

LETTER

Selecting for extinction: nonrandom disease-associated extinction homogenizes amphibian biotas

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Abstract

Studying the patterns in which local extinctions occur is critical to understanding how extinctions affect biodiversity at local, regional and global spatial scales. To understand the importance of patterns of extinction at a regional spatial scale, we use data from extirpations associated with a widespread pathogenic agent of amphibian decline, *Batrachochytrium dendrobatidis* (*Bd*) as a model system. We apply novel null model analyses to these data to determine whether recent extirpations associated with *Bd* have resulted in selective extinction and homogenization of diverse tropical American amphibian biotas. We find that *Bd*-associated extinctions in this region were nonrandom and disproportionately, but not exclusively, affected low-occupancy and endemic species, resulting in homogenization of the remnant amphibian fauna. The pattern of extirpations also resulted in phylogenetic homogenization at the family level and ecological homogenization of reproductive mode and habitat association. Additionally, many more species were extirpated from the region than would be expected if extirpations occurred randomly. Our results indicate that amphibian declines in this region are an extinction filter, reducing regional amphibian biodiversity to highly similar relict assemblages and ultimately causing amplified biodiversity loss at regional and global scales.

Keywords:

Amphibian chytrid, amphibian declines, beta diversity, biodiversity, biotic homogenization, chytridiomycosis, extinction, scale-dependence, similarity, wildlife disease.

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INTRODUCTION

Human activities are profoundly affecting global biodiversity, causing the ‘sixth mass extinction’ (Pimm *et al.* 1995; Vitousek *et al.* 1997; Daszak *et al.* 2000; Stuart *et al.* 2004; Wake & Vredenburg 2008). A contributing factor is that several important threats to biodiversity have become ‘globalized’ and now constitute subcategories of threat within the broad class of global change. For example, international trade has increased the magnitude and extent of species invasions (Ricciardi 2007), climate change is inherently global in scale and threat (Thomas *et al.* 2004) and the incidence of emerging infectious diseases of wildlife has been increasing globally (Daszak *et al.* 2000). Despite the widespread threat posed to biodiversity by global change, however, extinctions tend not to occur randomly or uniformly among species, even when the threat itself is relatively uniformly distributed (McKinney 1987; Eble 1999; Purvis *et al.* 2000b). If extinctions occur nonrandomly and

are selective with respect to species traits, identity or phylogeny, then some species or taxa will be more affected by these threats than others, potentially resulting in a disproportionate loss of some biotic features such as evolutionary history (Purvis *et al.* 2000a).

Less recognized, however, are the possible consequences of nonrandom patterns of extinction being repeated across a landscape of communities or biotas. One possible result is that the structuring of biodiversity among localities (i.e. beta diversity) will be altered. Such an outcome would be seen as a change in the biotic similarity of the remnant communities. For example, if the most common species across a landscape are disproportionately at risk of extirpation, then biotas will become dominated by idiosyncratic species, leading to decreased similarity and increased beta diversity (Olden & Poff 2003). In contrast, the disproportionate extirpation of relatively rare or endemic species or of particular phylogenetic or functional groups could result in the loss of regional biotic distinctiveness, causing an

underappreciated form of biodiversity loss known as biotic homogenization (McKinney & Lockwood 1999; Olden & Poff 2003; Olden & Rooney 2006). Perhaps most importantly, the repetition of extinction patterns across a landscape may also result in a greater than expected loss of diversity at large spatial scales as unique and rare species are lost from entire metacommunities or regions (McKinney 1997; Chase 2007). Thus, if repeated across a large enough spatial scale, local and regional losses of evolutionary or ecological history may be magnified to a global scale of finality.

Despite the general understanding that extinction selectivity may exacerbate losses of biodiversity (McKinney 1997; Purvis *et al.* 2000a), modern diversity assessments focus almost universally on numbers of extinctions rather than on the patterns in which they occur. Additionally, the consequences of a repeated syndrome of disproportionate extinction threat at a large spatial scale have yet to be empirically addressed. A more complete understanding of the present biodiversity crisis requires not only recognizing selective extinction events, but also understanding how they alter patterns of species, phylogenetic and ecological diversity, and potentially amplify the effects of local extinctions (McKinney & Lockwood 1999). Here, we use a unique data set from a modern extinction event based on surveys of tropical American amphibians before and after disease-associated declines as a model system to (1) determine whether extirpations are selectively distributed among species across locations, (2) determine whether species, phylogenetic or functional diversity are affected across space and (3) understand the consequences to regional biodiversity of nonrandom extinctions.

Amphibians as a group are an archetype of the modern biodiversity crisis, in part owing to the spread of an emerging pathogenic fungus of amphibians, *Batrachochytrium dendrobatidis* (Longcore, Pessier, and Nichols, 1999) (*Bd*) (Stuart *et al.* 2004; Lips *et al.* 2006; Wake & Vredenburg 2008). Although *Bd* has low host specificity and infects many amphibians (Daszak *et al.* 1999), growing evidence suggests that particular host physiological and ecological traits are predictive of *Bd*-associated declines and extinctions (Lips *et al.* 2003a; Woodhams *et al.* 2006; Bielby *et al.* 2008). Consequently, *Bd*-associated extinctions may be selective with respect to species, phylogeny or ecological function, in which case susceptibility to *Bd* and extinction probability could be nonrandomly distributed among species. In particular, if certain species are disproportionately at risk of local extirpation, then the widespread occurrence of *Bd* may create an extinction filter leading ultimately to the homogenization of diversity at the regional scale and the regional or global extinction of susceptible species (McKinney 1997).

Of the several regions in which *Bd*-associated amphibian declines and extinctions have occurred, the American tropics have suffered a particularly dramatic loss of amphibian diversity (Stuart *et al.* 2004). We compared the amphibian communities of eight sites across Lower Central America based on data from surveys conducted by one of us (K.R.L.) and from published amphibian surveys conducted before and after *Bd*-associated declines. We show that *Bd*-associated local extinction of amphibians was nonrandom and selective, resulting in reduced beta diversity and remnant amphibian communities that are homogenized in terms of composition, family-level phylogeny and ecology. Additionally, the particular pattern of local extirpations has led to a greater than expected loss of species diversity at the regional scale.

MATERIALS AND METHODS

Study system

The amphibian chytrid fungus, *Bd*, is a pathogenic fungus of amphibians that has decimated local populations of amphibians in western North America (Muths *et al.* 2003; Rachowicz *et al.* 2006), the tropical Americas (Lips *et al.* 2006), Europe (Bosch *et al.* 2001) and Australia (Berger *et al.* 1998). In the study system in Lower Central America, *Bd* has moved through the region in a wavelike fashion, producing a general pattern of stable populations when absent and catastrophic amphibian declines when present (Lips *et al.* 2006, 2008; Rohr *et al.* 2008). Although there is evidence that climate and other interacting environmental factors have played a role in several *Bd*-associated declines in other regions and at specific locales (e.g. Pounds *et al.* 1999; Blaustein & Kiesecker 2002; Bosch *et al.* 2007; Muths *et al.* 2008), recent analyses indicate that there is presently little direct evidence for a role of climate as the widespread, proximate cause of amphibian declines in Lower Central America (cf. Pounds *et al.* 2006; Lips *et al.* 2008; Rohr *et al.* 2008). Hence, the general scientific consensus indicates that epizootic disease caused by outbreaks of *Bd* is an important proximate cause of amphibian declines and extinctions in the American tropics (Lips *et al.* 2006, 2008; Pounds *et al.* 2006; Skerratt *et al.* 2007; Rohr *et al.* 2008; Woodhams *et al.* 2008). Additionally, as the goal of this study was to identify and assess patterns (and not mechanisms) of extinction, the role of multiple interacting drivers will not qualitatively affect our conclusions.

Data collection and comments

Our data come from previously published surveys of eight sites across *c.* 500 km in Costa Rica and Panama occurring in tropical wet, lowland, premontane and lower montane

rainforest (Table 1). One of us (K.R.L.) compiled species lists for each site based on a combination of transect surveys, incidental sightings, published data and museum specimens. At six of the eight sites, K.R.L. and field teams repeatedly surveyed multiple transects along streams and trails over several years (Lips 1999; Lips *et al.* 2003a,b, 2006 and unpublished data). In summary, survey teams of two to three people walked 200–400 m transects during both diurnal and nocturnal periods, searching for all species of amphibians through visual and aural detection. In all cases, species lists were compiled from surveys conducted across multiple years, both pre- and post-decline. Although many species at each site are relatively uncommon (both in site occupancy and local abundance), even these species were regularly documented via nocturnal aural surveys or by the presence of larvae for some year-round stream-breeding species. For two sites not visited by K.R.L., species lists were compiled from published accounts from similar studies (Table 1). Survey methods and data collection are described in detail in the original publications describing declines in these areas (Pounds *et al.* 1997b, 1999; Lips 1998, 1999; Lips *et al.* 2003a,b, 2006; Puschendorf *et al.* 2006).

Our primary goal in compiling these data was to ensure the most complete species list for each site for both pre-decline and post-decline survey periods. Thus, we chose to include all available data, rather than attempting to standardize data sets based on survey methods or effort. Because our data come from several sources across a large geographical area and include surveys conducted at different times using related, but not identical, survey methods, there

is substantial variation in survey effort among sites in our data. However, this additional variation would be expected to obscure statistical patterns and make any selective extinction less likely to detect. For this reason we do not expect variation in among-site survey methods to have introduced systematic bias in our data.

One potential source of bias in our data could arise from a systematic reduction in survey effort or efficacy between pre- and post-decline surveys, which could falsely lead to a conclusion of reduced species richness, especially of rare or difficult-to-detect species, and possibly an erroneous conclusion of reduced beta diversity. However, we are confident that intra-site variation in survey effort is not a source of bias in our data for several reasons. First, although the number of species and individuals captured in post-decline surveys declined precipitously, post-decline survey effort was often quantitatively similar to or greater than pre-decline survey effort (Table S1). Additionally, qualitatively, post-decline surveys were more efficient and thorough, as fewer individual amphibians were captured and processed per person-hour and hence more time was spent conducting surveys (e.g. average number of individual amphibians captured per person-hour pre-decline across five sites: 9.5; average number post-decline: 3.0; Table S1). Over time, surveys also became more efficient as survey crews became more experienced (e.g. figs 3 and 4 in Lips *et al.* 2006), and amphibian declines typically elicit increased research interest and survey effort from researchers. Thus, by several measures, post-decline surveys were likely to be more thorough than pre-decline surveys at our sites. Despite this,

Table 1 Site locations, local amphibian species richness and data sources. Sites are listed from west to east

Site	Elevation (m a.s.l.)	Pre-decline amphibian species richness	Post-decline amphibian species richness (% reduction)	Data source and relevant references
Monteverde Cloud Forest Preserve, Costa Rica	1400	60	31 (–48.3)	Published surveys (Pounds <i>et al.</i> 1997a; Pounds & Fogden 2000)
Zona Protectora La Selva, Costa Rica	30–2906	30	20 (–33.3)	Published survey (Puschendorf <i>et al.</i> 2006)
Finca Las Alturas, Costa Rica	1000–3100	30	17 (–43.3)	K.R.L. surveys (Lips <i>et al.</i> 2003a,b) and unpublished surveys
Jardin Botanico Wilson, Costa Rica	900–1280	40	21 (–47.5)	K.R.L. unpublished surveys and Scott (1983)
Zona Protectora Las Tablas	1900	21	12 (–42.9)	K.R.L. surveys (Lips 1998) and unpublished surveys
Reserva Forestal Fortuna, Panamá	1000–1400	58	34 (–41.4)	K.R.L. surveys (Lips 1999) and unpublished surveys
Parque Nacional Santa Fé, Panamá	500–800	50	19 (–62.0)	K.R.L. surveys (Brem & Lips in press) and unpublished surveys
Parque Nacional G. D. Omar Torrijos (El Copé), Panamá	500–800	69	30 (–65.0)	K.R.L. surveys (Lips <i>et al.</i> 2006)
Total regional richness		144	83 (–42.4)	

no new species were found during post-decline surveys, which suggests that pre-decline species lists were relatively complete.

Because detection probability of very rare species may be lower than that of common species, it is possible that exceptionally rare species may have been missed entirely in post-decline surveys. However, it is reasonable to expect that species undetected by extensive surveys may not comprise viable populations and are likely to be functionally extirpated. This is partially supported by our observation that no documented extirpated species have re-appeared during subsequent post-decline surveys, even in surveys conducted up to 8 years post-decline (K.R.L., personal observations). Finally, our post-decline species lists almost certainly include species in the process of decline and extirpation. Thus, we expect that our post-decline data are conservative with respect to the ultimate effects of amphibian declines in this region.

Analyses

Null model of similarity and distance relationship

We used a null model approach to test for nonrandom changes in compositional biotic similarity owing to local extirpations of amphibians. We developed a null model of biotic composition to calculate the deviation from expected biotic similarity based on random extinction. This model derives the observed deviation (which we call J_{dev}), from the null-expected value of Jaccard's index (JI) of compositional similarity based on random community assembly. The primary benefit of this approach is that it allows us to determine the degree to which biotic similarity among sites is structured relative to random assembly, independent of changes in species richness caused by amphibian declines (for a discussion of similar null models, see Connor & Simberloff 1978; Raup & Crick 1979). Specifically, we hypothesized that remnant amphibian biotas would be more similar to each other post-decline owing to selective local extinctions and a filtering effect of *Bd*-associated declines.

We calculated the deviation from expected biotic similarity (J_{dev}) by randomizing the observed species occurrence matrix via 10 000 Monte Carlo randomizations (for details on a similar analysis, see Chase 2007). We constrained the randomizations to (1) maintain the observed species richness at each site and (2) maintain the observed occupancy of each species across sites (i.e. column and row totals were fixed). For each randomized output matrix we calculated all pairwise JI values, the mean of which provided our null expected value of JI. We then calculated J_{dev} as the difference between the mean observed pairwise JI and the mean expected pairwise JI. Thus, positive values of J_{dev} indicate that biotic similarity is greater than would be expected by random chance, whereas negative values

indicate that biotas are more distinct than would be expected by random chance. This metric is similar to, but more informative than, the Raup–Crick metric of similarity (Raup & Crick 1979) and identical analyses conducted with the Raup–Crick metric produced the same qualitative results and are therefore not presented here. We calculated J_{dev} once for pre-decline species incidence data and once for post-decline incidence data to assess the effects of amphibian extirpations on biotic similarity in Lower Central America.

We also used J_{dev} to assess the importance of the geographical structuring of amphibian community composition before and after declines and extinctions. We hypothesized that isolation by distance would lead to greater dissimilarity (and therefore beta diversity) in community composition among more distant sites (Nekola & White 1999), but that selective extinction caused by *Bd* would reduce the importance of the distance–similarity relationship. To avoid error inflation owing to non-independence of multiple pairwise comparisons, we used Mantel's procedure to test for a relationship between natural log-transformed pairwise similarity (J_{dev}) and untransformed geographical distance matrices (Legendre & Legendre 1998; Nekola & White 1999). We conducted this analysis on data collected both before and after decline events to determine whether the pattern of extirpations changed the importance of geography in the structuring of amphibian species across the eight sites.

Analysis of phylogenetic and ecological distinctiveness

We were further interested in the possible ecological and evolutionary consequences of nonrandom extinction of the amphibian biotas of the region. To identify phylogenetic homogenization, if present, we therefore created two additional species incidence matrices in which we categorized amphibian species into a family-level taxonomy (following Frost *et al.* 2006), again before and after amphibian declines. We then applied our null model of compositional similarity, J_{dev} , to this new matrix to determine whether amphibian biotas have become homogenized at the family level. We conducted an identical analysis on an additional set of incidence matrices in which individual species were assigned to ecological categories based on reproductive mode and habitat association, to determine whether the pattern of species loss associated with amphibian declines has resulted in the homogenization of ecological functions across biotas. For this analysis, species were allocated to appropriate categories based on adult habitat (arboreal, terrestrial, riparian, fossorial, pond or ephemeral pool), egg deposition site (arboreal, terrestrial, riparian, fossorial, pond, ephemeral pool or carried by adults) and larval habitat (arboreal, riparian, pond, ephemeral pool or direct-developing). Finally, we also used these

same data in a similarity percentage analysis, SIMPER, to identify the ecological groups contributing most significantly to differences among pre- and post-decline biotic distinctiveness (Clarke 1993).

Null model of random extinction

We also created a null model for the loss of regional diversity under random local extinction. This model allows us to determine whether selective extirpations resulted in a repeated pattern of species losses across sites, leading to a greater loss of regional diversity than would be expected if local extinctions were non-selective and randomly distributed among species. We created a null prediction for the loss of regional species richness under random local extinction by first assigning each species at a site a fixed and equivalent probability of local extinction based on the observed number of species actually extirpated at that particular site. That is, for a site with i species, of which j disappeared after *Bd*-associated declines, our null prediction is that each species experiences a random probability of local extinction of j/i . We then conducted 10 000 iterations of the random extinction process and calculated the resultant regional species richness for each individual simulation. The mean value derived from these simulations forms our prediction of regional species richness under random extirpation. We then compared this value with the actual observed change in regional species richness owing to observed extirpations.

RESULTS

Loss of biotic distinctiveness

Prior to the appearance of *Bd* and associated amphibian declines, the eight geographical regions had high local amphibian species richness, with an average of 45 species observed per site (range 21–69 species; Table 1). Compositional difference among the communities was also high and the communities were significantly less similar than would be expected by random chance (randomization t -test of $J_{\text{dev}} \neq 0$, $t = -2.49$, $P = 0.019$; mean $J_{\text{dev}} = -0.04$). This indicates a high level of beta diversity, which is most likely an outcome of the high endemism of tropical American amphibian communities and the geographical separation of the study sites (Nekola & White 1999; Lamoreux *et al.* 2006; Lips *et al.* 2006; McKnight *et al.* 2007). Among the species in this study, 61 (*c.* 42%) were locally endemic, each occurring at only one of the eight sites. As would be expected at this spatial scale (range of inter-site distances: 10–493 km), the similarity of amphibian biotas was negatively associated with pairwise distance among sites (Mantel test: $r = -0.54$, $P = 0.007$, $n = 8$ sites; Fig. 1a). Based on the null model (J_{dev}), adjacent sites were more

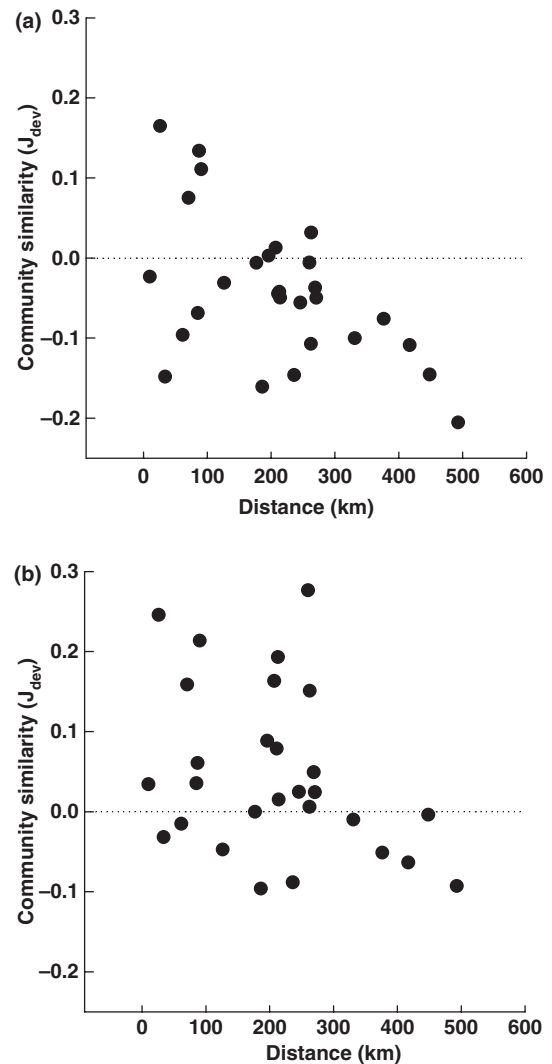


Figure 1 Biotic similarity by pairwise distance among sites for pre- and post-decline amphibian communities. Biotic similarity (J_{dev}) is the deviation from the null expected similarity based on JI of similarity (Materials and methods). The dotted line represents null-expected biotic similarity. (a) Prior to *Batrachochytrium dendrobatidis* (*Bd*)-associated declines and extinctions, biotic similarity was generally less than expected by chance and declined significantly with increasing pairwise distance among sites. (b) After *Bd*-associated declines and extinctions, amphibian communities were generally more similar than expected by chance ($J_{\text{dev}} > 0$) and the declining relationship between biotic similarity and pairwise distance was weaker.

similar than would be expected by random chance, while distant sites were more distinct. This common pattern is consistent with theory suggesting that a combination of historical biogeography, habitat specialization and dispersal limitation play important roles in the creation and maintenance of the diversity of these communities (Nekola & White 1999).

The loss of amphibian species following *Bd* epizootics fundamentally altered the way in which amphibian diversity was structured. After extirpations occurred at each site, observed local amphibian species richness declined sharply to an average of 23 species per site (range 12–34 species; Table 1). These local extinctions also homogenized the post-decline communities such that they became significantly more similar than would be expected by chance (randomization *t*-test of $J_{dev} \neq 0$, $t = 2.41$, $P = 0.023$; mean $J_{dev} = 0.05$). Additionally, the relationship between community similarity and pairwise distance among sites became weaker and only marginally detectable (Mantel test: $r = -0.34$, $P = 0.088$, $n = 8$ sites; Fig. 1b).

Because relatively rare, low-occupancy species create biotic distinctiveness and increase beta diversity (McKinney & Lockwood 1999; Olden & Poff 2003; Olden & Rooney 2006), our result of reduced beta diversity post-decline suggests that species occurring at only one or a few sites were disproportionately at risk of regional extinction. Although endemic species comprised *c.* 42% of the surveyed species, *c.* 59% of the regional extinctions were of endemics ($\chi^2 = 12.02$, $P < 0.001$, $n_1 = 83$, $n_2 = 61$), as would be expected. Despite this, site occupancy less reliably predicted the loss of species from individual sites. The result of individual logistic regressions for each site indicates that site occupancy influenced the probability of local extirpation at only four of eight sites (Table S2). Although increased occupancy of common species also could have caused a loss of beta diversity, we found that no species became more widespread after the decline events.

Loss of phylogenetic and ecological distinctiveness

Among-site biotic distinctiveness at the family level was also constrained after declines and extinctions took place relative to original biotic distinctiveness. Amphibian biotas were originally significantly more similar than would be expected by random chance, with a mean J_{dev} of 0.15 (95% CI: 0.09, 0.22). After declines and extinctions took place, family-level biotic similarity increased significantly to a mean of 0.26 (95% CI: 0.21, 0.31), indicating that phylogenetic similarity at the family level became even more similar than would be expected after declines took place across the eight sites.

Based on the diversity of reproductive modes and habitat associations of amphibians among the eight sites, we also found that extirpations associated with outbreaks of *Bd* resulted in an ecologically constrained set of communities. Whereas amphibian assemblages were originally only slightly more similar than would be expected by chance in terms of reproductive modes and habitat associations (mean $J_{dev} = 0.05$, 95% CI: 0.03, 0.08), post-decline communities were significantly more similar (mean $J_{dev} = 0.21$, 95% CI: 0.18, 0.24). This homogenizing effect of the pattern of post-

epizootic extirpation is evident when ecological composition is ordinated in non-metric space (Fig. 2).

We also found that the diversity of ecological and habitat affiliations changed significantly among pre- and post-decline communities (ANOSIM; $P = 0.018$). Our SIMPER analysis indicated that over 50% of the change in pre- and post-decline ecological similarity was attributable to changes in the number of species in four ecological groups. Specifically, species with terrestrial adults, terrestrial eggs and direct-developing larvae become the most distinctive components of post-decline sites as these three ecological groups became relatively more speciose post-decline. In contrast, the fourth distinguishing group, riparian adults, became relatively less dominant in terms of number of species per site (Table S3). In summary, amphibian assemblages became typified by terrestrial species without free-swimming larvae, at the expense of highly aquatic riparian species with aquatic larvae.

Loss of regional diversity

To determine the effects on regional diversity of the selective local extinction of rare species caused by *Bd*, we

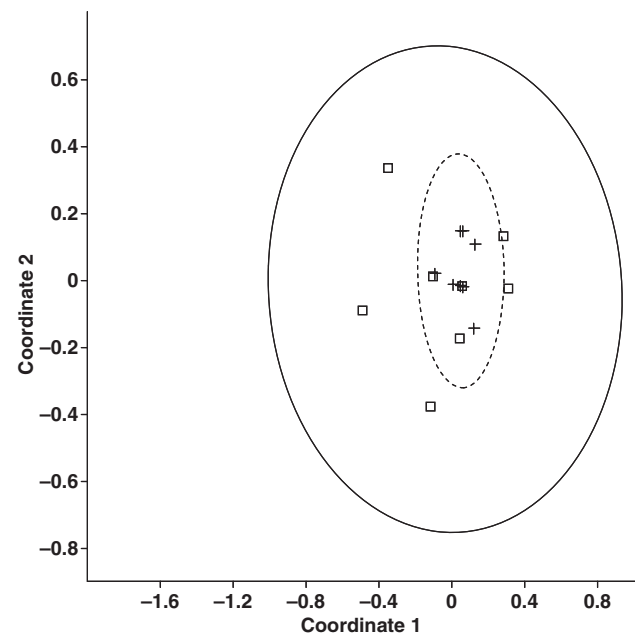


Figure 2 Non-metric multidimensional scaling (NMDS) ordination of amphibian ecological similarity before (squares) and after (crosses) amphibian extirpations in Lower Central America. NMDS illustrates biotic distinctiveness by ordinating compositional difference into two unitless dimensions, such that Euclidean distances between points are proportional to differences in ecological composition among the eight sites in this study. In this figure we use the Raup–Crick null model of compositional similarity. Ellipses represent 95% confidence intervals.

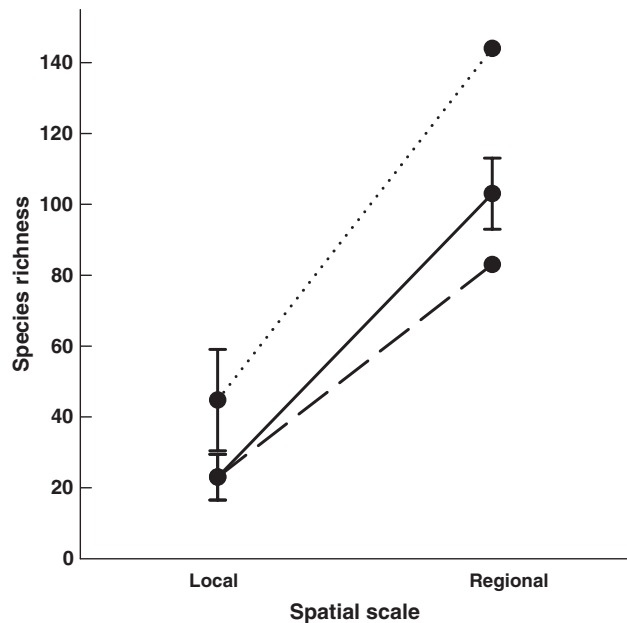


Figure 3 The scaling of local and regional species richness among tropical American amphibian communities. Local richness is mean number of species per site and regional richness is the total number of species across all eight sites. 95% confidence intervals are shown where applicable. Prior to the appearance of *Batrachochytrium dendrobatidis* (*Bd*; dotted line), beta diversity was high, seen as a rapid accumulation of species from local to regional scales. After *Bd*-associated extinctions (hashed line), beta diversity declined, and significantly fewer species were present both locally and regionally. The loss of regional diversity was greater than would be expected if local extinctions were random (solid line) (permutation test based on null model, $P < 0.0001$, 10 000 iterations; see Materials and methods).

compared the observed number of regional extinctions to our null model for the loss of regional diversity under random extinction. Our simulations show that a random pattern of local extinction would have resulted in 41 regional extinctions across the eight sites (95% confidence interval: 31, 51), whereas 61 regional extinctions were actually observed ($P = 0.0001$; Fig. 3). Thus, the particular pattern in which *Bd*-associated extinctions occurred resulted in a disproportionate and significantly greater loss of species at the regional scale when compared with random loss of species.

DISCUSSION

Our analyses yield several novel conclusions. First, that *Bd*-associated extinctions have caused a substantial loss of beta diversity in Lower Central American amphibian assemblages, resulting in compositional homogenization of the regional amphibian biota. Second, this loss of beta

diversity has also resulted in homogenization at the phylogenetic and ecological scales. Finally, we also found that the nonrandom pattern of extinctions has resulted in a greater than expected loss of regional, and potentially global, amphibian diversity.

The homogenization of tropical American amphibian faunas is a troubling result from a conservation perspective for several reasons. First, as noted previously, endemism is a primary component of beta diversity and biotic distinctiveness, so biotic homogenization in our system is indicative of a significant loss of endemism from one of the world's 'endemism hotspots' (Orme *et al.* 2005). Although locally endemic species were disproportionately likely to be extirpated at our sites, endemism did not perfectly predict extirpation. Of the 61 locally endemic species, less than half (25) were driven regionally extinct. Thus, geographical rarity does not fully explain susceptibility to *Bd*-associated decline and extirpation in this study. One explanation for this is that not all endemic species are 'rare' in the sense of demographic susceptibility to extinction (Rabinowitz 1981). For example, some of the locally endemic species in our study are actually widespread species at the margins of their ranges [e.g. *Lithobates forreri* (Boulenger, 1883)]. Additionally, it was not only geographically rare species that experienced regional extinction, as 41% of extinctions were of non-endemic species, and some species that were once widespread and common in the study area have disappeared completely [e.g. *Hylomantis lemur* (Boulenger, 1882)]. Therefore, in the case of tropical American amphibians, equating susceptibility to *Bd* with rarity oversimplifies the role of *Bd* as an agent of extinction and ignores the influence of other potentially significant factors (Blaustein & Kiesecker 2002; de Castro & Bolker 2005). Our study explicitly examines extinction patterns and not processes, but previous research in this and other systems suggests that the observed pattern of extinctions may arise from an interaction of demographic, ecological and physiological traits at the species level (Lips *et al.* 2003b; Woodhams *et al.* 2006). This is supported by our additional findings that selective extinction occurred at the level of habitat association, with the number of terrestrial species becoming relatively more dominant and riparian species becoming less speciose, a pattern observed in other studies (Lips *et al.* 2003b; Bielby *et al.* 2008). However, the significance of the nonrandom distribution of these traits among locations and communities has previously gone unrecognized.

A second troubling aspect of our results is that amphibian declines in this system have already resulted in a loss of some ecosystem functions, notably nutrient cycling in riparian systems owing to the loss of riparian tadpoles (Whiles *et al.* 2006). An unanswered question is whether the taxonomic homogenization we describe will result in a concomitant loss of unique functions (i.e.

functional homogenization), which may increase the probability of effects of amphibian declines cascading throughout or across ecosystems, as has been documented in other systems (Tilman *et al.* 1997). Although conducted at a coarse scale and based on variation in species richness of amphibian families and ecological groups at each site, our findings of family-level and ecological homogenization suggest that the ecological function and evolutionary trajectory of amphibian biotas in Lower Central America have changed significantly as a result of amphibian extirpations and extinctions. For example, the apparent complete loss of two rare families, Aromobatidae and Hemiphractidae, from the region illustrates that nonrandom extinctions can result in disproportionate losses of evolutionary history through the loss of higher taxa (Purvis *et al.* 2000a). In this case, this loss is coupled with the concomitant loss of a unique ecological group, as well: the marsupial frogs of Hemiphractidae.

It is important to note that our study does not address change in patterns of the abundance of individual species, in part because equivalent-effort abundance data were not available for each site. Therefore, we could not assess potentially important patterns at the level of species abundance relationships, despite observations that some species such as *Agalychnis callidryas* (Cope, 1862) and *Rhinella marina* (Linnaeus, 1758; formerly *Bufo marinus*) have become more abundant after *Bd*-associated declines (Lips *et al.* 2006). Because population abundances respond more quickly to changes in the ecological landscape than do site occupancies, future analyses on patterns of species abundance may foreshadow changes in occupancy as threat-tolerant species become numerically dominant (Cassey *et al.* 2008).

The apparent loss of geographical structuring of the amphibian biota across Lower Central America suggests that modern mass mortality and decline events, in this case decline events associated with a novel pathogen, can override historical biogeography as a contributor to community structure (Schluter & Ricklefs 1993; Nekola & White 1999). Although the primacy of *Bd* as a cause of amphibian declines, extirpations and extinctions in this region has been the subject of debate (Pounds *et al.* 1999, 2006; Lips *et al.* 2008; Rohr *et al.* 2008), there is no question that *Bd* has significantly contributed to the pattern of species losses documented here. Thus, our results suggest that the slate of ecological history in these assemblages has been partially erased and that amphibian biotas in this region may now primarily be structured by whether constitutive species survive epizootics of *Bd*.

We documented a greater than expected loss of regional diversity stemming from selective extinction associated with *Bd*. The primary implication of this result is that local extirpations of amphibians in the tropical Americas may

disproportionately translate into global extinctions. Thus, although the effects of *Bd* have previously been described as a startling loss of local amphibian diversity (e.g. Lips *et al.* 2006), our evidence also suggests an even greater loss of regional and global amphibian diversity. The continued spread of *Bd* in the region (Woodhams *et al.* 2008) suggests that if the pattern of extinction is repeated, even more unique species will be extirpated. Furthermore, our results suggest that the predicted losses of evolutionary history based on hypothetically nonrandom extinction in birds and mammals (Purvis *et al.* 2000a) may be foreshadowed by the real loss of phylogenetic diversity and evolutionary history in tropical American amphibians.

Local extinctions are increasingly well documented, but researchers only rarely assess extinction patterns across communities, sites or regions. As a result, it is often unknown whether local extirpations will result in regional and global extinctions. Although some threats to biodiversity are idiosyncratic and local, several significant threats such as global climate change (Thomas *et al.* 2004), emerging infectious diseases of wildlife (Daszak *et al.* 2000; Lips *et al.* 2006) and invasive species (Vitousek *et al.* 1997) inherently occur at regional or global scales. Our findings emphasize that when widespread threats cause selective extinctions, they may act as extinction filters, consistently removing vulnerable taxa from biotas at local and regional scales. In the case of tropical amphibian declines associated with disease outbreaks, this process has led to the loss of biogeographical, ecological and evolutionary history, and to a magnified loss of regional, and potentially global, biodiversity. Coming to terms with present and future threats to biodiversity will require addressing not only how many extinctions occur, but also how those extinctions are patterned across scales of space and diversity.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Summary of survey effort across five of the eight sites used in this study for which effort data are available.

Table S2 Results of logistic regression evaluating the effects of number of sites occupied on probability of local extirpation of amphibian species across eight sites in lower Central America.

Table S3 Change in relative species abundance of amphibians in 15 ecological categories, in terms of species per category, owing to amphibian declines across the eight sites in this study.

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