

UC Riverside

UC Riverside Previously Published Works

Title

Extinction debt and functional traits mediate community saturation over large spatiotemporal scales

Permalink

<https://escholarship.org/uc/item/4b17g1f4>

Journal

Journal of Animal Ecology, 92(11)

ISSN

0021-8790

Authors

Ramírez, Juan P

Reeder, Tod W

Spasojevic, Marko J

Publication Date

2023-11-01

DOI

10.1111/1365-2656.14009

Copyright Information

This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

RESEARCH ARTICLE

Extinction debt and functional traits mediate community saturation over large spatiotemporal scales

Juan P. Ramírez¹  | Tod W. Reeder¹ | Marko J. Spasojevic² 

¹Department of Biology, San Diego State University, San Diego, California, USA

²Department of Evolution, Ecology, and Organismal Biology, University of California, Riverside, California, USA

Correspondence

Juan P. Ramírez

Email: jramirezramirez@sdsu.edu

Handling Editor: Marta Rueda

Abstract

1. Determining if ecological communities are saturated (have a limit to the number of species they can support) has important implications for understanding community assembly, species invasions, and climate change. However, previous studies have generally been limited to short time frames that overlook extinction debt and have not explicitly considered how functional trait diversity may mediate patterns of community saturation.
2. Here, we combine data from biodiversity surveys with functional and phylogenetic data to explore if the colonisation events after the Great American Biotic Interchange (closure of the Panamanian Isthmus) resulted in increases in species richness of communities of the snake family Dipsadidae. We determined the number and the direction of dispersal events between Central and South America by estimating ancestral areas based on a Bayesian time-calibrated phylogenetic analysis. We then evaluated whether variation in community saturation was mediated by the functional similarity of six traits for the resident and colonizing snakes and/or local environmental conditions.
3. We found that colonised communities did not support more species than those that were not colonised. Moreover, we did not find an association between the functional diversity across sites and whether they were colonised by members from the lineages dispersing across the Isthmus or not. Instead, variation in species richness was predicted best by covariates such as time since colonisation and local environment.
4. Taken together, our results suggest that snake communities of the Dipsadidae across the neotropics are saturated. Moreover, our research highlights two important factors to consider in studies of community saturation: extinction debt and the functional differences and similarities in species' ecological roles.

KEYWORDS

Dipsadidae, dispersal, Great American Biotic Interchange, neotropics, snakes

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *Journal of Animal Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Understanding the processes responsible for determining how many species can coexist at a given site is a key goal for community ecology (Kraft et al., 2007; Vellend, 2010), with important implications for invasion biology (MacDougall et al., 2009) and predicting how communities will respond to global change (Chen et al., 2011; HilleRisLambers et al., 2013). Classically, much of the focus of such research has been on community saturation—if novel species can freely establish themselves in a new community or if the structure of the community prevents their establishment unless they replace native species (Elton, 1958; MacArthur, 1965; MacArthur & Levins, 1967; Ricklefs, 1987). To date, many studies have used biological invasions to test for saturation, focusing only on species richness (e.g. Myers & Harms, 2009; Sax et al., 2002; and studies cited in Sax & Gaines, 2003; see also Olivares et al., 2018). The assumption of many of these studies is that if the species richness of a community does not increase after the introduction of species from other regions (either naturally or through human action), the community is saturated, while if richness does increase, the community is unsaturated (Olivares et al., 2018). For example, the lack of extinction of native species after the introduction of non-native species, in many cases, has led researchers to suggest that many non-island communities are unsaturated (Gurevitch & Padilla, 2004; Sax et al., 2002, 2007; Smith & Shurin, 2006; Stohlgren et al., 2008).

Despite decades of research on saturation (e.g. Elton, 1950; MacArthur & Wilson, 1963; Terborgh & Faaborg, 1980), evidence for saturation is mixed, with many studies confounding saturation with stability or equilibrium (Olivares et al., 2018). More critically, much of the previous research on saturation suffers from two key issues that limit generalisation. First, much of the research on saturation is based on exploring the consequences of biotic introductions without considering *extinction debt*—that the exclusion of natives by introduced species (or vice-versa) is not observed because of the long-time frame required for competitive exclusion to occur (Gilbert & Levine, 2013). Indeed, most studies testing for saturation based on evaluating the impacts of colonizing taxa have done so in the context of modern-day biological invasions (see Olivares et al., 2018; Stachowicz & Tilman, 2005). While monitoring the effects of species introductions through long periods of time (i.e. over hundreds to millions of years) is obviously not feasible, integrating historical biogeography into studies of community saturation can provide important insights into the long-term implications of species invasions (Pinto-Sánchez et al., 2014) and resolve the issue of extinction debt. Specifically, historical biogeography allows us to determine the origin and timing of colonisation events that occurred in biological communities thousands or millions of years ago. Using ancestral area estimation to infer the geographical origin of taxa makes it possible to evaluate if communities involved in long-term colonisation events are also more speciose—a result that would support the hypothesis that communities are not saturated (Pinto-Sánchez et al., 2014).

A second limitation for assessing saturation is that determining if the species richness of communities differs if they were colonised

or not does not account for the differences and similarities in species' ecological roles. The number of ecological roles in a community can be determined by the size of the trait space filled by the species inhabiting it (i.e. functional richness; Cornwell et al., 2006) or the dissimilarity in functional strategies among species (e.g. functional dispersion; Laliberté & Legendre, 2010; or Mean Pairwise Distance [MPD]; Webb et al., 2002). Thus, examining how the functional diversity of communities relates to whether they were colonised or not can help infer the mechanisms by which these species were able to invade in the first place. For example, finding that novel species increase community functional richness (the total multivariate volume of the trait space for all the species in a community; Mason et al., 2005; Villéger et al., 2008) or mean pairwise distance (mean of the dissimilarities in trait values between all species pairs on a community, de Bello et al., 2016; Webb et al., 2002) would suggest that the new species bring new trait states to the community, expanding its original trait space (Gerhold et al., 2011). On the other hand, finding that the trait space of a community either diminishes or does not change upon invasion would suggest that the novel colonising species use portions of the niche space that were either empty or previously occupied by native species (with the latter suggesting niche limitation).

Here, we combine community composition data with a calibrated phylogeny and functional trait data to infer the processes underlying variation in community saturation after one of the largest biotic interchanges in recent Earth's history—the Great American Biotic Interchange (GABI)—the exchanges between the long-isolated North and South American biotas after the closure of the Panamanian Isthmus (Simpson, 1980; Stehli & Webb, 1985). The GABI, which occurred either 15 or 3 million years ago (see Montes et al., 2015; O'Dea et al., 2016 for debate about the exact date), provides unique insights for understanding the processes determining community saturation (Vermeij, 1991) and a complementary point of view from the one given by the study of human-mediated species introductions (Stachowicz & Tilman, 2005). Although the impacts on the native biotas of the taxa involved in this large-scale event have been discussed at the continental or regional scales (e.g. Marshall et al., 1982), they remain mostly unexplored at the community scale (Pinto-Sánchez et al., 2014). Here, we focus on the hyper-diverse snake family Dipsadidae, with its >800 species and 110 genera inhabiting many different environments from Canada to Argentina (Uetz et al., 2023). Members of the Dipsadidae are a major component of Neotropical snake communities, and a variety of ecological morphotypes can live in sympatry. First, we used a calibrated phylogeny of the group to determine the timing and direction of the dispersion events of the dipsadid subclades across the Panamanian Isthmus. We then compiled species composition data for 67 communities of dipsadid snakes ranging from Mexico to Argentina, as well as data for six life-history traits thought to mediate their ecological interactions. We then analysed if the total number of species in a community differs between those receiving or not lineages dispersing across the Isthmus to infer if dipsadid snake communities are saturated. At last, we tested if functional trait diversity varies between communities

involved or not in the GABI to assess if having members of colonizing lineages is associated with increased values of their overall functional diversity.

2 | MATERIALS AND METHODS

2.1 | Dataset

We established a database on local species composition and richness of snakes of the family Dipsadidae by compiling data from the literature for a total of 67 sites located between Mexico and Argentina, with 21 of them in North and Central America and 46 in South America (Figure 1a, the species composition for each site is available at <https://doi.org/10.5281/zenodo.8216311>). Sites ranged between 2 and 30 species per site, with an average of 9.69 ± 6.67 species (Table S1, Figure 1b), adding together to a total of 215 species across all sites. For each of the 67 sites included, we also compiled data on variables that may influence their species richness or functional trait space (summarised in Table S1). We first included variables related to sampling effort that may bias our analyses, such as area sampled, sampling effort (in units of person-hours), time of first colonisation (see below) or the type of sampling methodology used (i.e. if sampling methods different from visual searches, such as pitfall traps or drift fence arrays, were used or not).

Next, we included environmental variables for each site that may influence variation in richness or functional diversity. We first obtained site elevation from the original sources or Google Maps if not reported. We then extracted the 19 climatic variables from the WorldClim 2.0 repository using a resolution of 2.5 min of a degree (Fick & Hijmans, 2017). As many of these variables are correlated, we used a Principal Component Analysis (PCA) to describe the environment in four key axes of variation (Figure 2). PC1 explained 45.13% of the variation in our data, where high values of PC1 correspond with warm winter conditions (BIO6, 11 and 9), and smaller values indicate cold winter conditions. PC2 explained 23.16% of the variation in our data, where high values of PC2 correspond with drier and warmer conditions during the summer (BIO17, 14, and 5), and low values indicate rainier and colder summer conditions. PC3 explained 9.46% of the variation in our data, where high values of PC3 correspond with low-elevation sites with high summer temperatures but reduced precipitation seasonality (BIO15, elevation, and BIO10). Finally, PC4 explained 8.56% of the variation in our data, where high values of PC4 correspond with low precipitation during the winter (BIO13, 3, and 16), and reduced values correspond with increased winter rainfall. PCA loadings and summary values are summarised in Tables S2 and S3 (PCA score values are available at <https://doi.org/10.5281/zenodo.8216311>). At last, both the species richness and functional diversity of dipsadid snakes present at a given site are also influenced by their interactions with species from other groups

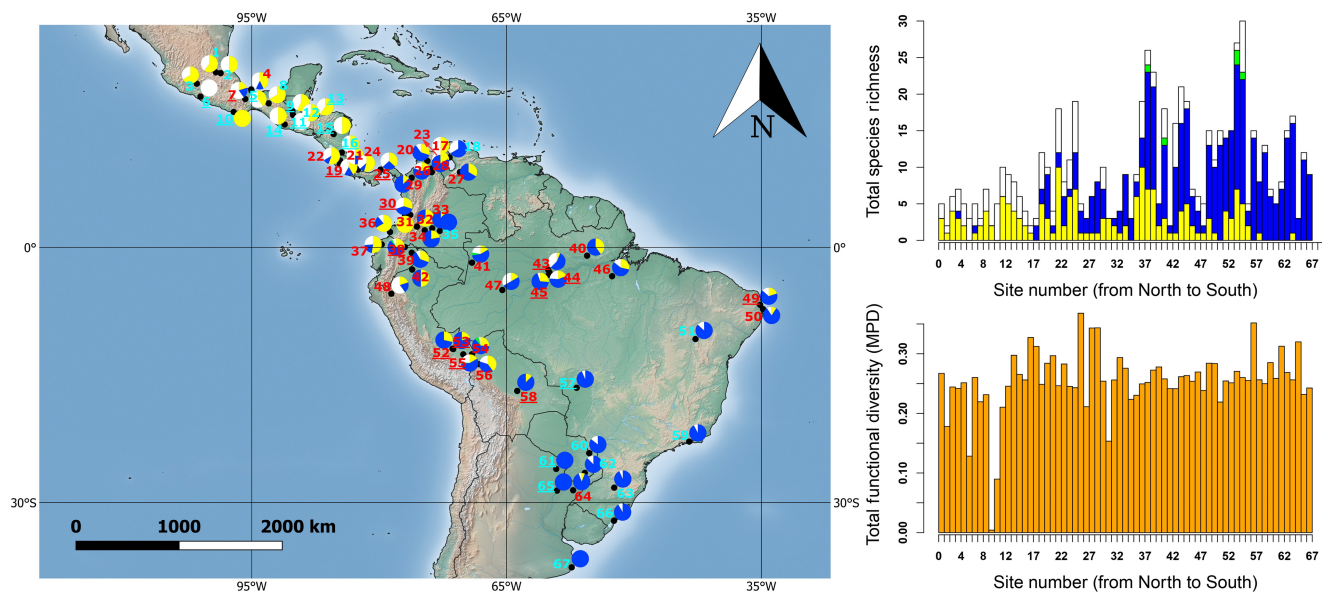


FIGURE 1 (a) Map showing the location of the 67 communities of snakes of the family Dipsadidae analysed in this study. Each site is represented with a circle, divided into yellow, blue, or green portions according to the proportion of taxa recovered by the analyses using BioGeoBEARS as having a Central American, South American, or both Central and South American ancestry, respectively. White portions of the circles indicate the proportion of species on each site from where there is not enough data to determine their continent of origin. (b) Total species richness per site, separated into the geographical origin of each species, as recovered by BioGeoBEARS. The colours of the histogram bars are as in the pie charts. (c) Total functional diversity (as measured with the Mean Pairwise Distance metric) per site. Each number corresponds to one of the localities referred to in Table S1. Numbers are coloured red or pale blue depending on whether the corresponding site was colonised across the Panamanian Isthmus by dipsadid taxa or not, respectively. Numbers were also underlined if corresponding to communities lacking data for any of the variables we compiled.

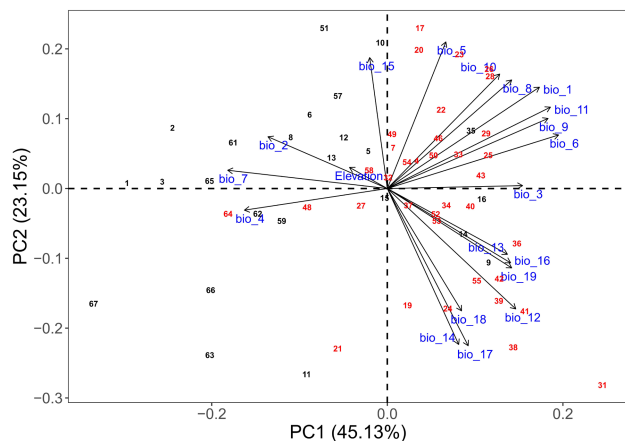


FIGURE 2 Principal Component Analysis (PCA) of the 19 WorldClim climatic variables (plus site elevation) of a series of communities of snakes of the family Dipsadidae across the Neotropics. Each community is indicated with a number, following the code used in Table S2. Numbers are coloured (i.e. red or black) according to whether their corresponding communities were colonised or not by members of lineages dispersing during the GABI. Arrows correspond to the 19 WorldClim variables used or to site elevation.

of snakes living in sympatry. Thus, we generated a list of the snake species from families other than the Dipsadidae found at each site (data available at <https://doi.org/10.5281/zenodo.8216311>) and calculated their species richness (Table S4).

2.2 | Phylogenetic reconstruction and ancestral area estimation

First, to build a phylogenetic tree of snakes of the family Dipsadidae, we compiled all sequences corresponding to five mitochondrial (12S, 16S, *cyt b*, ND2, and ND4) and four nuclear (BDNF, *c-mos*, NT3, and RAG2) genes publicly deposited in GenBank (up until October 2018). We also incorporated sequences from 24 species from 14 different families of Caenophidia that were used as outgroups. In total, we compiled sequence data from a total of 341 species. We then aligned sequences with the online version of MAFFT v7 (Katoh & Standley, 2013) under default parameters, except for the case of the 12S and 16S ribosomal genes, for which we used the Q-INS-i algorithm (which considers the secondary structure of RNA sequences, Katoh & Toh, 2008). We then performed a Bayesian phylogenetic analysis (BA) with BEAST 2 v4.8 (Bouckaert et al., 2014). We applied the bModelTest package of BEAST 2 to simultaneously explore the substitution model space and estimate the corresponding model parameters and the phylogeny (Bouckaert & Drummond, 2017). The sampling of the BEAST 2 analysis used two independent MCMC chains of 50 million generations each, with the first 50% of trees discarded as burn-in. The posterior distribution of trees was summarised as a Maximum Clade Credibility (MCC) timetree (shown as Figure S1) using TreeAnnotator

v2.4.8, part of BEAST 2. See Appendix 1 in Supporting Information for further details.

Next, to determine the number and the direction of dispersal events between Central America and South America, we estimated ancestral areas by implementing a model-based approach (the R package BioGeoBEARS, Matzke, 2013, 2014) using the resulting Bayesian time tree (see details in Appendix 1). Critically, these results permitted the identification of the geographic origin of each of the New World lineages of the Dipsadidae. We considered taxa as being involved in the GABI if they are part of a lineage whose ancestral area is in a different subcontinent than what was inferred for its immediate ancestor and if that dispersal event occurred more recently than 15 million years ago. Using a cut-off of 3 million years did not change the results of the analyses performed for this study (results not shown). The results of the ancestral area estimation also allowed us to obtain a rough estimate of the time when each site was first colonised by members of the Dipsadidae. To do so, we assumed that the time when dipsadids first arrived at a given site was the same as when the region where it is located was first colonised. We used the time of first colonisation of each region and not the ages of all posterior colonisation events, following Pinto-Sánchez et al. (2014) and the studies cited therein, which show that both approaches give similar results.

2.3 | Functional traits

To examine variation in functional diversity among sites, we extracted data from the literature for six life-history traits of the species they contain: microhabitat use, time of activity, reproductive mode, diet, total length and total mass (see details in Appendix 1 and data at <https://doi.org/10.5281/zenodo.8216311>). We selected these traits for them being commonly considered as important components of the life history of snakes (e.g. Henderson et al., 1979; Pianka et al., 2017; Shine, 1994). We then calculated the pairwise Gower distance (Gower, 1971) between all species in each community using the *gowdis* function from the 'FD' package (Laliberté & Shipley, 2011), as it can be calculated for both discrete and continuous traits (de Bello et al., 2016). The resulting dissimilarities were then used to obtain the MPD metric based on the presence of species at each site using the function *mpd* in the 'picante' package (Kembel et al., 2010) in R (R Development Core Team, 2020; summarised in Table S1). Considering that we do not have abundance data for the species in each community, using this function to calculate MPD values is adequate (de Bello et al., 2016). Although there are many metrics of functional diversity (reviewed by Mouchet et al., 2010; Schleuter et al., 2010), we focused here on MPD as it is independent of species richness (de Bello et al., 2016). However, our main results did not change (results not shown) when using Functional Dispersion, another metric of functional dissimilarity (Laliberté & Shipley, 2011). Finally, we also compiled data of the same six functional traits mentioned above from species of snake families apart from the Dipsadidae (data available at <https://doi.org/10.5281/>

zenodo.8216311). We then used those values to estimate the MPD of non-Dipsadidae snakes found at each site (Figure 1c; Table S4).

2.4 | Statistical analyses

To determine if sites containing species from lineages colonizing them across the Panamanian Isthmus exhibit greater species richness values than those that were not colonised, we first generated a global generalised linear model (GLM) with all variables and covariates of interest. The model included species richness as a response variable and whether each site received or not species from clades dispersing across the Isthmus as a fixed independent variable. We also included covariates of species richness such as trap use, sampling effort, local environmental conditions (as summarised into the four PC axes of climatic variation), time since first colonisation by members of Dipsadidae, as well as the species richness and MPD of other groups of snakes as additional fixed independent predictors. We used a quasipoisson error distribution and log link function, as the response variable (=the species richness of each site) only exhibits discrete values, and the data were overdispersed. We then used the R package 'MuMIn' (Barton, 2023) to generate subsets of this global model containing all possible combinations between the variable of whether sites were colonised or not and all the other predictors. The resulting models were ranked by their corrected quasi-Akaike information criteria (qAICc) values, which account for the increase in degrees of freedom caused by estimating the overdispersion parameter (Barton, 2023). All models within 2 qAICc units of the lowest value were retained and then subjected to a model averaging approach where the coefficients of variables missing from a given model were considered as having a value of zero (i.e. the "zero" or "full-average" method, Barton, 2023; Grueber et al., 2011).

To determine if sites receiving species from groups dispersing across the Panamanian Isthmus also exhibit greater values of MPD, we regressed the values of these two variables by using a Beta regression with a logit link function. Again, we considered the same six predictor variables described above, along with whether sites were colonised or not by species of lineages having originated on the opposite side of the Isthmus, as fixed independent variables. We used a Beta regression for this global model (as implemented in the R package 'betareg'; Cribari-Neto & Zeileis, 2010), as the response variable (MPD of each site) is continuous and ranges between zero and one without including these values. As done before, we generated subsets of this second global model corresponding to the possible combinations of the variable of whether communities were or not colonised after the GABI and all its covariates. However, in this case, models were ranked by their corrected Akaike information criterion (AICc) instead. Applying a model subsetting and averaging approach was necessary as both global models were close to overparametrisation due to their ratios of the number of observations against estimated parameters being less than the recommended value of 10–15 times (Babyak, 2004). Indeed, when considering that

25 sites had to be removed due to the lack of data on some of the variables of interest, the global models having species richness and functional diversity as response variables had ratios of 4.7 and 4.2 observations per estimated parameter, respectively.

For both the global GLM and Beta regression analyses we performed, we first determined if they conform to their assumption of no-multicollinearity by calculating the variance inflation factors (VIF) of each independent variable with the command *vif* of R package 'car'. After excluding site area (and the first climate PC axis for the global model where regional richness was the independent variable), all independent variables had VIFs lesser than the values commonly considered as indicating multicollinearity (VIF values of either 4 or 10, depending on the author; O'Brien, 2007). We also explored the degree of spatial autocorrelation in our data with a correlogram based on Moran's *I* metric (Koenig & Knops, 1998; Moran, 1950) for each of the global models we tested and for the best-fitting ones. To do so, we used the function *correlog* of the R package 'ncf' (Bjornstad & Cai, 2020). We evaluated the statistical significance of these results with a total of 1000 permutations under a null model assuming no spatial autocorrelation and upon applying a Bonferroni correction. For all analyses, we used a significance level (α) of 0.05.

3 | RESULTS

3.1 | Phylogenetic reconstruction and ancestral area estimation

The model with the best fit for our phylogenetic and distributional data corresponded to the BAYAREALIKE biogeographical model (Matzke, 2013) with the jump parameter (+j, Matzke, 2014; Table S5). The results of the ancestral area estimation indicate the existence of at least 24 dispersal events across the Panamanian Isthmus by members of the Dipsadidae (Table S6), with 19 of them estimated to have occurred after 15 million years ago. Of the latter, eight of them occurred from North to South America (all of them corresponding to members of Dipsadinae), and 11 of them in the opposite direction (with three of them involving members of the Dipsadinae, and eight from members of the Xenodontinae). A more detailed description of the results of the ancestral area estimation analysis is presented in Appendix 2 in Supporting Information.

3.2 | Community saturation

In our global models, we found that there was no relationship between local species richness and whether communities contained or not members of clades dispersing from the other side of the Isthmus (t -value = 0.153, p = 0.880, df = 41; Table 1; Figure S2), as expected if communities were saturated. Instead, variation in species richness was best predicted by the species richness of non-dipsadid snakes (t -value = 3.736; p = 7.03E-04; Table 1; Figure S2). Similarly, we did not find an association between the MPD values

TABLE 1 Results of the generalised linear model performed between the total species richness of 42 communities of snakes of the family Dipsadidae included in this study and whether they contain or not members of lineages dispersing across the Panamanian Isthmus, incorporating the effects of several confounding variables. A total of 25 additional communities were not considered for this analysis due to data missingness on any of the variables of interest. The variables indicated in bold were recovered as significant predictors of the dependent variable of the model. Parameters of the model are as follows: null deviance: 151.998 on 41 degrees of freedom; residual deviance: 79.356 on 32 degrees of freedom; dispersion parameter: 2.533.

Variable	Estimate	Standard error	z-values	p-value
Presence of colonizing lineages	3.06E-02	2.00E-01	0.15	0.88
Environmental PC2	-3.81E-02	4.35E-02	-0.88	0.39
Environmental PC3	9.61E-02	9.86E-02	0.98	0.34
Environmental PC4	-4.11E-03	1.07E-01	-0.04	0.97
MPD of non-dipsadid snakes	-2.48E-01	1.56E+00	-0.16	0.87
Species richness of non-dipsadid snakes	5.17E-02	1.38E-02	3.74	0.00
Time of first colonisation	2.82E-02	5.86E-02	0.48	0.63
Total sampling effort	1.97E-05	1.50E-05	1.31	0.20
Trap use	1.45E-01	2.10E-01	0.69	0.50

TABLE 2 Results of the Beta regression performed between the Mean Pairwise Distance (MPD) of 42 communities of snakes of the family Dipsadidae included in this study and whether they contain or not members of lineages dispersing across the Panamanian Isthmus, incorporating the effects of several confounding variables. A total of 25 additional communities were not considered for this analysis due to data missingness on any of the variables of interest. The variables indicated in bold were recovered as significant predictors of the dependent variable of the Beta regression. Parameters of the model are as follows: log-likelihood: 81.87 on 12 degrees of freedom; Pseudo R-squared: 0.344.

Variable	Estimate	Standard error	z-values	p-value
Presence of colonizing lineages	-2.00E-01	1.07E-01	-1.87	0.06
Environmental PC1	-2.08E-02	1.58E-02	-1.32	0.19
Environmental PC2	3.11E-02	1.36E-02	2.28	0.02
Environmental PC3	3.28E-02	3.68E-02	0.89	0.37
Environmental PC4	-1.53E-02	3.20E-02	-0.48	0.63
MPD of non-dipsadid snakes	-8.92E-02	4.80E-01	-0.19	0.85
Species richness of non-dipsadid snakes	7.36E-04	5.41E-03	0.14	0.89
Time of first colonisation	3.86E-02	1.81E-02	2.14	0.03
Total sampling effort	8.06E-07	7.14E-06	0.11	0.91
Trap use	-5.99E-02	6.34E-02	-0.95	0.34

of communities and if they were colonised or not by species from lineages dispersing across the Isthmus (z -value = -1.868; p = 0.062; df = 12, [Table 2](#); [Figure S2](#)), further in accordance with what would be expected if communities were saturated. In contrast, MPD values were better predicted by environmental PC2 (z -value = 2.280, p = 0.023, df = 12) and time of first colonisation (z -value = 2.137, p = 0.033, df = 12, [Table 2](#)).

In the model averaging approach we performed using site regional richness as the explanatory variable, the best-model subset contains a total of five models ([Table S7](#)). Of these models, all include the variable of species richness of non-dipsadid snakes, with three incorporating the environmental PC3 (including the model with higher $qAICc$). The variables of trap use and total sampling effort were included in three and two models, respectively ([Table S7](#)). The remaining covariates did not appear in any of the best models.

Of the model-averaged coefficient estimates, only the species richness of non-dipsadid snakes was recovered as statistically significant (0.0555, standard error of 0.0133, p -value of 4.95E-05; [Table 3](#)). On the other hand, the results of the model averaging approach with functional diversity (MPD) as the explanatory variable generated a subset of two models ([Table S8](#)). Both these models include the variables of time of first colonisation and the environmental PC2, with only the second-ranked model including the environmental PC1 as well ([Table S8](#)). The variables of time of first colonisation and PC2 had model-averaged coefficient estimates of 0.039 and 0.029, both of which were significant (standard errors of 0.014 and 0.012, p -values of 0.006 and 0.027, respectively; [Table 3](#)). Thus, in summary, the results of the global models and the model-averaging approach indicate the statistical significance of the same factors driving species richness and functional diversity of sites, which do not include

TABLE 3 Results of the model averaging approach implemented herein with models having either (a) species richness or (b) functional diversity (as measured with the Mean Pairwise Distance metric) as their response variables. Models within two $qAICc$ or $AICc$ values (respectively) from the highest-supported model were used to obtain the averaged estimate values shown. Variables in bold were found to be significant predictors of the response variables of the models resulting from the model averaging approach.

Variable	Estimate	Standard error	Adjusted standard error	z-values	p-value
(a)					
Environmental PC3	1.11E-01	9.52E-02	9.65E-02	1.151	0.25
Species richness of non-dipsadid snakes	5.55E-02	1.33E-02	1.37E-02	4.058	4.95E-05
Presence of colonizing lineages	-6.13E-03	1.85E-01	1.91E-01	0.032	0.974
Total sampling effort	7.44E-06	1.28E-05	1.30E-05	0.574	0.566
Trap use	1.49E-01	2.05E-01	2.07E-01	0.719	0.472
(b)					
Environmental PC2	0.028652	0.012543	0.012969	2.209	0.02715
Time of first colonisation	0.038858	0.013609	0.014072	2.761	0.00576
Presence of colonizing lineages	-0.07843	0.075707	0.077919	1.007	0.31413
(phi)					
Environmental PC1	153.3771	33.41882	34.55533	4.439	9.10E-06
Environmental PC1	-0.00365	0.009141	0.009336	0.391	0.69598

whether they were colonised or not. Finally, for neither the global nor best-fitting models, we found meaningful patterns of spatial structure/autocorrelation (Figures S3 and S4, respectively).

4 | DISCUSSION

While many short-term studies focusing on recent biological invasions have found that communities are unsaturated (e.g. Myers & Harms, 2009; Sax et al., 2002; Stohlgren et al., 2008; and the studies cited in Sax & Gaines, 2003), ours is one of the few using patterns of species introductions to find evidence for saturation over long temporal scales. Critically, most studies based on the impacts of modern-day biotic introduction events have generally not considered extinction debt or functional traits. As a result, the unsaturation of modern-day biological communities could correspond to a temporary artefact in which extinction debts will eventually be paid. In line with these modern-day studies, most studies investigating the impacts of biotic introductions that occurred millions of years ago also find patterns of unsaturation (Flynn et al., 1991; Lindberg, 1991; Patzkowsky & Holland, 2007; Vermeij, 1991; other references cited in Pinto-Sánchez et al., 2014; Smith & Shurin, 2006). However, these studies are generally based on evidence from the fossil record, so determining the coexistence of taxa at the community scale (and their identification at the species level) is difficult at best (Pinto-Sánchez et al., 2014). Interestingly, the only other study using historical biogeography for directly testing for community saturation at large temporal scales (i.e. Pinto-Sánchez et al., 2014) did not find evidence for community saturation. This discrepancy is surprising as both studies are based on analysing the impacts of the GABI on the species richness of Neotropical communities. However, the difference between our results and those of Pinto-Sánchez et al. (2014) may be due to the high levels of similarity in the ecological roles (e.g. functional traits) exhibited by the group of frogs (Terrarana) used by

Pinto-Sánchez et al. (2014) as compared to the snakes in the Dipsadidae. In parts of their distribution, many species of these frogs can live in sympatry without any apparent partitioning in habitat use or diet (e.g. Arroyo et al., 2008; Lieberman, 1986). The results of Pinto-Sánchez et al. (2014) likely indicate that, albeit the communities of frogs they studied are unsaturated in terms of species counts, these communities have already reached the limit of ecological entities they can harbour.

By merging historical biogeographic inferences (e.g. ancestral area reconstructions) with modern ecological approaches (e.g. functional traits), we provide a robust approach for examining community saturation that suggests that community saturation may occur more frequently than suggested by the current evidence. Critically, our framework satisfies the conditions needed to assess saturation recently proposed by Olivares et al. (2018): the existence of both *niche limitation* and either *equilibrium* or *stability* in numbers of species or ecological entities after accounting for potential covariates (e.g. local climate, time of first colonisation, site area, and sampling effort). Importantly, we explicitly quantified the functional space occupied by species. Metrics of the functional trait space (such as MPD or functional dispersion) consider the ecological redundancy and the roles that organisms have on ecosystems, aspects not considered by metrics of taxonomic diversity (Cadotte et al., 2011; Canning-Clode et al., 2010; Schleuter et al., 2010). However, functional trait space has only been quantified in a few studies testing for community saturation (e.g. Canning-Clode et al., 2010), none of which are based on studying the impacts of biotic introductions. As a result, it is possible that the common finding of community species richness being unsaturated may be obscured by not considering functional diversity.

We found that using metrics of the functional trait diversity while testing for community saturation is indicative of *niche limitation* in communities of Dipsadidae across the neotropics, as we focused on functional traits associated with different niche axes in snake communities. First, body length is among the most

important traits not only in snakes but in most other groups of organisms (see Boback & Guyer, 2003; Feldman et al., 2016; Shine, 1994; and references in Burbrink et al., 2012). Body length in snakes is correlated to their mass (Boback & Guyer, 2003; Feldman & Meiri, 2012), but more importantly, it has been shown that the diet of snakes is highly dependent on their body size. Indeed, the diet of larger snake species contains increased percentages of endotherms, while smaller species feed more on invertebrates (e.g. Pyron & Burbrink, 2009; Shine, 1994). Thus, it is likely that competition for food among snakes of different body lengths is limited. This is especially true considering the very specialised diets exhibited by some snakes, including several members of the Dipsadidae (such as the mollusc and annelid specialists *Dipsas* and *Sibon* [Ray et al., 2012], the small reptile eggs specialists *Enulius* and *Enuliophis* [Brown et al., 2018; Savage, 2002], or the crayfish specialist *Farancia* [Godley et al., 1984]). The role of predatory interactions between the snakes considered in this study (facilitated by differences in body size between species) is also likely to be reduced, as few seem to be ophiophagous (snake-eating). Similarly, two other traits considered herein (time of activity and microhabitat use) are also commonly considered to influence the biotic interactions between coexisting snake taxa (e.g. Burbrink & Myers, 2015; Henderson et al., 1979; Vitt, 1987). Thus, snake species similar in most other respects (including body length) could coexist if they differ in the times of activity and/or the resources they use due to inhabiting different microhabitats. Finally, both oviparity and viviparity can provide different competitive advantages, but their relative advantage often depends on the local climatic conditions (Blackburn, 1999). For example, viviparity is considered more advantageous in colder climates, as it allows development to occur faster, increasing the survival of young individuals (Bleu et al., 2012). By focusing on multiple niche axes, the traits we analysed are likely to link to the many biotic interactions that may influence the saturation of neotropical snake communities (Mlambo, 2014).

In addition to niche limitation, we also addressed the second condition needed to assess saturation recognised by Olivares et al. (2018): *equilibrium* or *stability* in numbers of species or ecological entities. In the case of contemporary biotic invasions, the term *stability* refers to whether the species richness of communities does not significantly change even as the colonisation events increase the size of the regional species pool (Olivares et al., 2018). In other words, site richness would be considered stable if it remained unchanged despite having the opportunity to increase along with the number of colonizing lineages. Our results are consistent with this expectation, as we found that the species richness of the communities of interest did not depend on whether they were colonised or not by taxa dispersing across the Panamanian Isthmus. Although it is impossible to know how the species richness of individual communities has changed through time, our results indicate that the general tendency was for the richness of colonised sites not to increase to a level that surpasses that of uncolonised sites. However, it is important to note that the lack of a significant difference in the species richness between colonised

and uncolonised communities does not necessarily indicate that they are saturated. Indeed, it is still possible that the increased dispersal (and posterior diversification) following the GABI could have increased the richness of colonised sites to a level comparable to that of uncolonised communities. Despite this, we did not find evidence suggesting that colonised communities harboured more taxa than uncolonised sites before the GABI occurred. Instead, we found that across the several variables we compared between them, colonised communities only tend to occur at lower latitudes and have higher winter temperatures than uncolonised sites (see Appendix 2). Considering that dipsadid snakes are ectotherms and currently exhibit a latitudinal species gradient (LDG) (J. P. Ramirez & T. W. Reeder, work in preparation), it is likely that such a pattern already existed before the GABI occurred, especially when considering that LDGs have existed for the last ~30–40 million years in other taxa (Mannion, 2020).

Importantly, saturation can only occur when stability or equilibrium in species numbers or ecological entities results from niche limitation and not from stochastic mechanisms (Olivares et al., 2018). Supporting this idea, we also did not recover significant differences in the functional diversity (MPD values) of the sites involved in the GABI and those that were not. Such a result indicates that colonizing lineages did not tend to increase the trait space of most of the communities to where they dispersed. As a result, in those cases, taxa dispersing across the Panamanian Isthmus had to either replace native taxa or use unoccupied portions of the trait space so that they could colonise while keeping it relatively unchanged (Gerhold et al., 2011), with both scenarios being indicative of niche limitation. Despite this, it is also possible that uncolonised communities used to have a reduced functional diversity (MPD), which increased to levels comparable to that of the trait space of colonised sites after the GABI. However, as discussed above regarding site species richness, we did not find support for the idea that uncolonised communities have reduced trait spaces than colonised communities or that they reached comparable levels afterward. Further, if that were the case, one would expect that colonizing lineages represent a considerable portion of the trait space of at least some of the communities of interest. Despite this, we found that the functional diversity (MPD) of sites involved in the GABI does not significantly differ whether calculated with or without considering the species of the lineages that colonised them (see Appendix 2). In summary, alternative explanations to our findings of a lack of association between site species richness or functional diversity (MPD) and whether communities were colonised are unlikely, thus supporting the idea that these patterns are indeed indicative of community saturation.

In summary, our finding that communities of dipsadid snakes across the Neotropics are saturated (both in terms of species counts and ecological entities) contrasts with previous studies using biotic introductions to test for community saturation. This discrepancy likely results from other studies not considering the existence of extinction debts or that saturation could be mediated by functional traits. Extinction debts can require hundreds or even thousands

of years to unfold (Figueiredo et al., 2019; Kitzes & Harte, 2015), with their extent determined by factors that can be taxon-specific or even fortuitous. Some of these factors include how frequently disturbances occur, the abundance distribution of the species involved, and if they exhibit traits associated with longer timespans (such as having increased longevity or dispersal ability, Figueiredo et al., 2019; Kitzes & Harte, 2015; Lalechère et al., 2019). As a result, assuming that unsaturation or saturation is the rule at any spatial or temporal scale may be unjustified and premature. Indeed, unsaturation could simply correspond to a temporary unstable stage in which communities or regions stay after suffering from a considerable disturbance before reaching a potential stable stage (i.e. transient stable states, Fukami & Nakajima, 2011). Moving forward, it is important to note that studies testing for community saturation across large temporal scales can also provide insights into the long-term impacts of modern-day species introductions and other disturbances not possible to be obtained from other methods. Such studies could also allow us to predict how the richness and functional diversity of communities and regions might be influenced by the predicted migrations of taxa caused by climate change and habitat homogenisation around the world.

AUTHOR CONTRIBUTIONS

Juan P. Ramírez and Marko J. Spasojevic conceived the ideas and designed the methodology. Juan P. Ramírez compiled and analysed the data under the guidance of Tod W. Reeder and Marko J. Spasojevic. Juan P. Ramírez and Marko J. Spasojevic led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

ACKNOWLEDGEMENTS

We thank past and previous members of the Spasojevic and Reeder laboratories for helpful discussions on this research. We also thank N. Barber for providing important insights into the statistical methods used herein. Finally, we acknowledge Cesar Barrio-Amorós (CRWild) for authorizing the use of his photograph of *Oxyrhopus peltolarius* in the graphical abstract.

CONFLICT OF INTEREST STATEMENT

The authors do not declare any conflicts of interest.

DATA AVAILABILITY STATEMENT

All data are available in the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.8216311> (Ramirez et al., 2023).

ORCID

Juan P. Ramírez  <https://orcid.org/0000-0002-0484-8047>

Marko J. Spasojevic  <https://orcid.org/0000-0003-1808-0048>

REFERENCES

- Arroyo, S. B., Serrano-Cardozo, V. H., & Ramírez-Pinilla, M. P. (2008). Diet, microhabitat and time of activity in a *Pristimantis* (Anura, Strabomantidae) assemblage. *Phyllomedusa*, 7, 109–119.

- Babyak, M. A. (2004). What you see may not be what you get: A brief, nontechnical introduction to overfitting in regression-type models. *Psychosomatic Medicine*, 66(3), 411–421.
- Barton, K. (2023). *MuMIn: Multi-model inference*. R package version 1.47.5. R Project for Statistical Computing.
- Bjornstad, O. N., & Cai, J. (2020). *ncf: Spatial covariance functions*. R package version 1.3-2. R Project for Statistical Computing.
- Blackburn, D. G. (1999). Viviparity and oviparity: Evolution and reproductive strategies. In T. E. Knobil & J. D. Neill (Eds.), *Encyclopedia of reproduction* (pp. 994–1003). Academic Press.
- Bleu, J., Heulin, B., Haussy, C., Meylan, S., & Massot, M. (2012). Experimental evidence of early costs of reproduction in conspecific viviparous and oviparous lizards. *Journal of Evolutionary Biology*, 25(7), 1264–1274.
- Boback, S. M., & Guyer, C. (2003). Empirical evidence for an optimal body size in snakes. *Evolution*, 57(2), 345–451.
- Bouckaert, R., Heled, J., Kühnert, D., Vaughan, T., Wu, C. H., Xie, D., Suchard, M. A., Rambaut, A., & Drummond, A. J. (2014). BEAST 2: A software platform for Bayesian evolutionary analysis. *PLoS Computational Biology*, 10(4), e1003537.
- Bouckaert, R. R., & Drummond, A. J. (2017). bModelTest: Bayesian phylogenetic site model averaging and model comparison. *BMC Evolutionary Biology*, 17(1), 42.
- Brown, T. W., van den Burg, M. P., Maryon, D. F., & Arrivillaga, C. (2018). Arboreality and diet in Pacific long-tailed snakes, *Enallius flavitorques* (Squamata: Dipsadidae), and a potential adaptive hypothesis for egg attendance in Honduran leaf-toed Geckos, *Phyllodactylus palmeus* (Squamata: Phyllodactylidae). *Reptiles & Amphibians*, 25(1), 31–34.
- Burbrink, F. T., Chen, X., Myers, E. A., Brandley, M. C., & Pyron, R. A. (2012). Evidence for determinism in species diversification and contingency in phenotypic evolution during adaptive radiation. *Proceedings of the Royal Society B: Biological Sciences*, 279(1748), 4817–4826.
- Burbrink, F. T., & Myers, E. A. (2015). Both traits and phylogenetic history influence community structure in snakes over steep environmental gradients. *Ecography*, 38(10), 1036–1048.
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48(5), 1079–1087.
- Canning-Clode, J., Maloney, K. O., McMahon, S. M., & Wahl, M. (2010). Expanded view of the local–regional richness relationship by incorporating functional richness and time: A large-scale perspective. *Global Ecology and Biogeography*, 19(6), 875–885.
- Cornwell, W. K., Schwillk, D. W., & Ackerly, D. D. (2006). A trait-based test for habitat filtering: convex hull volume. *Ecology*, 87(6), 1465–1471.
- Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333, 1024–1026.
- Cribari-Neto, F., & Zeileis, A. (2010). Beta Regression in R. *Journal of Statistical Software*, 34(2), 1–24.
- de Bello, F., Carmona, C. P., Lepš, J., Szava-Kovats, R., & Pärtel, M. (2016). Functional diversity through the mean trait dissimilarity: Resolving shortcomings with existing paradigms and algorithms. *Oecologia*, 180, 933–940.
- Elton, C. (1950). *The ecology of animals*. Methuen.
- Elton, C. S. (1958). *The ecology of invasions by animals and plants*. Methuen.
- Feldman, A., & Meiri, S. (2012). Length–mass allometry in snakes. *Biological Journal of the Linnean Society*, 108(1), 161–172.
- Feldman, A., Sabath, N., Pyron, R. A., Mayrose, I., & Meiri, S. (2016). Body sizes and diversification rates of lizards, snakes, amphibians and the tuatara. *Global Ecology and Biogeography*, 25(2), 187–197.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37(12), 4302–4315.

- Figueiredo, L., Krauss, J., Steffan-Dewenter, I., & Sarmiento Cabral, J. (2019). Understanding extinction debts: Spatio-temporal scales, mechanisms and a roadmap for future research. *Ecography*, 42(12), 1973–1990.
- Flynn, L. J., Tedford, R. H., & Zhanxiang, Q. (1991). Enrichment and stability in the Pliocene mammalian fauna of North China. *Paleobiology*, 17, 246–265.
- Fukami, T., & Nakajima, M. (2011). Community assembly: Alternative stable states or alternative transient states? *Ecology Letters*, 14(10), 973–984.
- Gerhold, P., Pärtel, M., Tackenberg, O., Hennekens, S. M., Bartish, I., Schaminée, J. H., Fergus, A. J. F., Ozinga, W. A., & Prinzing, A. (2011). Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *The American Naturalist*, 177(5), 668–680.
- Gilbert, B., & Levine, J. M. (2013). Plant invasions and extinction debts. *Proceedings of the National Academy of Sciences of the United States of America*, 110(5), 1744–1749.
- Godley, J. S., McDiarmid, R. W., & Rojas, N. N. (1984). Estimating prey size and number in crayfish-eating snakes, genus *Regina*. *Herpetologica*, 40(1), 82–88.
- Gower, J. C. (1971). General coefficient of similarity and some of its properties. *Biometrics*, 27, 857–871.
- Grueber, C. E., Nakagawa, S., Laws, R. J., & Jamieson, I. G. (2011). Multimodel inference in ecology and evolution: Challenges and solutions. *Journal of Evolutionary Biology*, 24, 699–711.
- Gurevitch, J., & Padilla, D. K. (2004). Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, 19(9), 470–474.
- Henderson, R. W., Dixon, J. R., & Soini, P. (1979). Resource partitioning in Amazonian snake communities. *Milwaukee Public Museum, Contributions in Biology and Geology*, 22, 1–11.
- HilleRisLambers, J., Harsch, M. A., Ettinger, A. K., Ford, K. R., & Theobald, E. J. (2013). How will biotic interactions influence climate change-induced range shifts? *Annals of the New York Academy of Sciences*, 1297, 112–125.
- Katoh, K., & Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution*, 30(4), 772–780.
- Katoh, K., & Toh, H. (2008). Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics*, 9(4), 286–298.
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26(11), 1463–1464.
- Kitzes, J., & Harte, J. (2015). Predicting extinction debt from community patterns. *Ecology*, 96(8), 2127–2136.
- Koenig, W. D., & Knops, J. M. (1998). Testing for spatial autocorrelation in ecological studies. *Ecography*, 21(4), 423–429.
- Kraft, N. J., Cornwell, W. K., Webb, C. O., & Ackerly, D. D. (2007). Trait evolution, community assembly, and the phylogenetic structure of ecological communities. *The American Naturalist*, 170(2), 271–283.
- Lalechère, E., Archaux, F., & Jabot, F. (2019). Relative importance of landscape and species characteristics on extinction debt, immigration credit and relaxation time after habitat turnover. *Population Ecology*, 61(4), 383–395.
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305.
- Laliberté, E., & Shipley, B. (2011). *FD: Measuring functional diversity from multiple traits, and other tools for functional ecology*. R package version 1.0-12. R Project for Statistical Computing.
- Lieberman, S. S. (1986). Ecology of the leaf litter herpetofauna of a Neotropical rain forest. La Selva, Costa Rica. *Acta Zoologica Mexicana*, 15, 1–72.
- Lindberg, D. R. (1991). Marine biotic interchange between the northern and southern hemispheres. *Paleobiology*, 17, 308–324.
- MacArthur, R., & Levins, R. (1967). The limiting similarity, convergence, and divergence of coexisting species. *The American Naturalist*, 101(921), 377–385.
- MacArthur, R. H. (1965). Patterns of species diversity. *Biological Reviews*, 40(4), 510–533.
- MacArthur, R. H., & Wilson, E. O. (1963). An equilibrium theory of insular zoogeography. *Evolution*, 17, 373–387.
- MacDougall, A. S., Gilbert, B., & Levine, J. M. (2009). Plant invasion and the niche. *Journal of Ecology*, 97, 609–615.
- Mannion, P. D. (2020). A deep-time perspective on the latitudinal diversity gradient. *Proceedings of the National Academy of Sciences of the United States of America*, 117(30), 17479–17481.
- Marshall, L., Webb, S., Sepkoski, J., Jr., & Raup, D. (1982). Mammalian evolution and the great American interchange. *Science*, 215, 1351–1357.
- Mason, N. W., Moullot, D., Lee, W. G., & Wilson, J. B. (2005). Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos*, 111(1), 112–118.
- Matzke, N. J. (2013). Probabilistic historical biogeography: New models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography*, 5(4), 242–248.
- Matzke, N. J. (2014). Model selection in historical biogeography reveals that founder-event speciation is a crucial process in Island clades. *Systematic Biology*, 63, 951–970.
- Mlambo, M. C. (2014). Not all traits are 'functional': Insights from taxonomy and biodiversity-ecosystem functioning research. *Biodiversity and Conservation*, 23(3), 781–790.
- Montes, C., Cardona, A., Jaramillo, C., Pardo, A., Silva, J. C., Valencia, V., Ayala, C., Pérez-Angel, L. C., Ramírez, V., & Niño, H. (2015). Middle Miocene closure of the central American seaway. *Science*, 348, 226–229.
- Moran, P. A. (1950). Notes on continuous stochastic phenomena. *Biometrika*, 37(1/2), 17–23.
- Mouchet, M. A., Villéger, S., Mason, N. W., & Moullot, D. (2010). Functional diversity measures: An overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24(4), 867–876.
- Myers, J. A., & Harms, K. E. (2009). Seed arrival, ecological filters, and plant species richness: A meta-analysis. *Ecology Letters*, 12(11), 1250–1260.
- O'Brien, R. M. (2007). A caution regarding rules of thumb for variance inflation factors. *Quality & Quantity*, 41(5), 673–690.
- O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L., Collins, L. S., de Queiroz, A., Farris, D. W., Norris, R. D., Stallard, R. F., Woodburne, M. O., Aguilera, O., Aubry, M. P., Berggren, W. A., Budd, A. F., Cozzuol, M. A., Coppard, S. E., Duque-Caro, H., ... Jackson, J. B. (2016). Formation of the isthmus of Panama. *Science Advances*, 2(8), e1600883.
- Olivares, I., Karger, D. N., & Kessler, M. (2018). Assessing species saturation: Conceptual and methodological challenges. *Biological Reviews*, 93(4), 1874–1890.
- Patzkowsky, M. E., & Holland, S. M. (2007). Diversity partitioning of a late Ordovician marine biotic invasion: Controls on diversity in regional ecosystems. *Paleobiology*, 33(2), 295–309.
- Pianka, E. R., Vitt, L. J., Pelegrin, N., Fitzgerald, D. B., & Winemiller, K. O. (2017). Toward a periodic table of niches, or exploring the lizard niche hypervolume. *The American Naturalist*, 190(5), 601–616.
- Pinto-Sánchez, N. R., Crawford, A. J., & Wiens, J. J. (2014). Using historical biogeography to test for community saturation. *Ecology Letters*, 17(9), 1077–1085.
- Pyron, R. A., & Burbrink, F. T. (2009). Body size as a primary determinant of ecomorphological diversification and the evolution of mimicry in the lamprolittinid snakes (Serpentes: Colubridae). *Journal of Evolutionary Biology*, 22(10), 2057–2067.

- R Development Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Ramirez, J. P., Reeder, T. W., & Spasojevic, M. J. (2023). Data from: Extinction debt and functional traits mediate community saturation over large spatiotemporal scales. *Zenodo Digital Repository* <https://doi.org/10.5281/zenodo.8216311>
- Ray, J. M., Montgomery, C. E., Mahon, H. K., Savitzky, A. H., & Lips, K. R. (2012). Goo-eaters: Diets of the neotropical snakes *Dipsas* and *Sibon* in Central Panama. *Copeia*, 2012(2), 197–202.
- Ricklefs, R. E. (1987). Community diversity: Relative roles of local and regional processes. *Science*, 235(4785), 167–171.
- Savage, J. M. (2002). *The amphibians and reptiles of Costa Rica* (p. 934). University of Chicago Press.
- Sax, D. F., & Gaines, S. D. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology & Evolution*, 18(11), 561–566.
- Sax, D. F., Gaines, S. D., & Brown, J. H. (2002). Species invasions exceed extinctions on islands worldwide: A comparative study of plants and birds. *The American Naturalist*, 160(6), 766–783.
- Sax, D. F., Stachowicz, J. J., Brown, J. H., Bruno, J. F., Dawson, M. N., Gaines, S. D., & O'Connor, M. I. (2007). Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, 22(9), 465–471.
- Schleuter, D., Daufresne, M., Massol, F., & Argillier, C. (2010). A user's guide to functional diversity indices. *Ecological Monographs*, 80(3), 469–484.
- Shine, R. (1994). Allometric patterns in the ecology of Australian snakes. *Copeia*, 1994, 851–867.
- Simpson, G. G. (1980). *Splendid isolation: The curious history of south American mammals*. Yale University Press.
- Smith, S. A., & Shurin, J. B. (2006). Room for one more? Evidence of invasibility and saturation in ecological communities. In M. W. Cadotte, S. M. MacMahon, & T. Fukami (Eds.), *Conceptual ecology and invasion biology: Reciprocal approaches to nature* (pp. 423–447). Springer.
- Stachowicz, J. J., & Tilman, D. (2005). Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In D. F. Sax, J. J. Stachowicz, & S. D. Gaines (Eds.), *Species invasions: Insights into ecology, evolution, and biogeography* (pp. 41–64). Sinauer Associates Inc.
- Stehli, F. G., & Webb, S. D. (Eds.). (1985). *The great American biotic interchange*. Topics in geobiology. Plenum Press.
- Stohlgren, T. J., Barnett, D. T., Jarnevich, C. S., Flather, C., & Kartesz, J. (2008). The myth of plant species saturation. *Ecology Letters*, 11(4), 313–322.
- Terborgh, J. W., & Faaborg, J. (1980). Saturation of bird communities in the West Indies. *The American Naturalist*, 116(2), 178–195.
- Uetz, P., Freed, P., & Hošek, J. (Eds.). (2023). The reptile database. <http://www.reptile-database.org>
- Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, 85(2), 183–206.
- Vermeij, G. J. (1991). When biotas meet: Understanding biotic interchange. *Science*, 253(5024), 1099–1104.
- Villéger, S., Mason, N. W., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301.
- Vitt, L. J. (1987). Communities. In R. A. Seigel, J. T. Collins, & S. S. Novak (Eds.), *Snakes: Ecology and evolutionary biology* (pp. 335–365). McGraw-Hill.
- Webb, C. O., Ackerly, D. D., McPeck, M. A., & Donoghue, M. J. (2002). Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, 33(1), 475–505.

SUPPORTING INFORMATION

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

Table S1. Information about the 67 communities of snakes of the family Dipsadidae included in this study, including their area, coordinates, elevation, species richness, functional dispersion, and the number of species from clades colonizing from the other side of the Isthmus that they contain.

Table S2. Loadings of the first four Principal Component (PC) Axes of the PC analyses performed with the values of the 19 WorldClim variables corresponding to each of the sites included in this work.

Table S3. Summary of the Principal Component (PC) Axes of the PC analyses performed with the values of the 19 WorldClim variables corresponding to each of the sites included in this work.

Table S4. Species richness and functional dispersion of the sympatric snakes from other families present in the 67 communities of snakes of the family Dipsadidae included in this study.

Table S5. Comparison among biogeographic models, as evaluated with 'BioGeoBEARS' for the analysis performed defined in the text. For each model, the following values are reported: log-likelihood (LnL), numbers of parameters, and their corresponding value of the corrected Akaike information criterion (AIC weights and AICc).

Table S6. List of the dispersal events of Dipsadidae snakes across the Panamanian Isthmus, indicating the direction and estimated age in which they occurred, according to the results of the BioGeoBEARS analyses.

Table S7. Summary of the models tested for this work having species richness as the response variable.

Table S8. Summary of the models tested for this work having functional diversity (as measured with the MPD metric) as the response variable.

Table S9. Best-fit partitioning scheme for the protein-coding genes and models of nucleotide substitution for each partition, based on the corrected Akaike information criterion (AICc) as implemented in PartitionFinder 2 (Lanfear et al., 2016). The abbreviation 'pos.' refers to codon position.

Table S10. Calibration points used for obtaining the Bayesian timetree used for this work and reported as Figure S1. Modified from Zaher et al. (2018) and Head et al. (2016).

Table S11. Values of per-species diversification, speciation, and extinction rates averaged across all taxa inhabiting each of the communities of the Dipsadidae considered for this study.

Table S12. Values of functional dispersion of the 67 communities of dipsadid snakes included in this study calculated after removing the species from lineages colonizing them from across the Panamanian Isthmus.

Table S13. Results and statistics of the t-tests performed to test for possible differences in several variables between communities of dipsadid snakes involved or not in the Great American Biotic Interchange.

Figure S1. Timetree of the family Dipsadidae derived with the software Beast 2, calibrated with the fossils presented in the Table S10.

Figure S2. Relationship between (a) species richness or (b) functional dispersion and the number of species per site from taxa colonizing across the opposite side of the Panamanian Isthmus.

Figure S3. Moran's I spatial correlograms corresponding to the residuals of the global models evaluated in this study, having either (a) total Species Richness or (b) functional diversity (as measured with the MPD metric) as their response variables.

Figure S4. Moran's I spatial correlograms corresponding to the residuals of the best-fitting models evaluated in this study, having either (a) total Species Richness or (b) functional diversity (as measured with the MPD metric) as their response variables.

Figure S5. Map of the biogeographic regions considered in the biogeographic analyses performed herein (modified after Morrone, 2014). The location of the 67 sites or communities that served as the basis for our study is also indicated.

Appendix 1. Extended methods.

Appendix 2. Additional details about the methodology and results of the biogeographic analyses performed for this study.

How to cite this article: Ramírez, J. P., Reeder, T. W., & Spasojevic, M. J. (2023). Extinction debt and functional traits mediate community saturation over large spatiotemporal scales. *Journal of Animal Ecology*, 92, 2228–2239. <https://doi.org/10.1111/1365-2656.14009>