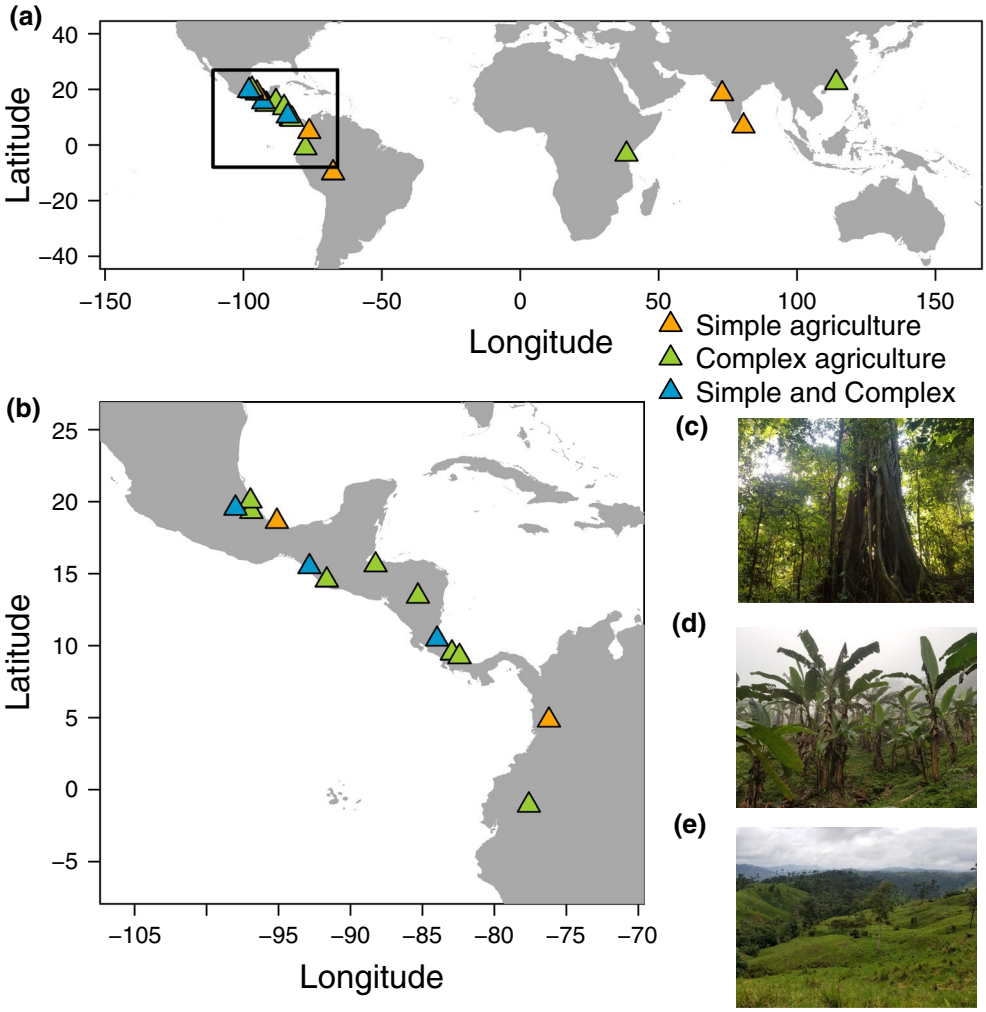


FIGURE 1 (a) Distribution of 18 study locations included in our analysis. (b) The greatest concentration of studies ($n = 14$) is in Central America and northern South America. All studies contained (c) primary forest, while 13 contained (d) complex agriculture, and 8 studies contained (e) simple agriculture [Colour figure can be viewed at wileyonlinelibrary.com]

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 that 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 analysed data set. 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 data set) 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 four continents, with the greatest number of studies from Central America (Figure 1).

2.2 | 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 (Figure 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 understorey (1), in midstorey (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-storey and a quarter of time in the understorey 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-storey and half of the time from the understorey 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 in which eggs are laid and the habitat where larvae 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 (a) terrestrial direct developers that forgo a larval stage, (b) lotic species, that have aquatic larvae that develop in moving water (lotic habitat), or (c) 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 data set did not contain many. Detailed descriptions of amphibian trait scoring are contained in Supporting Information Appendix S2. All references for data sources can be found in Supporting Information Appendix S1.

2.3 | Analysis

To test the hypotheses that (a) species that use higher vegetative strata will be most severely reduced following conversion of tropical forest, and (b) that this reduction will be most severe in structurally simple agriculture, we implemented a generalized linear mixed effect model. Doing so allowed us to analyse 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

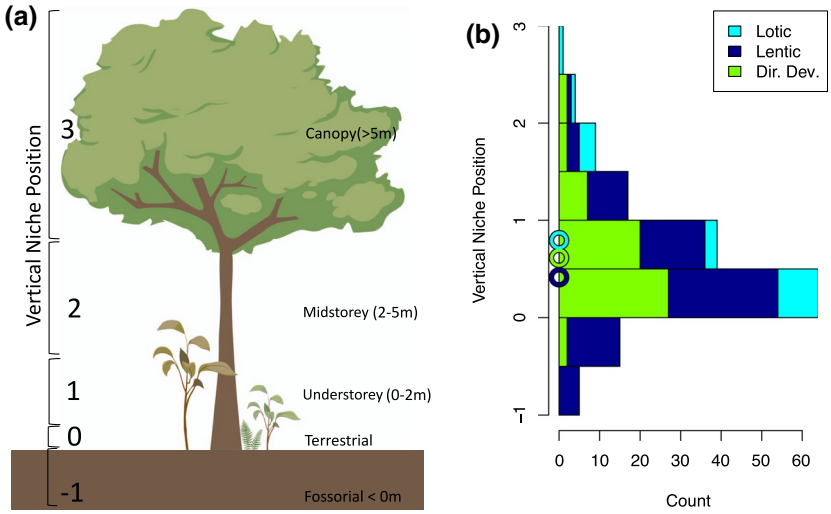


FIGURE 2 (a) Schematic depicting how vertical niche position was scored numerically based on species accounts of the height and/or vegetative stratum where species occurred. (b) Histogram of species' vertical niche position within each reproductive mode. There was a total of 75 species whose larvae developed 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 colour-coded open circle [Colour figure can be viewed at wileyonlinelibrary.com]

amphibian abundance and present results of latitude and the other climate variables in Supporting Information Appendix S3. We obtained environmental data from the WorldClim data set (Fick & Hijmans, 2017). We extracted the climatic variables at the individual sites within studies at a 2.5-min scale, a resolution suitable for detecting large biogeographic 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 (R core team 2019) using the 'glmmTMB' package to implement generalized linear mixed effect models. We conducted model comparison of a full suite of models using Akaike information criterion (AIC), and tested for term significance through likelihood ratio tests of nested models, evaluated against a chi-square distribution (Supporting Information Appendix S3 contains full model information). We calculated r^2 values for each model using the r.squaredGLMM function from the 'MuMIn; package in R (Barton & Barton, 2019; Johnson, 2014; Nakagawa et al., 2013). To ensure our results were robust to phylogenetic non-independence, we incorporated phylogeny into our models using the glmmTMB_phylo function in R (Brooks et al., 2017). 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) (Tables 1, 2; Supporting Information Table S2). All models presented in the main text are phylogeny models; we present AIC values for non-phylogenetic models in Supporting Information Table S2. Inclusion of phylogeny does not alter the direction or significance of parameters' effects.

3 | RESULTS

After filtering our data, we retained 18 studies with 154 species, and over 6,700 individual observations of species within sites (Figure 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 centred between terrestrial and understorey (mean vertical niche position of 0.54; Figure 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 ($n = 19$; Figure 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; Figure 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* × *land use* interaction, $df = 2$, $\chi^2 = 30.74$, $p < .001$, 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 two-way interactions. We find that interactions between traits did not influence how species respond to habitat conversion (*reproductive mode* × *vertical niche* × *land use* interaction, $df = 4$ $\chi^2 = 4.734$, $p = .32$), 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* × *land use* interaction, $df = 4$, $\chi^2 = 277.4$, $p < .001$, 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 (Figure 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 Supporting Information 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* × *reproductive mode* × *land use* interaction, $df = 4$, $\chi^2 = 16.323$, $p = .0026$; Figure 4, Table 2, Supporting Information Figure S3.7). 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* × *vertical niche position* × *land use* interaction, $df = 2$, $\chi^2 = 26.25$, $p < .001$ Figure 5, Table 3, Supporting Information Figure S3.6).

4 | DISCUSSION

Overall the hypothesis that arboreality leads to increased sensitivity to habitat conversion is supported, as arboreal species decline

TABLE 1 All models predicting amphibian abundance

#	Model type	Model	ΔAIC	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
1	Land use only	LU	396	10,515	.07	2		***													
2	Trait models	LU × NP	367	10,486	.16	5												***			
3		LU × RP	107	10,226	.25	8									***						
4	Environment models	LU × MT	402	10,521	.07	5															
5	Trait-by-trait	LU × NP × RP	92	10,211	.32	17															
6	Trait-by-environment	LU × NP × MT	348	10,467	.22	11															
7		LU × RP × MT	0	10,119	.28	17															
								Additive terms						Trait × LU						Trait × Trait	

Note.: AIC = Akaike information criterion;R^2m = marginal R^2. Terms [LU = land use; RP = reproductive mode; 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 ($p < .05$), while lightly shaded colours $p < .1$. 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 $p > .1$ (NS), $p < .01$ (**), $p < .001$ (***), 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 ($n = 154$).

TABLE 2 Model summary for model 6 (Table 1.)

Model 6 : LU * Max Temp * Niche Pos			
Fixed effects			
Parameters	**Parameter estimate**	**Standard error**	***p*-value**
Intercept	0.07	0.23	
Comp Ag	−0.38	0.13	**
Simp Ag	−1.14	0.14	***
Max Temp	0.09	0.13	
Niche Pos	−0.16	0.10	
Comp Ag : Max Temp	−0.04	0.13	
Simp Ag : Max Temp	−0.06	0.10	
Comp Ag : Niche Pos	0.23	0.08	**
Simp Ag : Niche Pos	−0.63	0.15	***
Max Temp : Niche Pos	−0.06	0.05	
Comp Ag : Niche Pos : Max Temp	0.22	0.08	**
Simp Ag : Niche Pos : Max Temp	0.51	0.12	***
Random effects			
	Standard deviation		
Species	1.02		
Study	0.79		
Site	0.50		

Note: We denote whether each parameter is significant $p < .01$ (**), $p < .001$ (***) based on Wald tests. Negative binomial dispersion parameter, phi = 5.85. Pagel's lambda = .23. Terms [LU = land use; Niche Pos = niche position; Comp Ag = complex agriculture; Simp Ag = simple agriculture; Max Temp = maximum temperature (Bio5 from WorldClim)].

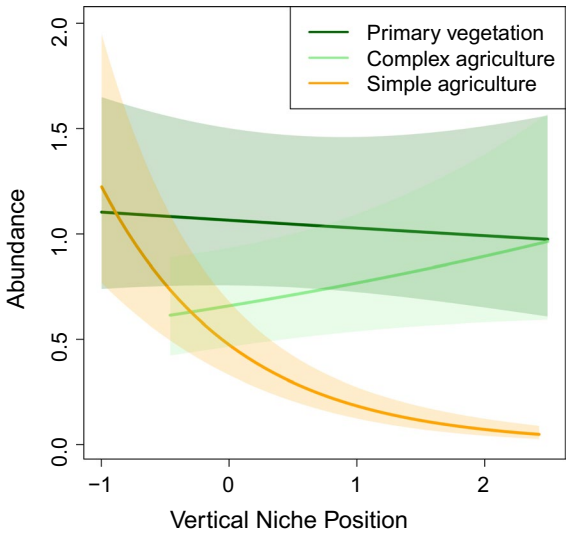
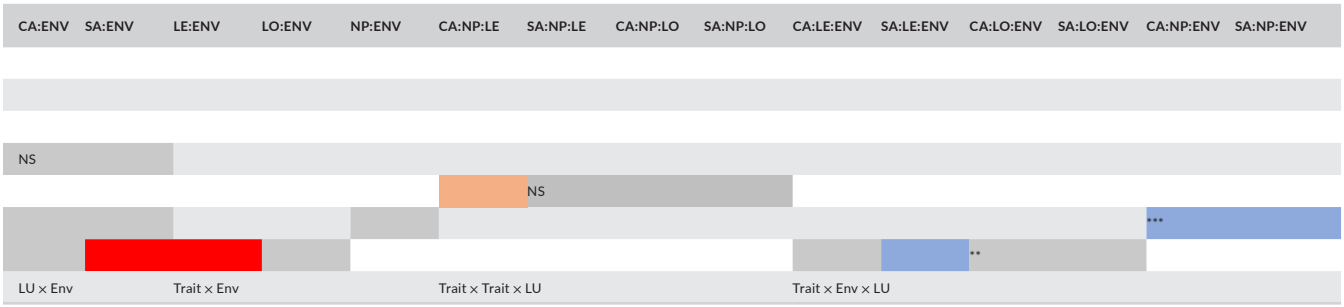


FIGURE 3 Model-predicted relationship between vertical niche position and abundance in three different land uses. Line segments span the range of niche position for which we had data within a given land use. Shaded regions represent standard error for model predictions, predictions shown here correspond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

most severely in converted habitats with only short vegetation remaining (Figure 3). However, arboreal species do not decline in converted habitats with taller vegetation, such as plantations, or coffee farms—instead abundances of terrestrial and understorey 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 understorey 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 understorey 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 dwelling 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 unfavourable 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 effects 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, Supporting Information 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, Watling, et al., 2018, 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, Figure 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.

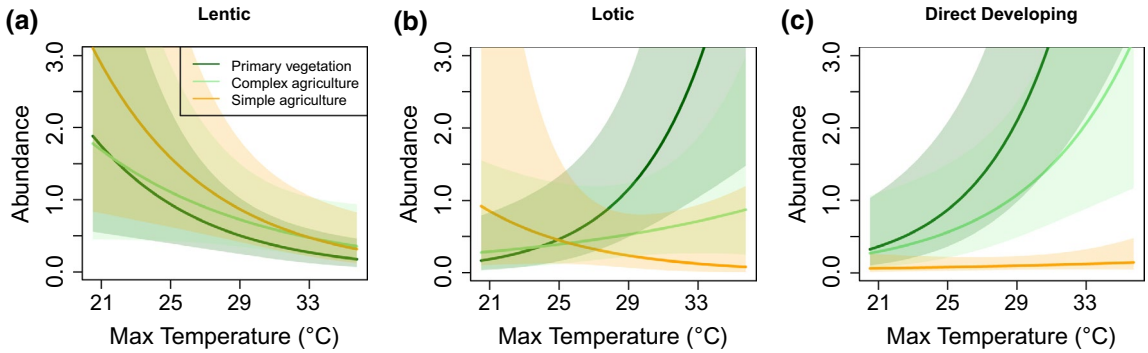


FIGURE 4 Model-predicted relationship between reproductive mode and abundance in three different land uses for (a) lentic breeding species (pond breeders), (b) lotic breeding species (stream breeders), and (c) direct developing species (model 7, Table 3). Shaded regions represent standard error [Colour figure can be viewed at wileyonlinelibrary.com]

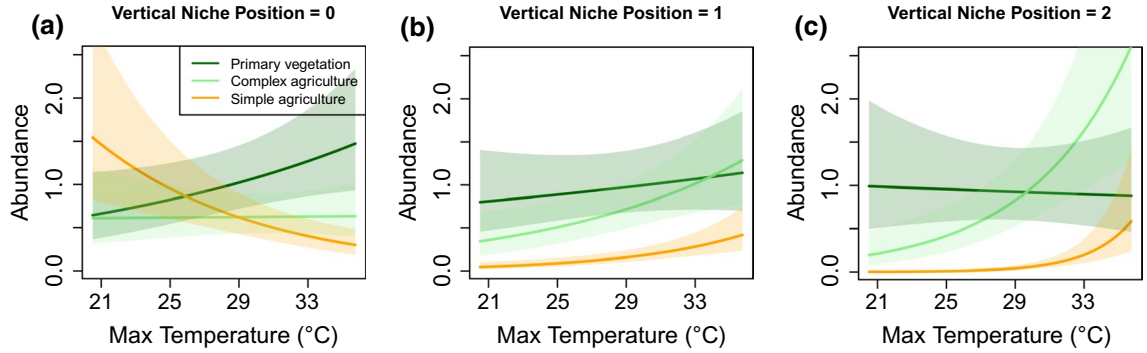


FIGURE 5 Model-predicted relationship between vertical niche position and abundance across land uses for climate zones (model 6, Table 2). Vertical niche position 0 (a) represents a species that is terrestrial; (b) vertical niche position 1 represents a species primarily found in the understorey; (c) vertical niche position 2 represents a species primarily found in the midstorey. Shaded regions represent standard error [Colour figure can be viewed at wileyonlinelibrary.com]

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 beetle 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 (Supporting Information Appendix S3, Figure S3.1–S3.5, Table S1).

Regional temperature gradients influence species- and assemblage-level responses to habitat conversion (Frishkoff et al., 2019; Mantyka-pringle et al., 2012; Nowakowski, Frishkoff, Agha, et al., 2018). For example, species turnover and reduced abundances associated with habitat conversion are most pronounced in warm, tropical regions (Mantyka-pringle et al., 2012; Nowakowski, Frishkoff, Agha, et al., 2018). 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, Watling, Thompson, et al., 2018) 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, 2016; Nowakowski, Watling, Thompson, et al., 2018; 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, 2019; Frishkoff & Karp, 2019; Orme et al., 2019).

We find that arboreal amphibians are less sensitive to habitat conversion in warmer areas. In fact, 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 pre-adaption to climate extremes. Because they live above thermally buffered forest understorey, 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 that accompany habitat conversion. Further, arboreal species are often more resistant to water loss than terrestrial

TABLE 3 Model summary for model 7 (Table 1.)

Model 7: LU * Max Temp * RP			
Fixed effects			
Parameters	**Parameter estimate**	**Standard error**	***p*-value**
Intercept	0.86	0.29	**
Comp Ag	−0.74	0.14	***
Simp Ag	−3.30	0.22	***
Max Temp	0.61	0.14	***
Lentic	−1.82	0.22	***
Lotic	−0.46	0.35	
Comp Ag : Max Temp	−0.15	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	1.16	0.66	.
Max Temp : Lentic	−1.03	0.11	***
Max Temp : Lotic	0.05	0.18	
Comp Ag : Max Temp : Lentic	0.28	0.17	
Simp Ag : Max Temp : Lentic	0.47	0.18	*
Comp Ag : Max Temp : Lotic	−0.27	0.22	
Simp Ag : Max Temp : Lotic	−0.63	0.40	
Random effects			
	Standard deviation		
Species	1.03		
Study	0.98		
Site	0.47		

Note: We denote whether each parameter is significant $p < .1$ (.), $p < .05$ (*), $p < .01$ (**), $p < .001$ (***) based on Wald tests. Negative binomial dispersion parameter, phi = 3.86. Pagel's lambda = .21. Terms [LU = land use; RP = reproductive mode; Comp Ag = complex agriculture; Simp Ag = simple agriculture; Max Temp = maximum temperature (Bio5 from WorldClim)].

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 that help prevent desiccation (Delfino et al., 1998; Mc Clanahan et al., 1978), while others, such as *Smilisca baudinii*, have evolved the ability to form cocoons that 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 (Figure 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 that 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.

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AUTHOR CONTRIBUTIONS

A.H.M. and L.O.F. conceived the paper; all co-authors contributed to discussions of the content; A.H.M. gathered amphibian trait data; A.H.M. and L.O.F.; performed analyses; A.H.M. wrote the first draft of manuscript with guidance from L.O.F.; all authors contributed to writing and editing of manuscript.

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

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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