Received: 8 January 2019 | Accepted: 31 May 2019

DOI: 10.1111/1365-2664.13510

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

When are extinctions simply bad luck? Rarefaction as a framework for disentangling selective and stochastic extinctions

Kevin G. Smith[1,2] | **Ryan J. Almeida**[1,3]

[1]Department of Biology, Davidson College, Davidson, NC, USA

[2]Department of Environmental Studies, Davidson College, Davidson, NC, USA

[3]Department of Ecology, Evolution, and Natural Resources, Rutgers University, New Brunswick, NJ, USA

Correspondence
Kevin G. Smith
Email: kgsmith@davidson.edu

Funding information
Davidson College; Davidson College Biology Department; Davidson Research Initiative; National Science Foundation, Grant/Award Number: DEB-1650554

Handling Editor: Silvia Carvalho

Abstract

1. A key challenge in conservation biology is that not all species are equally likely to go extinct when faced with a disturbance, but there are multiple overlapping reasons for such differences in extinction probability. Differences in species extinction risk may represent extinction selectivity, a non-random process by which species' risks of extinction are caused by differences in fitness based on traits. Additionally, rare species with low abundances and/or occupancies are more likely to go extinct than common species for reasons of random chance alone, that is, bad luck. Unless ecologists and conservation biologists can disentangle random and selective extinction processes, then the prediction and prevention of future extinctions will continue to be an elusive challenge.
2. We suggest that a modified version of a common null model procedure, rarefaction, can be used to disentangle the influence of stochastic species loss from selective non-random processes. To this end we applied a rarefaction-based null model to three published data sets to characterize the influence of species rarity in driving biodiversity loss following three biodiversity loss events: (a) disease-associated bat declines; (b) disease-associated amphibian declines; and (c) habitat loss and invasive species-associated gastropod declines. For each case study, we used rarefaction to generate null expectations of biodiversity loss and species-specific extinction probabilities.
3. In each of our case studies, we find evidence for both random and non-random (selective) extinctions. Our findings highlight the importance of explicitly considering that some species extinctions are the result of stochastic processes. In other words, we find significant evidence for bad luck in the extinction process.
4. *Policy implications*. Our results suggest that rarefaction can be used to disentangle random and non-random extinctions and guide management decisions. For example, rarefaction can be used retrospectively to identify when declines of at-risk species are likely to result from selectivity, versus random chance. Rarefaction can also be used prospectively to formulate minimum predictions of species loss in response to hypothetical disturbances. Given its minimal data requirements and

familiarity among ecologists, rarefaction may be an efficient and versatile tool for identifying and protecting species that are most vulnerable to global extinction.

KEYWORDS
biodiversity, extinction, extinction risk, null model, rarefaction, rarity, selectivity, stochastic

1 | INTRODUCTION

Why do some species go extinct when faced with a disturbance, while others persist? This question is fundamentally an issue of extinction selectivity (Payne, Bush, Heim, Knope, & McCauley, 2016). Extinction selectivity results when some taxa have higher extinction probabilities than others, for example, as caused by mismatches between species' traits and the environment ('fair game extinction', Raup, 1994; 'Darwinian extinction', Webb, 2003). If species phenotypes are responsible for these differences in extinction probability, then extinction selectivity may reveal traits that are causally associated with risk of extinction (e.g. Boyer, 2010; Chiba & Roy,2011a). Ultimately, identifying such causal relationship can help predict risk of extinction for extant taxa faced with similar threats (Payne et al., 2016), leading to more efficient and effective allocation of scarce conservation resources.

A significant complication to identifying extinction selectivity is that not all differences in extinction probability are caused by trait selectivity, but rather are the result of random chance (Hedrick, Lacy, Allendorf, & Soulé, 1996; Lande, 1993; Raup, 1981, 1994, 1992; Shaffer, 1981). This leads to confusion as to whether extinctions are truly associated with a suite of particular traits, or rather are the result of bad luck. For example, for low abundance or endemic populations that happen to exist where and when a significant disturbance occurs, it may be impossible to tell if an extinction was the result of trait-based selectivity, or if the rare species was simply 'at the wrong place at the wrong time' (Raup, 1981, 1994). This may be a common issue; analyses have found that many modern extinctions are of endemic, small-range, and low-abundance species (Boyer, 2010; Chiba & Roy 2011a,b; Lips, Reeve, & Witters, 2003; Smith, Lips, & Chase, 2009). Did these extinctions occur simply because the species were rare and subject to stochastic extinction, or because of true trait-based extinction selectivity?

We suggest that the importance of random chance in the extinction process, while recognized, may be underestimated. In the worst case, if random chance is not taken into account, stochastic extinctions may be erroneously classified as having been caused by trait-based, selective processes. While it is unlikely that patterns of modern extinction are strictly the result of random processes (Smith et al., 2009), it is clear that population abundance and range size vary dramatically among taxa (e.g. Rabinowitz, 1981). As a result, we should expect large variation in extinction probability and rate among taxa owing to random chance alone, even when environmental disturbances are relatively uniform and themselves random. This suggests an important question for studies aiming to identify and explain extinction selectivity: How can we determine when extirpations and extinctions are the result of trait-based selectivity, and not the result of the interaction between a stochastic disturbance and differences in abundance or range size?

We propose that research on extinction selectivity among taxa would benefit from the use of more informative null hypotheses for species extinctions. To this end we describe a modification of a well-established, simulation-based null-model method, rarefaction, and its application to the study of extinction selectivity. The outputs of our analysis are expected numbers of extinctions and random extinction probabilities (p_e), which can be used to inform conservation decision-making via an explicit consideration of whether observed extinctions were likely to have occurred as the result of random chance alone (e.g. a high p_e). In this paper, we describe our modification of rarefaction for this purpose and apply this analysis to three case studies of biodiversity decline, extirpation and extinction events to illustrate our approach's application, interpretation, strengths and limitations.

1.1 | Rarefaction as a null model for extinction

Although it was not designed for this explicit purpose, rarefaction can be modified to assess random extinction probabilities among taxa with different abundances or spatial occupancies. As typically used in ecological studies, rarefaction produces estimates of expected species richness such that larger species assemblages, habitats, or communities with more individuals can be compared to smaller communities with fewer individuals (Gotelli, 2001; Gotelli & Colwell, 2001; Gotelli & Graves, 1996; Simberloff, 1972). Rarefaction is a backward simulation down a species accumulation curve and is an explicit test of the degree to which random sampling effects alone cause differences in species richness among sites or communities. Rarefaction eliminates the influence of these random sampling effects (Gotelli & Colwell, 2001), allowing for more rigorous identification of non-random selective effects (sensu Vellend, 2010) such as competition, predation, or environmental change.

Within the context of biodiversity loss and extinction, we propose using rarefaction to compare a species assemblage to itself, before and after a significant disturbance or biodiversity loss event that causes a reduction in assemblage size. This is a minor conceptual change to how rarefaction is applied. When applied this way, rarefaction estimates the effects of the random loss of individuals and produces as an output the expected number of species in the smaller (i.e. post-disturbance) community. A further modification to rarefaction procedures is the conversion of this output to its complement, the expected number of extirpations or extinctions, assuming a random loss of individuals from a species assemblage (Figure 1a). This output can be used as a null model for extinction. When significantly more species are lost from an assemblage than expected, this provides strong evidence that some of the species losses associated with the disturbance are statistically unexpected, non-random, and therefore selective (Smith et al., 2009; Woods, Biro, Yang, & Smith, 2016).

We also made a more substantive modification to rarefaction, with the goal of identifying unexpected extinctions, that is, species with low random extinction probabilities, p_e, that were nonetheless driven extinct. Specifically, for a given decline from n_{pre} to n_{post} individuals (where $n_{pre} > n_{post}$) at a location, each individual rarefaction simulation results in a rarefied species richness $S_{rarefied}$, which is always $\leq S_{original}$. The individual species that occur in $S_{original}$ but not $S_{rarefied}$ represent stochastic extirpations/extinctions. From these principles, we define the random probability of local extinction, $p_{eL}(i)$ for each species i as the proportion of rarefaction runs that result in an abundance of zero (local extinction) for species i. This approach can be extended to a network of locations (a multi-site region), allowing for the calculation of $p_{eR}(i)$, the random probability of regional extinction of species i from all sites in the study region. These calculated p_e values explicitly reflect the influence of species abundance and range size on extinction probability (Figure 1b) and can be used to assess agreement or disagreement between stochastic extinction probabilities and observed extinctions.

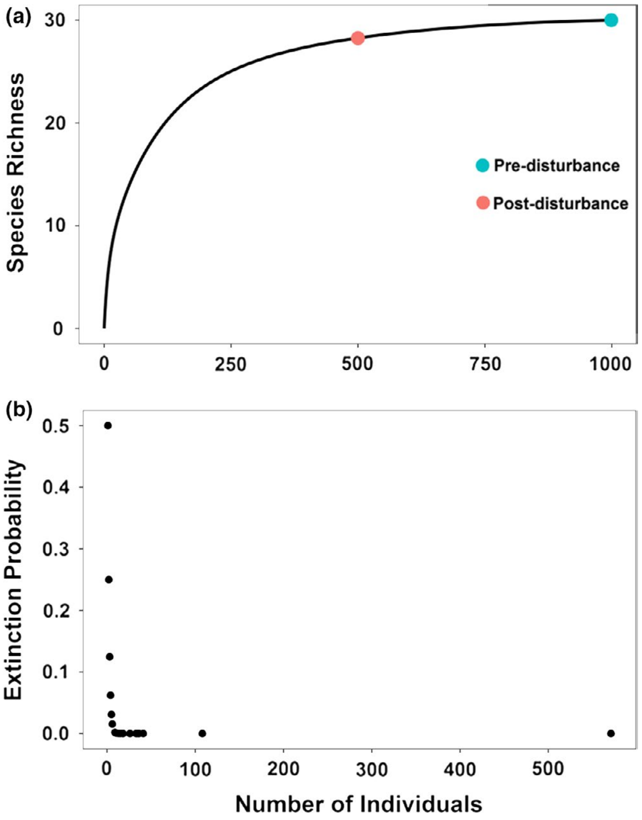

FIGURE 1 (a) Graphical representation of rarefaction-based null model for a simulated community of 30 species. Under the assumptions of the null model, species loss is dictated solely by the random removal of individuals. Rarefaction predicts a post-disturbance species richness of 28.9 species (a loss of one species) following a 50% loss of individuals in the community. (b) Relationship between species extinction probability and species abundance, based on simulated data for a community of 30 species drawn from a log series. Each point represents the null-expected extinction probability for a species based on its abundance alone. Extinction probabilities were calculated via rarefaction, simulating the effects of a random loss of 50% of the individuals in the original community. Rare species have high random extinction probabilities that quickly decline as abundance increases

2 | MATERIALS AND METHODS

2.1 | Data overview

We used data from three real-life disturbance events in which there was an observed decline of biodiversity and for which biodiversity data were collected both before and after the disturbance. Here, we use the term ‘disturbance’ in a broad sense to include abiotic or biotic changes leading to dramatic biodiversity change over ecological timescales, including for example, habitat loss, invasive species, and emergent pathogens. We compared pre-decline and post-decline datasets in the form of species-by-site matrices, which contained either presence/absence or abundance data for communities assessed prior to and following an absolute reduction in total number of individuals. If data were only available at a single site, our analyses required abundance data to perform individual based rarefaction (Figure 1a,b). If the data included multiple sites, however, then a sample-based rarefaction could be used to assess regional selectivity using only presence/absence data. We demonstrate both cases in our analyses. Importantly, because rarefaction is explicitly designed to correct for discrepancies in sampling effort between communities, we were able to compare sampling periods in which the pre-disturbance and post-disturbance survey effort differed (Heck, van Belle, & Simberloff, 1975; Hurlbert, 1971). We provide a summary of our three datasets in Table S1.

2.2 | Rarefaction analyses

We developed a rarefaction-based null model using R (R Core Team, 2018) to characterize the role of random processes in each of our case study extinction events. Each rarefaction analysis consisted of 1,000 iterations of the repeated random subsampling of a community from N_{pre} to N_{post} individuals, where each iteration of the rarefied community at N_{post} was stored in the column of a species × simulation output matrix. We then derived null-expected (rarefied) species abundances, $S_{rarefied}$, and p_e values from this output. We additionally calculated a probability of observed decline, p_{OD}, which represents the proportion of times a species was simulated through rarefaction to undergo its observed decline or a more extreme decline. p_{OD} allows for the identification of non-random decline when a species did not go extinct but exhibited greater than expected declines in abundance, another form of ecological selectivity. $S_{rarefied}$ and p_e values can also be derived from the package

TABLE 1 Comparison of simulated to observed declines in West Virginia bat species

Species	Pre-white-nose syndrome (WNS) abundance	Simulated post-WNS abundance (95% CI)	Observed post-WNS abundance	Interpretation
Corynorhinus townsendii virginianus	**130**	**14.1 (7, 21)**	**0**	**Unexpected extirpation**
Eptesicus fuscus	**1,349**	**149.7 (129, 171)**	**433**	**More abundant than expected**
Lasionycteris noctivagans	**84**	**9.2 (4, 15)**	**0**	**Unexpected extirpation**
Lasiurus borealis	**1,297**	**143.4 (122, 165)**	**332**	**More abundant than expected**
Lasiurus cinereus	148	16.4 (9, 24)	14	—
Myotis leibii	**151**	**16.6 (10, 24)**	**6**	**Less abundant than expected**
Myotis lucifugus	**2,966**	**328.4 (300, 356)**	**155**	**Less abundant than expected**
Myotis septentrionalis	**4,829**	**534.7 (502, 567)**	**314**	**Less abundant than expected**
Myotis sodalis	36	4.0 (1, 8)	1	—
Nycticeius humeralis	1	0.1 (0, 1)	0	—
Perimyotis subflavus	**742**	**82.5 (66, 99)**	**49**	**Less abundant than expected**
Unknown	98	10.9 (5, 17)	6	—

Note: Simulated post-disturbance abundances were the average rarefied species abundance across 1,000 simulations. Numbers in parentheses indicate upper and lower bounds of 95% confidence intervals when applicable. Statuses in bold represent changes in abundance that were statistically improbable (p_{OD} < .05) under assumptions of random processes.

vegan in R (Oksanen et al., 2019). Within vegan, the rarefy() function provides expected species richness when given a community matrix and a sample size. In our case, this expected species richness can be viewed as null-expected post-disturbance richness. Probabilities of species occurrence can be obtained from the function drarefy(); in the context of extinction, p_e is calculated simply by taking the complement 1 − probability of occurrence. These are the random probabilities that species do not occur following a disturbance, that is, random extinction probabilities. We calculated S_{rarefied} and p_e values at both the local (p_{eL}) and regional scales (p_{eR}; among several sites) when appropriate. We provide example code demonstrating the use of our model as Supporting Material.

3 | RESULTS

3.1 | Bat declines associated with white nose fungus

We analysed generalized bat declines associated with the spread of the fungal infection white-nose syndrome (WNS; Francl, Sparks, & Brack, 2012a,2012b). WNS has led to the rapid decline of populations of several species of hibernating bats in the eastern United States, especially in the genus *Myotis* (Blehert et al., 2009; Verant et al., 2018). Species that were once widespread throughout North America now face local and regional extinction in WNS-epizootic areas (Frick et al., 2010; Warnecke et al., 2012). WNS is caused by the fungus *Pseudogymnoascus destructans* and affects many, but not all, North American bat species (Francl, Sparks, Brack, & Timpone, 2011; Verant et al., 2018). Given the breadth and magnitude of effects of WNS on bat populations, a better understanding of this pathogen's taxonomic selectivity may help understand its past impacts and predict future effects in new locations and taxa.

The data we use are abundance data in the form of captures via mist-netting, collected before and after WNS emerged in West Virginia (Francl et al., 2011). We calculated expected post-epizootic abundances for each species (Table 1) as well as p_{OD} and p_{eL} values (ST1). Based on rarefaction, the observed reduction in bat abundance from the original sample size of 11,734 bats corresponds to an expected loss of only 0.9 species. In contrast to this prediction, three species were not recorded in the post-WNS survey, suggesting local extirpation or dramatic decline of these species (Table 1). Furthermore, four species (*Myotis leibii*, *M. lucifugus*, *M. septentrionalis*, and *Perimyotis subflavus*) experienced greater declines than predicted by the null model (p_{OD} = .002, 0, 0, 0, respectively), suggesting that these species may be particularly susceptible to the WNS pathogen and are experiencing trait-based, selective declines, despite still being present at observable abundance. Two species (*Eptesicus fuscus* and *Lasiurus borealis*) were more abundant than expected by chance, suggesting some degree of selective tolerance or resistance to WNS by these species (Table 1).

This case study highlights a simple example of rarefaction's potential utility for analysing extinction selectivity during decline events. Rarefaction is conventionally used to correct for discrepancies in sampling effort to allow for comparisons of species richness across communities. Unequal sampling effort is a potential roadblock to analysing species decline, especially when post-decline sampling effort is less than pre-decline effort, as was the case in Francl et al. (2012a,b). Rarefaction helps address this complication. Half of the pre-decline bat species underwent greater declines than would be expected based on the smaller sample alone, suggesting an important role for taxonomic selectivity in WNS (Table 1). Notably, these findings confirm previous observations that species in the genus *Myotis* and *Perimyotis* are especially susceptible to the disease, which causes permanent and devastating tissue damage in these genera (Francl et al., 2011; Langwig et al., 2015; Reichard & Kunz, 2009). Importantly, our results also suggest the potential susceptibility of *Corynorhinus townsendii virginianus*, which is not generally recognized as vulnerable to the pathogen (Coleman & Reichard, 2014; Silvis, Perry, & Ford, 2016). Further, these results confirm recent findings that *E. fuscus* may have species-specific, trait-based resistance to WNS (Frank et al., 2014; Frank, Sitler-Elbel, Hudson, & Ingala, 2018), as its abundance was greater than expected post-decline.

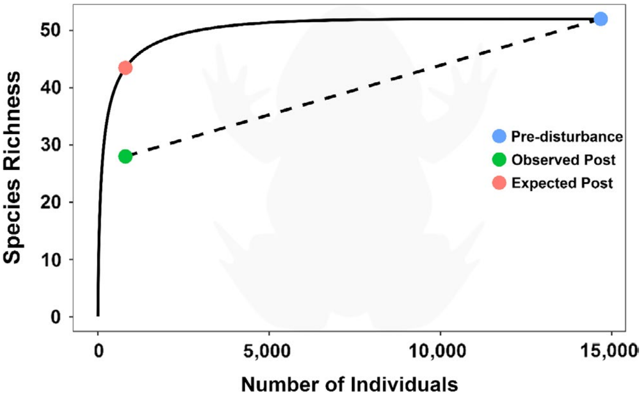

FIGURE 2 Comparison of expected species loss and observed species loss of amphibians in El Copé, Panama, after the introduction of chytrid fungus. Based on a total loss of 13,879 individuals, the rarefaction-based null model predicts a post-disturbance community richness of 43.5 species. Instead, there were 28 species after chytrid fungus appeared at El Copé, indicating a loss of richness greater than would be expected by neutrally stochastic processes and suggesting an important role for selectivity in chytrid-associated amphibian extirpations

3.2 | Amphibian chytrid and amphibians declines in a highly diverse community

We also analyse data documenting dramatic declines, extirpations, and extinctions of amphibians caused by the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (hereafter, *Bd*) in central Panama (Crawford, Lips, & Bermingham, 2010). The data include abundance data for amphibian species occurring in El Copé, Panama, collected throughout two sampling periods, one prior to the chytrid fungus epizootic (2000–2003) and one after (2007). Species lacking sufficient abundance data were excluded from the analyses (see Table S3, Crawford et al., 2010). Crawford et al. grouped species into four categories based on the severity of each species' decline between 2000–2003 and 2007 (Table S3, Crawford et al., 2010): Least Concern, Declined, Critical, and Extirpated. We compared these designations to our results based on p_e and p_{OD} values as produced by our rarefaction model. Our working hypothesis was that species with improbably large declines (i.e. low p_{OD} values) should be among those of greatest conservation concern and likely represent species that are selectively susceptible to *Bd*.

Over the 8-year sampling period, researchers identified 24 amphibian extirpations, while the rarefaction null model estimated only 8.5 expected extirpations based on the magnitude of the decline (Figure 2). This large difference between the expected number of extinctions and the actual number suggests an important role for species-specific susceptibility to *Bd*, a phenomenon that has been documented previously (Lips et al., 2003; Smith et al., 2009). Two factors could lead to there being more extinctions than expected based on population declines alone. First, common species with low null extinction probabilities may have been disproportionately susceptible to *Bd*, leading to unexpected extinctions. This was the case for three abundant species of *Pristimantis*, for example, *P. podiciferus* (125 individuals pre-chytrid, p_{OD} = .003) and *P. puntariolus* (877 individuals pre-chytrid, p_{OD} = 0), and *P. vocator* (47 individuals pre-chytrid, p_{OD} = .064). Each species had a low probability of observed decline (p_{OD}) and yet they were extirpated nonetheless, providing clear examples of the selective nature of these extirpations; even high local abundance did not protect these species from extirpation. Second, although rare species are randomly expected to be more susceptible to extinction than common species, phenomena such as Allee effects and extinction thresholds can lead to even more extinctions than would be expected based on rarity alone. Therefore, although it is easier to detect selectivity in common taxa (e.g. *Pristimantis* as described above) and it is never truly unexpected when rare species are extirpated, non-random extinction may also take the form of more rare species extinctions occurring than would be expected.

In addition to comparing expected and observed numbers of extinctions, we hypothesized that species that were selectively susceptible to *Bd*, seen as low p_{OD} values, should be those that are categorized as being at the greatest risk of extinction. Indeed, Crawford et al.'s categories of decline severity were statistically associated with p_{OD}; lower p_{OD} values were associated with more severe designation by Crawford et al. (Figure 3; Kruskal–Wallace test: $\chi^2 = 25.69$, $df = 3$, $p = .0005$). Despite this pattern, species were extirpated across a wide range of p_{OD} values. For example, *Colostethus pratti* (7 individuals pre-chytrid, p_{OD} = .675) and *Pristimantis taeniatus* (four individuals pre-chytrid, p_{OD} = .798) are two locally rare (in the context of the study) species that were extirpated, with concomitantly high probabilities of observed decline, suggesting that their extirpation is not surprising, given their low original abundances and the large loss of individuals from El Copé. *Colostethus pratti* is a regionally abundant species and has an IUCN conservation priority rating of 'Least Concern' (Gagliardo et al., 2008). Without the explicit acknowledgement of its small local population size, it would be easy to conflate this loss with evidence of selective extinction, under the assumption that this was an extirpation of a widely abundant species. Collectively, these results suggests that using p_{OD} values may be an efficient way to quickly and objectively convert observed declines into risk levels.

3.3 | Extinctions of endemic island gastropods

Our third case study focuses on extinction patterns among the endemic terrestrial gastropods of the Ogasawara archipelago (Bonin Islands) of Japan (Chiba & Roy, 2011a,b). Chiba and Roy

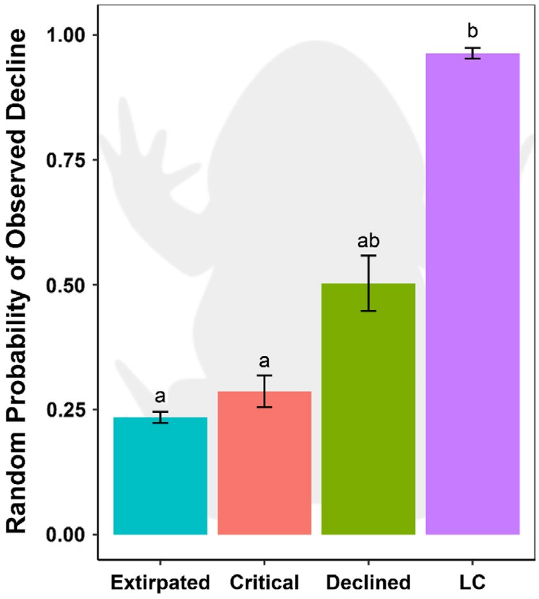

FIGURE 3 Probability of amphibian species declines as defined by the null model compared to decline categories defined by Crawford et al. Probabilities of species declines are defined as the likelihood of a species undergoing its observed decline or a decline due to chytrid fungus more severe than expected assuming only the random loss of individuals. Decline categories are assigned by Crawford et al. (ST02) and are listed in order of decreasing severity. p_{OD} differed significantly among decline category (Kruskal–Wallace test: $\chi^2 = 25.69$, $df = 3$, $p = .0005$); significant differences between groups are designated using different letters (Nemenyi-tests). Error bars represent standard error

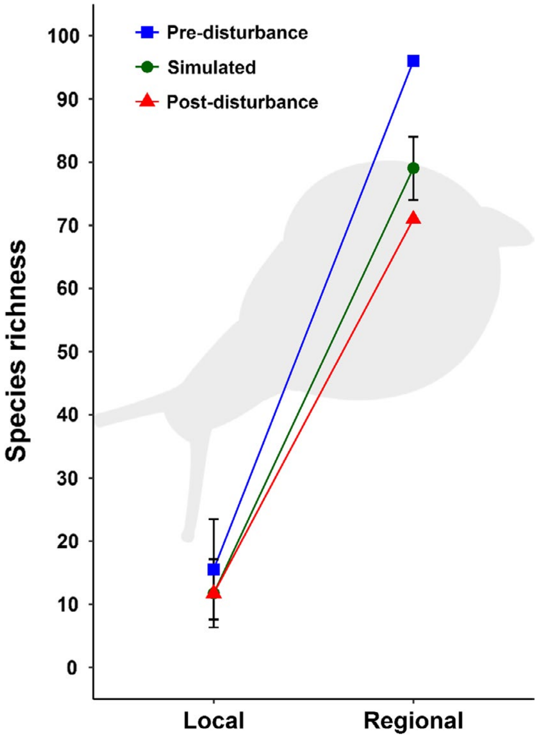

FIGURE 4 Regional scaling of changes in gastropod richness caused by anthropogenic threats. Local species richness is the mean number of species occurring at each site ($n = 16$) observed prior to and after anthropogenic-induced gastropod declines. Regional species richness is the total number of species that were present at any of the 16 islands. 95% confidence intervals are shown when applicable. Regional species richness was significantly lower in the post-survey than would be expected assuming only stochastic extinction processes (expected richness: 79.06; 95% CI: 74, 84; observed richness: 71)

applied a trait-based approach to identify extinction selectivity across two sampling periods (1987–1991 and 2004–2009). Unlike our previous case studies, the dataset does not include abundance data, but rather an index of range size based on occupancy among 16 islands in the archipelago. We therefore adapt rarefaction to these data by rarefying species richness on each island such that each species on each island has an equal local extinction probability (p_{eL}) defined by the proportion of species lost from that island. The product of our analysis was the probability of extinction at the regional level, p_{eR}, for each species (see Materials and Methods).

Across the two sampling periods, 25 of the original 96 species of gastropod disappeared from their entire range across the Ogasawara Islands (Chiba & Roy, 2011a,b). This is in contrast to the 17 regional extinctions predicted by rarefaction (Figure 4). Random extinction probability was a significant predictor of observed regional extinctions, which were concentrated among low-occupancy and endemic (single island) species (Figure 5; Logistic regression: OR = 1.12, $df = 95$, $p \sim 0$). Although rarefaction underestimated the number of gastropod extinctions, extinctions were concentrated among species with high p_{eR} values, that is, species with small range sizes that happened to overlap with high levels of disturbance (Figure 5). In contrast, widespread species with low predicted extinction probabilities almost universally survived, at least on some islands, and are therefore still extant (Figure 5).

Unique to this case study was the use of rarefaction using incidence data only. Although this requires the critical assumption of equiprobable local extinction probabilities for each species, we suggest that occupancy-based data can be used with caution in the absence of abundance data, provided an appropriate spatial scale to perform sample-based rarefaction (i.e. occupancy across sites is required). Rarefaction-based p_{eR} values strongly correspond with observed extinctions at the regional scale, suggesting an important role for occupancy/range size alone as a predictor of regional extinction in this system (Figure 5). We also find significantly more biodiversity loss than predicted by rarefaction, providing evidence that selective extinctions were also occurring (Figure 4). These differences were relatively modest, however, with 68% of the observed extinctions consistent with predictions from random species loss from islands. This case study highlights the value of assessing stochastic biodiversity loss via a rarefaction-based null model; while both random and non-random processes drive patterns of extinction in a community, inferring the dominance of either factor without considering the interplay between the two may lead to less robust characterizations of species risks of extinction.

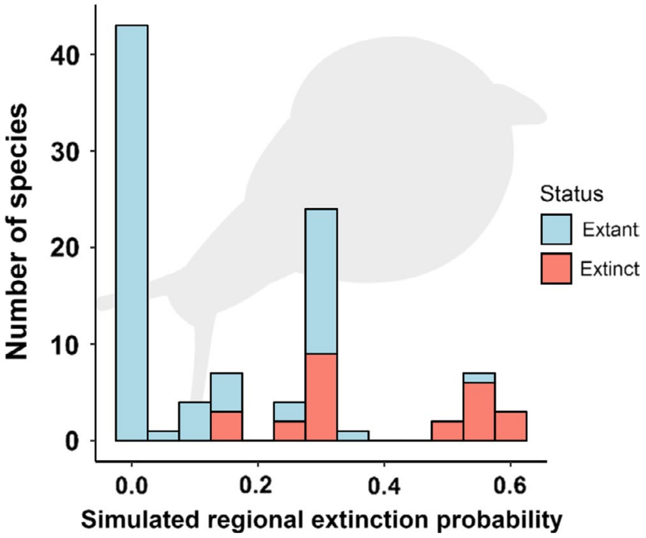

FIGURE 5 Distribution of simulated regional extinction probabilities grouped by observed gastropod extinction status in second sampling survey. Extinction probabilities are null-simulated p_e values representing a species' probability of going extinct based on observed declines in species richness if species losses were strictly random. Simulated risk of extinction is a significant predictor of whether species went extinct from the region (Logistic regression: OR = 1.12, $df = 95$, $p \sim 0$)

4 | DISCUSSION

If there is a first law of extinction, it is that rare species are more likely than common species to go extinct. This is a function of random probability (e.g. figure 1 and Simberloff, 1986) but also logic: to become extinct, even common species must first pass through rarity. And yet although rarity and random chance contribute to extinction, species abundance alone does not explain all extinctions, particularly during severe disturbances (Barnosky et al., 2011; Jablonski, 1991; Lockwood, Ross, & Sah, 2003). This confluence of random (abundance-based) and non-random (trait-based) mechanisms of extinction contributes to the difficulty of predicting extinctions (e.g. Tracy & George, 1992). We addressed this challenge by applying rarefaction to the study of extinctions. This approach allows us to generate null expectations for the number of extinctions based on abundance and random chance alone. These null expectations also allowed us to identify the signature of trait-based extinctions, based on the observed extinction of species with low random extinction probabilities (p_e). We extended this process to identify species declines that were unexpectedly large, allowing for the identification of non-random and putatively trait-based declines of individual species. Across several recent decline and extinction events, we find that although abundance and range size/occupancy do not fully explain patterns of extinction, stochastic processes play a prominent role in driving biodiversity loss, suggesting the disentanglement of stochastic and selective extinction events is necessary to evaluating species risk of extinction.

Our results confirm a primary role for stochastic processes in the extinction process, in that rare species are overwhelmingly likely to be the ones lost to extirpation or extinction as a result of ecological disturbances. In some ways, this is an unsurprising result that is consistent with global patterns of extinctions, which are dominated by rare species (Davies, Margules, & Lawrence, 2004; Diamond, 1989; Wood et al., 2017). While the importance of rarity to extinction is well known (Hedrick et al., 1996; Lande, 1993; Raup, 1981, 1992; Shaffer, 1981, 1994), the importance of stochastic extinction to species conservation is often underemphasized. It is important to note this finding does not suggest that scientists should deemphasize the importance of selective extinction events; trait-based approaches are foundational to our understanding of extinction (Fritz & Purvis, 2010; Jablonski, 1989; McKinney, 1997; McKinney & Lockwood, 1999; Pearson et al., 2014; Webb, Brook, & Shine, 2002) and the identification of non-random declines is essential to preventing future extinctions (Gaston, 2010; Gaston & Fuller, 2007, 2008; Lindenmayer et al., 2011). Rather, we propose that a conceptual shift is needed such that the relative influences of stochastic and selective processes on an extinction event are both considered.

Previous extinction studies have used a variety of alternative analytical approaches to account for the role rarity plays in driving biodiversity loss (Boyer, 2010; Green & Côté, 2014; McKinney, 1997). However, these studies differ from ours in that they account for rarity (e.g. in the forms of abundance, range size, endemism) in a trait-based framework, highlighting rarity as a 'trait' that can lead to selective extinction (Boyer, 2010; McKinney, 1997), or weighting model parameters by abundance as a covariate or nuisance variable (Green & Côté, 2014). In our view, these approaches inadvertently deemphasize the importance of random chance in the extinction process. While such approaches are analytically sound they imply that extinction is a strictly non-random process, which it is not. We also suggest that it is inappropriate to consider rarity (or commonness) a species trait; rather, it is the emergent outcome of the interaction between species traits and the environment. And yet rarity is still an essential component of extinction filters. Our approach therefore provides a method for disengtangling the random filtration of species based on rarity on the one hand and the trait-based, selective filtering of species on the other. Given that stochastic and selective processes act in tandem (Vellend et al., 2014), we cannot robustly characterize a disturbance as selective without addressing the influence of chance-based extinction on biodiversity.

The issue of whether extinctions are selective or stochastic is more than an academic distinction. The most common approach to estimating extinctions, the species-area method (e.g. Brooks et al., 2002), implicitly assumes that species will be lost randomly as habitat is lost. Importantly, the species-area method also makes no claim as to which species will be lost. Rarefaction by itself will also assume stochastic loss, but can provide insight as to which species are most likely to be lost based on the distribution of threat and each species' local abundance and regional occupancy. In our application of rarefaction as a method of analysing past extinctions we were able to identify unexpected species declines, extirpations, or extinctions. For example, three abundant species of *Pristimantis* that were extirpated after exposure to amphibian chytrid and the bat *C. townsendii virginianus*, which is not generally considered to be among the species most affected by white-nose fungus. These are examples of cases in which conservation managers will benefit the most from our suggested analyses. The early identification of non-random and unexpected extinctions is increasingly critical. Although managers are often prepared for the fact that rare species are at risk of extinction, identifying when common and widespread species are at risk is more of a challenge. Successfully doing so can provide essential information for deciding when scarce conservation resources are best applied to the surprising situations when common species are under threat of decline and extinction (Gaston, 2010; Gaston & Fuller, 2007, 2008; Lindenmayer et al., 2011).

Our approach has several potential management applications. First, when selective extinctions are identified, then they can be analysed for correlations with phylogenetic or trait similarity among taxa. These correlates of extinction risk (Boyer, 2010) potentially can be used to predict threat to similar species in other areas. This will be particularly important for identifying common or widespread species that may not be expected to suffer extinction owing to their abundance. Second, because our approach allows for the identification of larger-than-expected declines (via p_{OD}), selectivity can be identified before a species reaches its extinction threshold. This approach may be especially helpful in rapid response analyses, such as in response to emergent pathogens, the expansion of invasive species, or sudden environmental changes. As illustrated in our amphibian case study, p_{OD} values may also provide an efficient and objective way to place declining species in risk categories. Finally, although not illustrated here, rarefaction can also be applied in a prospective manner. For example, the estimated number of expected extinctions caused by habitat loss can be explored via rarefaction, for example, via a hypothetical loss of 50% of the individuals of a community. Although this would assume random processes alone, such an analysis would provide a minimum benchmark for an expected number of local extinctions and, importantly, the species most likely to be extirpated.

Overall, our rarefaction-based null model provides surprisingly informative minimum predictions for species risk of extinction in the absence of trait-based information. Being able to make use of existing information is critical to protecting global biodiversity (Forest, Crandall, Chase, & Faith, 2015). While this approach is not without limitations, its minimal data requirements and foundation in a widely used statistical technique suggest it can be a versatile reference point for the analysis of extinction events. Without disentangling the influence of stochastic processes from selection, we risk allocating resources towards species that may not be as vulnerable to global extinction as others. Ultimately, we propose that use of the rarefaction-based null model may provide biologists with a more robust understanding of why certain species go extinct while others survive and contribute to improved conservation decision-making.

ACKNOWLEDGEMENTS

We thank K. Lips and S. Chiba for sharing data used in this paper. K. Lips provided comments on an earlier version of this manuscript. This research benefited from discussions over the years with E. Biro, L. Woods, A. Boyer, and students in the spring 2019 offering of Diversity & Extinction Analysis at Davidson College (M. Begley, J. Clary, W. Goode, A. Lippert, S. Lowen, E. Sasser, E. Scott, M. Seagle, and L. Soifer). Carlos Vargas translated the abstract for the online version of this paper. This paper is based on work supported by Davidson College, the Davidson College Biology Department, the Davidson Research Initiative and the National Science Foundation under grant number DEB-1650554. Any opinions, findings and conclusions or recommendations expressed in this material are those of the authors and do not necessarily reflect the views of the National Science Foundation.

AUTHORS' CONTRIBUTIONS

K.G.S. developed the analyses, designed the study and wrote and edited the manuscript. R.J.A. performed the analyses and wrote and edited the manuscript. Both authors gave final approval for the publication of the manuscript.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.533534r (Smith & Almeida, 2019), except for the data used in our analysis of Crawford et al., 2010, as, while requested, we did not obtain permission to publicly archive these third party data. To request access to this dataset, author contact information can be found at https://biology.umd.edu/karen-lips.html.

ORCID

Kevin G. Smith https://orcid.org/0000-0001-9691-9625
Ryan J. Almeida https://orcid.org/0000-0003-3400-0052

REFERENCES

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., … Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, *471*(7336), 51–57. https://doi.org/10.1038/nature09678

Blehert, D. S., Hicks, A. C., Behr, M., Meteyer, C. U., Berlowski-Zier, B. M., Buckles, E. L., … Stone, W. B. (2009). Bat white-nose syndrome: An emerging fungal pathogen? *Science*, *323*(5911), 227–227. https://doi.org/10.1126/science.1163874

Boyer, A. G. (2010). Consistent ecological selectivity through time in Pacific island avian extinctions. *Conservation Biology*, *24*(2), 511–519. https://doi.org/10.1111/j.1523-1739.2009.01341.x

Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., Rylands, A. B., Konstant, W. R., … Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*, *16*(4), 909–923. https://doi.org/10.1046/j.1523-1739.2002.00530.x

Chiba, S., & Roy, K. (2011a). Selectivity of terrestrial gastropod extinctions on an oceanic archipelago and insights into the anthropogenic extinction process. *Proceedings of the National Academy of Sciences* *of the United States of America*, *108*(23), 9496–9501. https://doi.org/10.1073/pnas.1100085108

Chiba, S., & Roy, K. (2011b). Data from: Selectivity of terrestrial gastropod extinctions on an oceanic archipelago and insights into the anthropogenic extinction process. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.533534r

Coleman, J. T. H., & Reichard, J. D. (2014, December). Bat White-nose syndrome in 2014: A brief assessment seven years after discovery of a virulent fungal pathogen in North America. *Outlooks on Pest Management*, *25*, 374–377. https://doi.org/10.1564/v25_dec_08

Crawford, A. J., Lips, K. R., & Bermingham, E. (2010). Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of central Panama. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(31), 13777–13782. https://doi.org/10.1073/pnas.0914115107

Davies, K. F., Margules, C. R., & Lawrence, J. F. (2004). A synergistic effect puts rare, specialized species at greater risk of extinction. *Ecology*, *85*(1), 265–271. https://doi.org/10.1890/03-0110

Diamond, J. M. (1989). The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *325*(1228), 469–477. https://doi.org/10.1098/rstb.1989.0100

Forest, F., Crandall, K. A., Chase, M. W., & Faith, D. P. (2015). Phylogeny, extinction and conservation: Embracing uncertainties in a time of urgency. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1662), 20140002. https://doi.org/10.1098/rstb.2014.0002

Francl, K. E., Ford, W. M., Sparks, D. W., & Brack, V. (2012a). Capture and reproductive trends in summer bat communities in West Virginia: Assessing the impact of white-nose syndrome. *Journal of Fish and Wildlife Management*, *3*(1), 33–42. https://doi.org/10.3996/062011-JFWM-039

Francl, K. E., Ford, W. M., Sparks, D. W., & Brack, V. (2012b). Capture and reproductive trends in summer bat communities in West Virginia: Assessing the impact of white-nose syndrome. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.533534r

Francl, K. E., Sparks, D. W., Brack, V., & Timpone, J. (2011). White-nose syndrome and wing damage index scores among summer bats in the northeastern United States. *Journal of Wildlife Diseases*, *47*(1), 41–48. https://doi.org/10.7589/0090-3558-47.1.41

Frank, C. L., Michalski, A., McDonough, A. A., Rahimian, M., Rudd, R. J., & Herzog, C. (2014). The resistance of a North American bat species (*Eptesicus fuscus*) to white-nose syndrome (WNS). *PLoS ONE*, *9*(12), e113958. https://doi.org/10.1371/journal.pone.0113958

Frank, C., Sitler-Elbel, K., Hudson, A., & Ingala, M. (2018). The antifungal properties of epidermal fatty acid esters: Insights from white-nose syndrome (WNS) in bats. *Molecules*, *23*(8), 1986. https://doi.org/10.3390/molecules23081986

Frick, W. F., Pollock, J. F., Hicks, A. C., Langwig, K. E., Reynolds, D. S., Turner, G. G., … Kunz, T. H. (2010). An emerging disease causes regional population collapse of a common North American bat species. *Science*, *329*(5992), 679–682. https://doi.org/10.1126/science.1188594

Fritz, S. A., & Purvis, A. (2010). Selectivity in mammalian extinction risk and threat types: A new measure of phylogenetic signal strength in binary traits. *Conservation Biology*, *24*(4), 1042–1051. https://doi.org/10.1111/j.1523-1739.2010.01455.x

Gagliardo, R., Crump, P., Griffith, E., Mendelson, J., Ross, H., & Zippel, K. (2008). The principles of rapid response for amphibian conservation, using the programmes in Panama as an example. *International Zoo Yearbook*, *42*(1), 125–135. https://doi.org/10.1111/j.1748-1090.2008.00043.x

Gaston, K. J. (2010). Valuing common species. *Science*, *327*(5962), 154–155. https://doi.org/10.1126/science.1182818

Gaston, K. J., & Fuller, R. A. (2007). Biodiversity and extinction: Losing the common and the widespread. *Progress in Physical Geography*, *31*(2), 213–225. https://doi.org/10.1177/0309133307076488

Gaston, K. J., & Fuller, R. A. (2008). Commonness, population depletion and conservation biology. *Trends in Ecology & Evolution*, *23*(1), 14–19. https://doi.org/10.1016/j.tree.2007.11.001

Gotelli, N. J. (2001). Research frontiers in null model analysis. *Global Ecology and Biogeography*, *10*(4), 337–343. https://doi.org/10.1046/j.1466-822X.2001.00249.x

Gotelli, N. J., & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, *4*(4), 379–391. https://doi.org/10.1046/j.1461-0248.2001.00230.x

Gotelli, N. J., & Graves, G. R. (1996). *Null models in ecology*. Smithsonian Institution Press.

Green, S. J., & Côté, I. M. (2014). Trait-based diet selection: Prey behaviour and morphology predict vulnerability to predation in reef fish communities. *Journal of Animal Ecology*, *83*(6), 1451–1460. https://doi.org/10.1111/1365-2656.12250

Heck, K. L., van Belle, G., & Simberloff, D. (1975). Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*, *56*(6), 1459–1461. https://doi.org/10.2307/1934716

Hedrick, P. W., Lacy, R. C., Allendorf, F. W., & Soulé, M. E. (1996). Directions in conservation biology: Comments on Caughley. *Conservation Biology*, *10*(5), 1312–1320. https://doi.org/10.1046/j.1523-1739.1996.10051312.x

Hurlbert, S. H. (1971). The nonconcept of species diversity: A critique and alternative parameters. *Ecology*, *52*(4), 577–586. https://doi.org/10.2307/1934145

Jablonski, D. (1989). The biology of mass extinction: A palaeontological view. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *325*(1228), 357–368. https://doi.org/10.1098/rstb.1989.0093

Jablonski, D. (1991). Extinctions: A paleontological perspective. *Science*, *253*(5021), 754–757. Retrieved from http://www.jstor.org/stable/2879116

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, *142*(6), 911–927. https://doi.org/10.2307/2462690

Langwig, K. E., Hoyt, J. R., Parise, K. L., Kath, J., Kirk, D., Frick, W. F., … Kilpatrick, A. M. (2015). Invasion dynamics of white-nose syndrome fungus, Midwestern United States, 2012–2014. *Emerging Infectious Diseases*, *21*(6), 1023–1026. https://doi.org/10.3201/eid2106.150123

Lindenmayer, D. B., Wood, J. T., McBurney, L., MacGregor, C., Youngentob, K., & Banks, S. C. (2011). How to make a common species rare: A case against conservation complacency. *Biological Conservation*, *144*(5), 1663–1672. https://doi.org/10.1016/j.biocon.2011.02.022

Lips, K. R., Reeve, J. D., & Witters, L. R. (2003). Ecological traits predicting amphibian population declines in central America. *Conservation Biology*, *17*(4), 1078–1088. https://doi.org/10.1046/j.1523-1739.2003.01623.x

Lockwood, J. L., Ross, M. S., & Sah, J. P. (2003). Smoke on the water: The interplay of fire and water flow on Everglades restoration. *Frontiers in Ecology and the Environment*, *1*(9), 462–468. https://doi.org/10.1890/1540-9295(2003)001[0462:SOTWTI]2.0.CO;2

McKinney, M. L. (1997). Extinction vulnerability and selectivity: Combining ecological and paleontological views. *Annual Review of Ecology and Systematics*, *28*, 495–516. https://doi.org/10.1146/annurev.ecolsys.28.1.495. Retrieved from http://www.jstor.org/stable/2952502

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends* *in Ecology & Evolution*, *14*(11), 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Oksanen, J., Guillaume Blanchet, F., Friendly, M., Friendly, L. R., Legendre, P., McGlinn, D.… Wagner, H. (2019). vegan: Community Ecology Package. R package version 2.5-6. Retrieved from http://CRAN.R-project.org/package=vegan

Payne, J. L., Bush, A. M., Heim, N. A., Knope, M. L., & McCauley, D. J. (2016). Ecological selectivity of the emerging mass extinction in the oceans. *Science*, *353*(6305), 1284–1286. https://doi.org/10.1126/science.aaf2416

Pearson, R. G., Stanton, J. C., Shoemaker, K. T., Aiello-Lammens, M. E., Ersts, P. J., Horning, N., … Akçakaya, H. R. (2014). Life history and spatial traits predict extinction risk due to climate change. *Nature Climate Change*, *4*(3), 217–221. https://doi.org/10.1038/nclimate2113

R Core Team (2018). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Rabinowitz, D. (1981). Seven forms of rarity. In H. Synge (Ed.), *The biological aspects of rare plant conservation* (pp. 205–217). Chichester, UK: Wiley.

Raup, D. M. (1981). Extinction: Bad genes or bad luck? *Acta Geologica Hispanica*, *16*, 25–33.

Raup, D. M. (1992). *Extinction: Bad genes or bad luck?*. New York, NY: W. W. Norton & Company.

Raup, D. M. (1994). The role of extinction in evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *91*(15), 6758–6763. https://doi.org/10.1073/pnas.91.15.6758

Reichard, J. D., & Kunz, T. H. (2009, December). White-nose syndrome inflicts lasting injuries to the wings of little brown myotis (*Myotis lucifugus*). *Acta Chiropterologica*, *11*, 457–464. https://doi.org/10.3161/150811009X485684

Shaffer, M. L. (1981). Minimum population sizes for species conservation. *BioScience*, *31*(2), 131–134. https://doi.org/10.2307/1308256

Shaffer, M. L. (1994). Population viability analysis determining nature's share. In G. K. Meffe, & C. R. Carroll (Eds.), *Principles of Conservation Biology* (pp. 195–196). Sunderland, MA: Sinauer Associates.

Silvis, A., Perry, R., & Ford, W. M. (2016). *Relationships of three species of bats impacted by white-nose syndrome to forest condition and management* (Vol. *214*, pp. 1–48). Gen. Tech. Rep. SRS–214. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. Retrieved from https://www.fs.usda.gov/treesearch/pubs/52250

Simberloff, D. (1972). Properties of the rarefaction diversity measurement. *The American Naturalist*, *106*(949), 414–418. https://doi.org/10.1086/282781. Retrieved from http://www.jstor.org/stable/2459787

Simberloff, D. (1986). The proximate causes of extinction. In D. M. Raup & D. Jablonski (Eds.), *Dahlem workshop reports. Patterns and processes in the history of life* (pp. 259–276). Berlin, Germany: Springer-Verlaghttps://doi.org/10.1007/978-3-642-70831-2_14

Smith, K., & Almeida, R. (2019). Data from: Rarefaction as a conceptual framework for disentangling stochastic and selective extinctions. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.533534r

Smith, K. G., Lips, K. R., & Chase, J. M. (2009). Selecting for extinction: Nonrandom disease-associated extinction homogenizes amphibian biotas. *Ecology Letters*, *12*(10), 1069–1078. https://doi.org/10.1111/j.1461-0248.2009.01363.x

Tracy, C. R., & George, T. L. (1992). On the determinants of extinction. *The American Naturalist*, *139*(1), 102–122. https://doi.org/10.1086/285315

Vellend, M. (2010). Conceptual synthesis in community ecology. *The Quarterly Review of Biology*, *85*(2), 183–206. https://doi.org/10.1086/652373

Vellend, M., Srivastava, D. S., Anderson, K. M., Brown, C. D., Jankowski, J. E., Kleynhans, E. J., … Xue, X. (2014). Assessing the relative importance of neutral stochasticity in ecological communities. *Oikos*, *123*(12), 1420–1430. https://doi.org/10.1111/oik.01493

Verant, M. L., Bohuski, E. A., Richgels, K. L. D., Olival, K. J., Epstein, J. H., & Blehert, D. S. (2018). Determinants of *Pseudogymnoascus destructans* within bat hibernacula: Implications for surveillance and management of white-nose syndrome. *Journal of Applied Ecology*, *55*(2), 820–829. https://doi.org/10.1111/1365-2664.13070

Warnecke, L., Turner, J. M., Bollinger, T. K., Lorch, J. M., Misra, V., Cryan, P. M., … Willis, C. K. R. (2012). Inoculation of bats with European *Geomyces destructans* supports the novel pathogen hypothesis for the origin of white-nose syndrome. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(18), 6999–7003. https://doi.org/10.1073/pnas.1200374109

Webb, C. (2003). A complete classification of Darwinian extinction in ecological interactions. *The American Naturalist*, *161*(2), 181–205. https://doi.org/10.1086/345858

Webb, J. K., Brook, B. W., & Shine, R. (2002). What makes a species vulnerable to extinction? Comparative life-history traits of two sympatric snakes. *Ecological Research*, *17*(1), 59–67. https://doi.org/10.1046/j.1440-1703.2002.00463.x

Wood, J. R., Alcover, J. A., Blackburn, T. M., Bover, P., Duncan, R. P., Hume, J. P., … Wilmshurst, J. M. (2017). Island extinctions: Processes, patterns, and potential for ecosystem restoration. *Environmental Conservation*, *44*(4), 348–358. https://doi.org/10.1017/S0376892917 00039X

Woods, L. M., Biro, E. G., Yang, M., & Smith, K. G. (2016). Does regional diversity recover after disturbance? A field experiment in constructed ponds. *PeerJ*, *4*, e2455. https://doi.org/10.7717/peerj.2455

SUPPORTING INFORMATION

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

How to cite this article: Smith KG, Almeida RJ. When are extinctions simply bad luck? Rarefaction as a framework for disentangling selective and stochastic extinctions. *J Appl Ecol*. 2020;57:101–110. https://doi.org/10.1111/1365-2664.13510