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Disease alters macroecological patterns of North American bats

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ABSTRACT

Aim We investigated the effects of disease on the local abundances and distributions of species at continental scales by examining the impacts of white-nose syndrome, an infectious disease of hibernating bats, which has recently emerged in North America.

Location North America and Europe.

Methods We used four decades of population counts from 1108 populations to compare the local abundances of bats in North America before and after the emergence of white-nose syndrome to the situation in Europe, where the disease is endemic. We also examined the probability of local extinction for six species of hibernating bats in eastern North America and assessed the influence of winter colony size prior to the emergence of white-nose syndrome on the risk of local extinction.

Results White-nose syndrome has caused a 10-fold decrease in the abundance of bats at hibernacula in North America, eliminating large differences in species abundance patterns that existed between Europe and North America prior to disease emergence. White-nose syndrome has also caused extensive local extinctions (up to 69% of sites in a single species). For five out of six species, the risk of local extinction was lower in larger winter populations, as expected from theory, but for the most affected species, the northern long-eared bat (*Myotis septentrionalis*), extinction risk was constant across winter colony sizes, demonstrating that disease can sometimes eliminate numerical rarity as the dominant driver of extinction risk by driving both small and large populations extinct.

Main conclusions Species interactions, including disease, play an underappreciated role in macroecological patterns and influence broad patterns of species abundance, occurrence and extinction.

Keywords

Disease ecology, extinction risk, macroecology, population monitoring, *Pseudogymnoascus destructans*, white-nose syndrome.

INTRODUCTION

Abundance of organisms varies enormously both within and among species, and group sizes range from solitary individuals to aggregations of millions, which are often patchily distributed across seemingly suitable habitats. Although characterizing patterns in sociality, abundance and distribution has long fascinated ecologists, understanding the mechanisms that underlie these patterns remains challenging, in part due to the difficulty in quantifying species interactions across broad temporal and spatial scales (Brown & Maurer, 1989; Brown, 1999; Gaston & Blackburn, 2000; Smith *et al.*, 2008). Identifying the mechanisms that drive macroecological patterns can improve our understanding of the forces that shape ecological communities (Brown, 1995; Kerr *et al.*, 2007) and aids conservation by identifying species at risk of extinction (Johnson, 1998).

Infectious diseases are important conservation threats and produce effects at scales from individuals to ecosystems (Daszak *et al.*, 2000; Tompkins *et al.*, 2011). The fungal disease chytridiomycosis, for example, has caused population declines and extinctions of amphibian populations across the world (Lips *et al.*, 2006; Skerratt *et al.*, 2007; Kilpatrick *et al.*, 2010). The role of disease in shaping macroecological patterns has not been well documented, however. This is despite substantial theoretical work on the role of disease in population regulation and as a driver of extinction risk (Anderson & May, 1979; de Castro & Bolker, 2004) and empirical work on the population ecology of invasive species that have escaped their pathogens (Torchin *et al.*, 2003). Theory suggests that disease can regulate host abundance to much lower levels when transmission increases with host density (Anderson & May, 1979), but relatively few empirical examples exist of host regulation by disease (Hudson *et al.*, 1998; Hochachka & Dhondt, 2000) and none has examined the role of disease in regulating abundance for taxa across multiple continents. Disease can also drive species extinct if transmission does not decrease as hosts become rare, which can be caused by social interactions among hosts (e.g. mate-seeking), alternative hosts or abiotic reservoirs (de Castro & Bolker, 2004; McCallum, 2012). The importance of disease in determining macroecological patterns has been difficult to quantify, because host–pathogen dynamics are often difficult to isolate from other ecological factors that influence population abundance, especially at broad spatial scales. The introduction of a novel pathogen to a new continent can provide an opportunity to quantify the potential impact of disease on patterns of abundance and distribution.

White-nose syndrome (WNS), a multihost disease of hibernating bats caused by the fungal pathogen *Pseudogymnoascus destructans* (Blehert & Gargas) Minnis & D. L. Lindner (formerly *Geomyces destructans*), emerged in North America in 2006 (Blehert *et al.*, 2009). The disease is characterized by cutaneous infection (Meteyer *et al.*, 2009) during hibernation (Langwig *et al.*, 2015), disrupting natural torpor cycles and causing morbidity and mortality (Warnecke *et al.*, 2012). WNS caused massive initial declines in bat populations in the three years after it was first detected in North America (Frick *et al.*, 2010;

Langwig *et al.*, 2012). In contrast, although *P. destructans* infects numerous hibernating bat species throughout Europe there have been no reports of mass mortality, despite decades of population monitoring (Martínková *et al.*, 2010; Puechmaillé *et al.*, 2010, 2011a; Wibbelt *et al.*, 2013).

We used four decades of population-monitoring data across 1108 winter colonies of 16 hibernating bat species in North America and Europe to assess how the emergence of disease has altered local abundance patterns. We hypothesized that disease emergence would reduce the abundance of bats in eastern North America to levels similar to those in Europe, where the disease is endemic (Martínková *et al.*, 2010; Puechmaillé *et al.*, 2011a,b; Pikula *et al.*, 2012; Bandouchova *et al.*, 2014; Zukal *et al.*, 2014). We compared colony sizes in North America before and after the emergence of WNS to colony sizes in Europe, accounting for differences in habitat and climate, in order to determine the effects of disease on species abundance patterns. We also hypothesized that disease emergence would alter the distributions of species by causing local extinctions at hibernacula, and that the probability of local extinction through disease would be lower where colonies were larger prior to the disease's emergence.

MATERIALS AND METHODS

Species selection and estimating local abundance

No bat species occur in both North America and Europe, so we focused on species in the family Vespertilionidae, which has members from multiple genera on both continents (Fig. S1 in Supporting Information). We estimated local abundance for 10 species in Europe and six species in North America using annual counts of hibernating bats from 1976 to 2013 at 468 winter colonies in six US states where WNS has been present for at least four years (Vermont, New York, Pennsylvania, Maryland, West Virginia and Virginia) and 640 colonies in eight European countries (United Kingdom, Norway, the Netherlands, Belgium, France, Portugal, the Czech Republic and Bulgaria). Infections of *P. destructans* have been confirmed in bats in each of these European countries except Norway, where no surveys for the pathogen/disease have yet been completed. We use the term white-nose syndrome (WNS) to refer to the disease defined by cutaneous infection, as described by Meteyer *et al.* (2009).

We determined winter colony size by estimating the carrying capacity at a site from repeated annual surveys (5–26 annual surveys per site; mean, 8 surveys per site), using three different methods to account for differences in data availability (Fig. S2). We use colony size synonymously with local abundance to describe species-specific aggregations of individuals at a hibernation site. We estimated the carrying capacity rather than average counts in order to eliminate temporal trends (increasing or decreasing) in the raw count data (Frick *et al.*, 2010; Langwig *et al.*, 2012). We restricted analyses to sites where we had at least five annual counts, although this did not alter our qualitative conclusions (see data subset comparison below; Fig. S4). For sites where we had consecutive winter counts, we estimated the

carrying capacity for each species at each site with the discrete-time, density-dependent model $N_{t+1} \sim N_t + r \times N_t \times (1 - N_t/K)$, where N_t is the count in year t , and r and K are parameters fitted with a negative binomial distribution by maximum-likelihood estimation (Fig. S2a). For sites where we had non-consecutive year counts, we calculated the average of the upper quartile of counts (Fig. S2b). Finally, we estimated K at sites in eastern North America where WNS had been detected for at least three years by using the most recent count (Fig. S2c). Previous analyses suggested that most populations stabilized or were extirpated within four years of WNS being detected (Langwig *et al.*, 2012).

Data subset comparison

We restricted our analyses to sites with at least five annual counts in order to provide robust estimates of colony size that accounted for temporal trends in the raw data. If abundance at a site were to influence annual survey frequency, then restricting the data to well-sampled sites could introduce bias. For example, sites with large populations take substantial effort to count accurately and if large sites were therefore counted less frequently they could have been excluded from our analysis (e.g. a few large colonies of *Pipistrellus pipistrellus* were not included in our

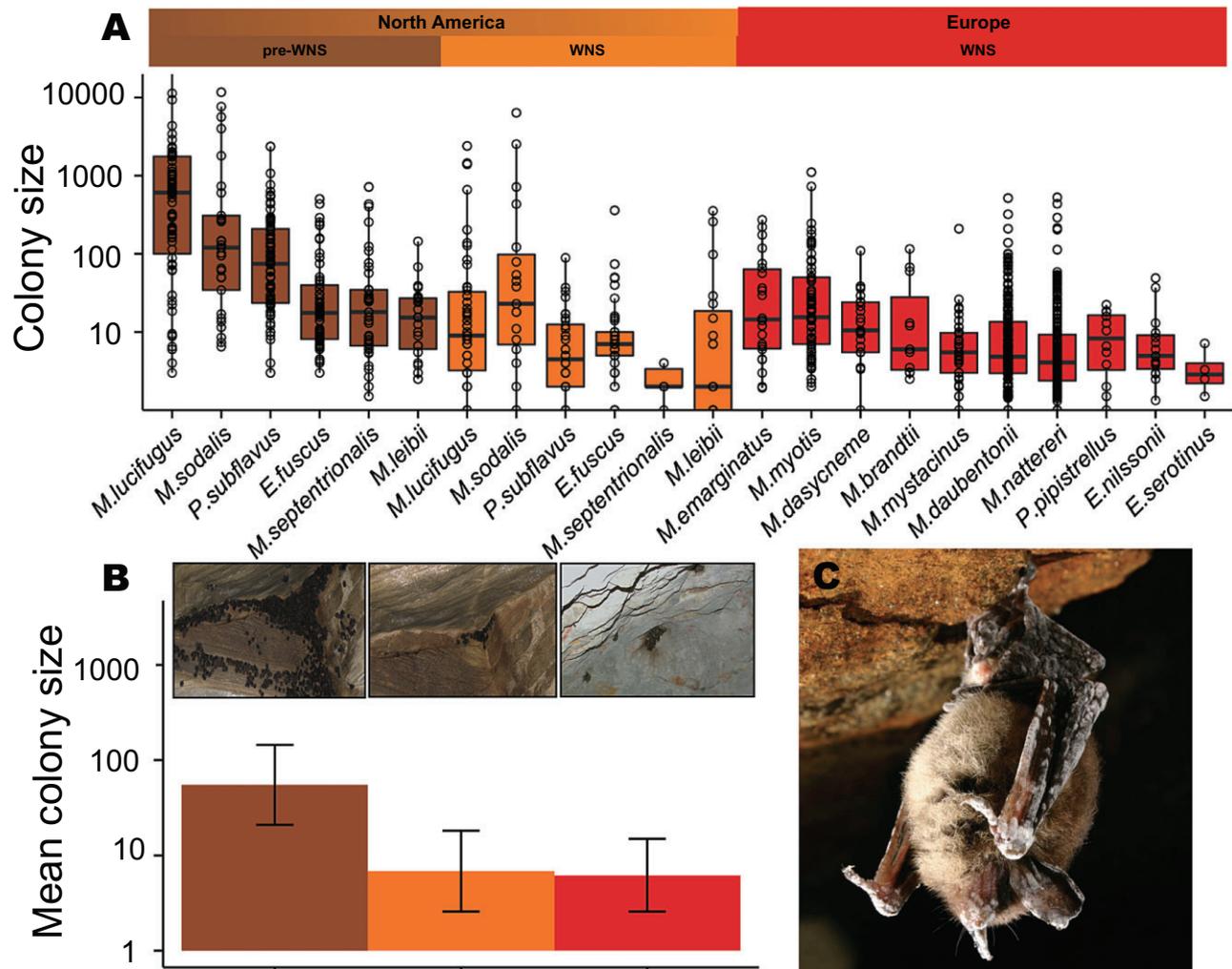


Figure 1 Changes in colony sizes of hibernating bats in North America, before and after the emergence of white-nose syndrome (WNS), compared to Europe. (a) Colony sizes of species in North America, before and after the emergence of WNS, compared to European species, where the disease is endemic. In each boxplot, box hinges show first and third quartiles, black horizontal lines show medians, and points are the estimated colony sizes. (b) Mean colony sizes for bat species in North America pre-WNS (brown), North America WNS (orange) and Europe WNS (red), calculated using the best-fitting model equation and continent-specific averages of ecological covariates measured at hibernacula. Error bars are standard errors. Photos above bars show representative aggregations of hibernating bats. From left to right: *Myotis lucifugus* hibernating in Vermont before WNS, the same colony after WNS, and *Myotis myotis* in the Czech Republic. (c) *Myotis septentrionalis* with WNS. This species is proposed for listing as endangered under the Endangered Species Act in the USA due to concerns about its global extinction risk from WNS. Photographs provided by A. Hicks and I. Horáček. Full species names are provided in Fig. S1.

dataset; Nagy & Szántó, 2003; Nagy & Postawa, 2010). Conversely, sites with small colonies may not be prioritized for sampling in areas where larger aggregations are available for population monitoring. We tested whether excluding infrequently sampled sites (fewer than five annual surveys) biased our comparison between North American and European abundances. We calculated an arithmetic mean of annual counts for colonies surveyed in fewer than five years ($n = 1728$). We fitted a linear mixed-effects model with dataset (full versus restricted) and continent as fixed effects, and site and species as random effects, and found qualitatively identical results to those from analyses using the more robust subset (Fig. S3).

Phylogenetic analysis

We created a pruned phylogenetic tree for the 16 species analysed (6 North American, 10 European; Fig. S1) and tested for phylogenetic signal in the species-abundance data based on this tree to examine whether abundance patterns were strongly influenced by phylogeny (Felsenstein, 1985). We retrieved sequences for the 16 focal species and six closely related or outgroup species from GenBank. The sequence data included the full cytochrome *b* mitochondrial gene (*cytb*; 1140 bp) and partial sequences of the recombination activator 2 gene (*RAG2*; 1151 bp). We retrieved both genes for all species, although some were not of full length and were completed with Ns. We conducted a Bayesian analysis in BEAST 1.7.5 using the Akaike information criterion in jMODELTEST 2.1.5, and determined GTR + Γ + I to be the best substitution model. We applied a strict molecular clock, did not specify an outgroup, and used the Yule process as a tree prior. The unweighted pair group method with arithmetic averages (UPGMA) was used to construct the starting tree. We ran 10,000,000 Markov chain Monte Carlo generations, sampling every 500 generations, and discarding the first 10% as burn-in. We performed three replicate analyses to ensure convergence, and combined the results of all three. We visually checked traces for convergence, and the effective sample sizes (ESS) of all parameters were greater than 800. We tested for phylogenetic signal in the species-abundance data using phylogenetically independent contrasts relative to tip-shuffling randomization (Blomberg *et al.*, 2003) using the 'phylosignal' function in the PICANTE package (Kembel *et al.*, 2010) in R 3.0.2 (R Core Team, 2013), and found no evidence of phylogenetic signal either before or after the emergence of WNS (European and North American pre-WNS, $K = 0.54$, $P = 0.42$; European and North American post-WNS, $K = 0.47$, $P = 0.64$). Although the number of species in our analysis is relatively low, reducing our ability to detect phylogenetic signal, the representation of members in multiple genera from both continents and the very weak evidence for phylogenetic signal ($P > 0.4$ in both cases) suggest that phylogeny is unlikely to be driving the observed patterns.

Habitat and climate covariates

To account for ecological factors that could influence local abundance at hibernation sites, we included eight variables

related to habitat and climatic conditions as covariates in our general linear mixed-effects model that compared abundances between North America, before and after WNS emergence, and Europe (Table S1). We measured habitat and climate variables within 140 km of a hibernaculum to represent the landscape that bats experience year-round, based on the distance between winter and summer colonies (Davis & Hitchcock, 1965; Hutterer *et al.*, 2005). We included five habitat variables related to bat activity and habitat use (Walsh & Harris, 1996; Gehrt & Chelvig, 2003; Mehr *et al.*, 2011; Akasaka *et al.*, 2012), including land cover of agriculture, forest and impervious surface area (a measure of urban area) as well as the surface areas of rivers and other bodies of water (Table S1). We used the total area of karst within the 140-km radius as an approximate measure of available hibernacula habitat. We note that bats also use anthropogenic structures, such as mines, tunnels and military bunkers for hibernacula in North America and Europe, but geographical data layers for mines and bunkers were not available at the geographical scope of this analysis. These structures are likely to constitute an important element of bats' winter habitat availability that is unaccounted for in our analysis. We used average annual temperatures and precipitation over the period 1950–2000 to characterize climate.

Statistical analyses

We compared local abundances in North America, both before and after WNS emerged, to those in Europe, using linear mixed-effects models with species and site as random effects, and con-

Table 1 Estimated model coefficients and standard errors from the best-fitting model and continent-specific means for each ecological variable used to estimate the mean abundance of six hibernating bats in North America prior to white-nose syndrome (WNS), in North America after WNS emergence, and in Europe, where the disease is endemic. Europe WNS was used as the reference group.

Model term	Coefficient	Std. error	Means	
			Europe	North America
Intercept – Europe WNS	–0.59	0.38		
North America WNS	–0.45	0.24		
North America pre-WNS	0.58	0.24		
Agriculture	5.24	0.85	0.49	0.04
Agriculture ²	–6.07	1.12	0.27	0.00
Forest	1.51	0.27	0.17	0.89
Impenetrable surface area	–0.16	0.05	4.39	2.84
Impenetrable surface area ²	0.02	0.01	21.44	12.65
Precipitation	0.03	0.01	66.85	102.07
Precipitation ²	0.00	0.00	4871	10434
(log ₁₀ River) ²	–0.06	0.01	32.06	28.15
(log ₁₀ Water) ²	0.08	0.01	15.48	13.35
log ₁₀ Karst	0.11	0.02	4.78	5.26

continent, disease and the ecological variables described above as fixed effects. We used manual backwards selection by removing parameters with t -values less than 2 – which corresponds to $P < 0.05$ for large sample sizes – to find the best-fitting model (Ramsey & Schafer, 2002). We used a likelihood-ratio test to compare the best-fitting model to a model without the group term of continent–WNS status, and Tukey’s honestly significant difference method (Crawley, 2007) for post-hoc independent contrasts among continent–disease groups (pre-WNS North America, WNS North America and WNS Europe). We estimated differences among groups using the best-fitting model equation and continent-specific means for each ecological variable measured at hibernacula. We also compared the variation in median abundances among species in North America, before and after WNS emergence, and species in Europe, using a modified robust Brown–Forsythe Levene-type test for homogeneity of variance using group medians (Ramsey & Schafer, 2002).

We analysed local extinctions in North America by fitting generalized linear models with a binomial distribution and logit

link to the presence or absence of each species three years after the detection of WNS at sites that were occupied by a given species for at least five years prior to the emergence of WNS. We compared five a priori candidate models (Table 2) to determine the influence of colony size and species effects on the probability of extinction. All statistical analyses were conducted in R 3.0.2 (R Core Team, 2013). We used the package *BBMLE* (Bolker & R Development Core Team, 2013) for maximum-likelihood estimation.

RESULTS

Species abundances

WNS caused an order-of-magnitude decrease in colony size within seven years of detection in North America and eliminated differences in local abundance between North America prior to WNS emergence and Europe (Fig. 1). The best-fitting model for explaining the variation in local abundance included

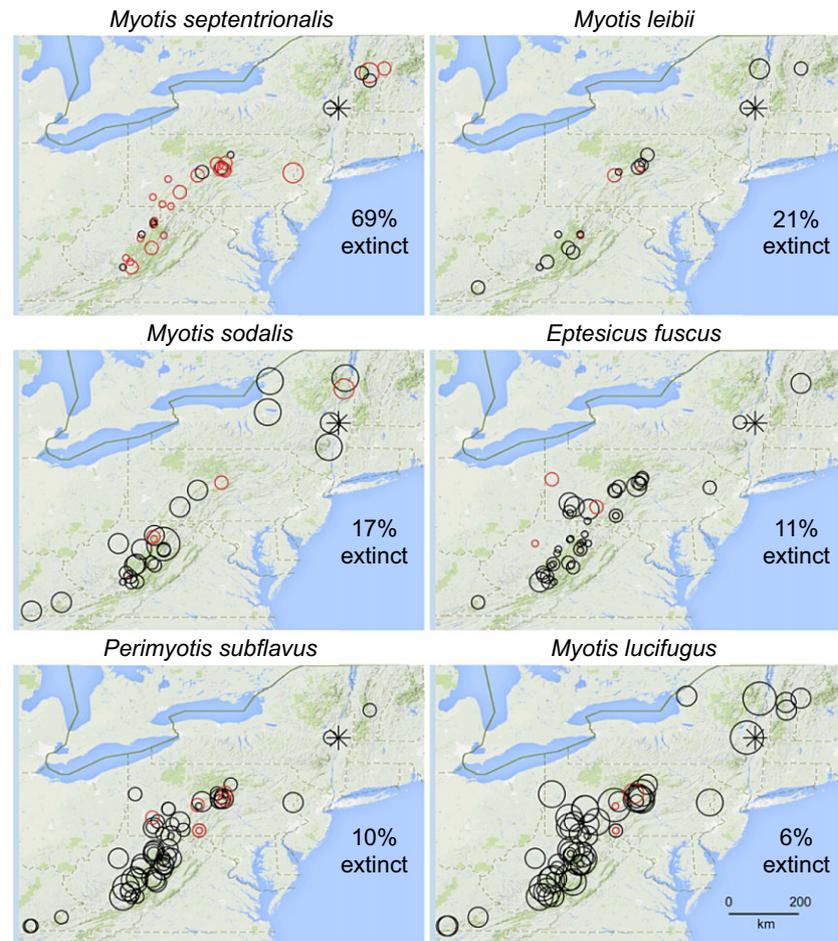


Figure 2 Local extinctions in six species of hibernating bats in North America seven years after white-nose syndrome (WNS) emerged in New York. Size of the circle indicates pre-WNS colony size; black circles are extant and red circles are extinct colonies. The black star shows where WNS emerged near Albany, New York, in 2006.



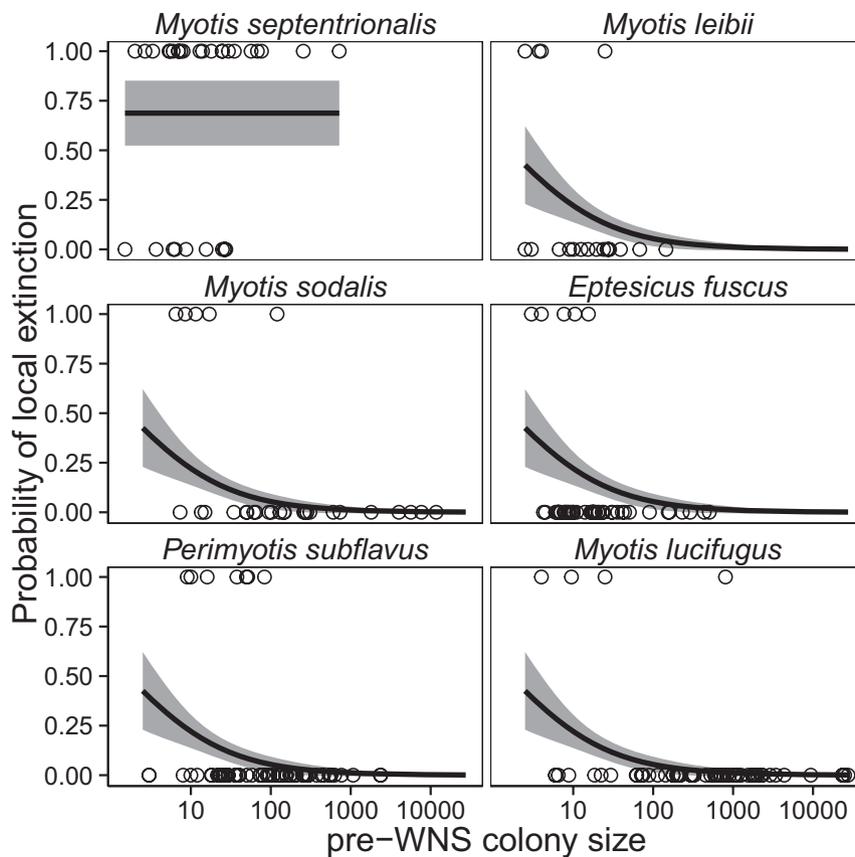


Figure 3 Probability of local extinction and local abundance of hibernating bats in North America. Line and 95% confidence bands show the fitted relationship [probability of extinction = $1/(1 + e^{0.33-1.59 \times \text{colony size}})$ where $a = 0.33-1.59 \times \text{colony size}$] for the five species where colony size influenced extinction probability, based on the best-fitting model after removing *M. septentrionalis* (Table 2).

seven habitat and climatic variables (Fig. S4, Table 1). There were continental differences in some land-cover types, including much higher forest cover and less agricultural area in eastern North America than in Europe (Fig. S4), but these were not sufficient to explain the continental differences in local abundance patterns (likelihood-ratio test of models with and without continent–disease: $\chi^2 = 244$, d.f. = 2, $P < 0.0001$). After accounting for mean habitat and climatic conditions, colony sizes were 10 times larger in eastern North America prior to WNS than in Europe (Tukey’s HSD, $P < 0.03$), whereas after WNS emergence, there was no significant difference between colony sizes in eastern North America and Europe (Tukey’s HSD, $P < 0.13$). Declines in median abundances occurred in all North American species and ranged from 60% to 98%.

Variation in median abundances among species in North America prior to WNS (variance = 0.40) was significantly greater than in Europe (variance = 0.06; Brown–Forsythe Levene test: 6.3, $P = 0.02$). The emergence of WNS in North America eliminated this difference between continents in the variation in median abundances between species (variance = 0.17, Brown–Forsythe Levene test: 2.0, $P = 0.18$).

Distributions and extinctions

Local extinctions occurred in all six species in North America, with the highest probability of extinction occurring in *Myotis septentrionalis* (Trouessart, 1897), which has disappeared from

69% of its former known hibernacula (Fig. 2). The probability of local extinction was significantly related to the colony size prior to the emergence of WNS for five of the six species affected by WNS, such that extinction probability was highest in colonies that were small before WNS emerged. In contrast, there was no significant relationship between pre-WNS colony size and extinction risk for *M. septentrionalis* (Fig 3., Table 2). The results from model comparisons after removing *M. septentrionalis* showed little support for the inclusion of a species term (Table 2), suggesting that the other five species exhibited the same relationship between probability of extinction and pre-WNS colony size.

DISCUSSION

The emergence of WNS altered the macroecological patterns of hibernating bats in North America by reducing local abundance by an order of magnitude and causing extensive local extinctions. The impact of WNS emergence on North American bats raises the question of whether hibernating bat colonies in Europe were substantially larger and more variable prior to the presence of the disease in Europe and, more broadly, whether disease is a hidden force behind macroecological patterns across continents in other taxa and regions. Furthermore, extensive local extinctions and predicted global extinction of *M. septentrionalis* due to WNS (Langwig *et al.*, 2012) highlights the possibility that past extinctions of bat species may have occurred when the disease first emerged in Europe.

Table 2 Influence of colony size and species differences on probability of extinction for six hibernating bats in North America. Best-fitting models in bold. Likelihood-ratio test (LRT) results shown for models with $\Delta\text{AIC} < 4$ from best-fitting model.

Model	AIC	χ^2 (d.f.)	LRT
All species included			
Pr(extinction) ~ species \times \log_{10} (pre-WNS colony size)	185.9		
Pr(extinction) ~ species + \log_{10}(pre-WNS colony size)	189.8	13.8 (5)	$P = 0.017^*$
Pr(extinction) ~ species	205.2		
Pr(extinction) ~ \log_{10} (pre-WNS colony size)	215.4		
Pr(extinction) ~ null	248.1		
Excluding <i>Myotis septentrionalis</i>			
Pr(extinction) ~ \log_{10} (pre-WNS colony size)	136.8		
Pr(extinction) ~ species + \log_{10}(pre-WNS colony size)	137.9	6.9 (4)	$P = 0.14^\dagger$
Pr(extinction) ~ species \times \log_{10} (pre-WNS colony size)	143.2		
Pr(extinction) ~ null	159.9		
Pr(extinction) ~ species	163.4		

*Likelihood-ratio test (LRT) P -value represents significant support for inclusion of the interaction term between species and \log_{10} (pre-WNS colony size). † LRT P -value represents no statistical support for inclusion of additive species effect.

Theory and extensive empirical work both suggest that small populations are generally at greater risk of extinction (Lande, 1993; Purvis *et al.*, 2000; de Castro & Bolker, 2004). We found that the probability of local extinction decreased with colony size for all six species, except *M. septentrionalis*, and those five species all showed the same relationship between local extinction and abundance, with larger colonies less likely to go locally extinct (Fig. 3, Table 2). Abundance prior to WNS detection had no significant effect on the probability of local extinction for *M. septentrionalis*. In fact, *M. septentrionalis* was subject to a much higher extinction probability than the two other species that had similar pre-WNS colony sizes: *M. leibii* Audubon & Bachman, 1842 and *Eptesicus fuscus* (Palisot de Beauvois, 1796) (Fig. 3). This result, which is at odds with theory on extinction risk from stochastic factors, is partly explained by previous work showing that the initial impacts of disease were greater in larger colonies of *M. septentrionalis* (Langwig *et al.*, 2012). Density-dependent declines in this species eliminated the influence of numerical rarity as a driver of extinction risk by making the probability of local extinction equally high for large and small colonies.

In addition to disease, colony sizes are also influenced by ecological, social and environmental differences between Europe and North America. Our comparisons accounted for some ecological factors related to bat–habitat interactions (Walsh & Harris, 1996; Mehr *et al.*, 2011), but other factors that influence local abundance (e.g. differences in roost quality and availability) were difficult to measure and could not be included. Nonetheless, the patterns shown here suggest that disease may indeed be an important driver of macroecological patterns and can rapidly alter local abundance patterns for a suite of species.

There are numerous examples of unexplained variation in the abundance of closely related and ecologically similar taxa across or between continents (Brown, 1995; Gaston & Blackburn, 2000; Smith *et al.*, 2008), and species distributions often have substantial gaps that are often difficult to explain with simple measures of climate, habitat or other abiotic factors. Species

interactions have been proposed as a possible cause for these differences in abundance and gaps in distributions, but their role is difficult to demonstrate due to their often invisible nature (Travis, 1996). Our results demonstrate how disease can be a strong force in shaping macroecological patterns by altering host abundances and distribution across sites at broad spatial scales.

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REFERENCES

- Akasaka, T., Akasaka, M. & Nakamura, F. (2012) Scale-independent significance of river and riparian zones on three sympatric *Myotis* species in an agricultural landscape. *Biological Conservation*, **145**, 15–23.
- Anderson, R.M. & May, R.M. (1979) Population biology of infectious diseases: part I. *Nature*, **280**, 361–367.
- Bandouchova, H., Bartonicka, T., Berkova, H., Brichta, J., Cerny, J., Kovacova, V., Kolarik, M., Köllner, B., Kulich, P., Martinkova, N., Rehak, Z., Turner, G.G., Zukal, J. & Pikula, J. (2014) *Pseudogymnoascus destructans*: evidence of virulent

- skin invasion for bats under natural conditions, Europe. *Transboundary and Emerging Diseases*, doi:10.1111/tbed.12282.
- Blehert, D.S., Hicks, A.C., Behr, M., Meteyer, C.U., Berlowski-Zier, B.M., Buckles, E.L., Coleman, J.T.H., Darling, S.R., Gargas, A., Niver, R., Okoniewski, J.C., Rudd, R.J. & Stone, W.B. (2009) Bat white-nose syndrome: an emerging fungal pathogen? *Science*, **323**, 227.
- Blomberg, S.P., Garland, T. & Ives, A.R. (2003) Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution*, **57**, 717–745.
- Bolker, B.M. & R Development Core Team (2013) *bbmle: tools for general maximum likelihood estimation*. Available at: <http://cran.r-project.org/package=bbmle> (accessed 20 September 2013).
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.
- Brown, J.H. (1999) Macroecology: progress and prospect. *Oikos*, **87**, 3–14.
- Brown, J.H. & Maurer, B.A. (1989) Macroecology: the division of food and space among species on continents. *Science*, **243**, 1145–1150.
- de Castro, F. & Bolker, B. (2004) Mechanisms of disease-induced extinction. *Ecology Letters*, **8**, 117–126.
- Crawley, M.J. (2007) *The R book*. John Wiley & Sons, Chichester, UK.
- Daszak, P., Cunningham, A.A. & Hyatt, A.D. (2000) Emerging infectious diseases of wildlife – threats to biodiversity and human health. *Science*, **287**, 443–449.
- Davis, W.H. & Hitchcock, H.B. (1965) Biology and migration of the bat, *Myotis lucifugus*, in New England. *Journal of Mammalogy*, **46**, 296–313.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *The American Naturalist*, **125**, 1–15.
- Frick, W.F., Pollock, J.F., Hicks, A.C., Langwig, K.E., Reynolds, D.S., Turner, G.G., Butchkoski, C.M. & Kunz, T.H. (2010) An emerging disease causes regional population collapse of a common North American bat species. *Science*, **329**, 679–682.
- Gaston, K.J. & Blackburn, T.M. (2000) *Patterns and process in macroecology*. Blackwell Science, Cambridge, UK.
- Gehrt, S.D. & Chelsvig, J.E. (2003) Bat activity in an urban landscape: patterns at the landscape and microhabitat scale. *Ecological Applications*, **13**, 939–950.
- Hochachka, W.M. & Dhondt, A.A. (2000) Density-dependent decline of host abundance resulting from a new infectious disease. *Proceedings of the National Academy of Sciences USA*, **97**, 5303–5306.
- Hudson, P.J., Dobson, A.P. & Newborn, D. (1998) Prevention of population cycles by parasite removal. *Science*, **282**, 2256–2258.
- Hutterer, R., Ivanova, T., Meyer-Cords, C. & Rodrigues, L. (2005) *Bat migrations in Europe: a review of banding data and literature*. Federal Agency for Nature Conservation, Bonn.
- Johnson, C.N. (1998) Species extinction and the relationship between distribution and abundance. *Nature*, **394**, 272–274.
- Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D.D., Blomberg, S.P. & Webb, C.O. (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, **26**, 1463–1464.
- Kerr, J.T., Kharouba, H.M. & Currie, D.J. (2007) The macroecological contribution to global change solutions. *Science*, **316**, 1581–1584.
- Kilpatrick, A.M., Briggs, C.J. & Daszak, P. (2010) The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends in Ecology and Evolution*, **25**, 109–118.
- Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, **142**, 911–927.
- Langwig, K.E., Frick, W.F., Bried, J.T., Hicks, A.C., Kunz, T.H. & Kilpatrick, A.M. (2012) Sociality, density-dependence and microclimates determine the persistence of populations suffering from a novel fungal disease, white-nose syndrome. *Ecology Letters*, **15**, 1050–1057.
- Langwig, K.E., Frick, W.F., Reynolds, R., Parise, K.L., Drees, K.P., Hoyt, J.R., Cheng, T.L., Kunz, T.H., Foster, J.T. & Kilpatrick, A.M. (2015) Host and pathogen ecology drive the seasonal dynamics of a fungal disease, white-nose syndrome. *Proceedings of the Royal Society B: Biological Sciences*, **282**, 20142335.
- Lips, K.R., Brem, F., Brenes, R., Reeve, J.D., Alford, R.A., Voyles, J., Carey, C., Livo, L., Pessier, A.P. & Collins, J.P. (2006) Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences USA*, **103**, 3165–3170.
- McCallum, H. (2012) Disease and the dynamics of extinction. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **367**, 2828–2839.
- Martínková, N., Bačkor, P., Bartonička, T. *et al.* (2010) Increasing incidence of *Geomyces destructans* fungus in bats from the Czech Republic and Slovakia. *PLoS ONE*, **5**, e13853.
- Mehr, M., Brandl, R., Hothorn, T., Dziöck, F., Förster, B. & Müller, J. (2011) Land use is more important than climate for species richness and composition of bat assemblages on a regional scale. *Mammalian Biology*, **76**, 451–460.
- Meteyer, C.U., Buckles, E.L., Blehert, D.S., Hicks, A.C., Green, D.E., Shearn-Bochsler, V., Thomas, N.J., Gargas, A. & Behr, M.J. (2009) Histopathologic criteria to confirm white-nose syndrome in bats. *Journal of Veterinary Diagnostic Investigation*, **21**, 411–414.
- Nagy, Z.L. & Postawa, T. (2010) Seasonal and geographical distribution of cave-dwelling bats in Romania: implications for conservation. *Animal Conservation*, **14**, 74–86.
- Nagy, Z.L. & Szántó, L. (2003) The occurrence of hibernating *Pipistrellus pipistrellus* (Schreber, 1774) in caves of the Carpathian Basin. *Acta Chiropterologica*, **5**, 155–160.
- Pikula, J., Bandouchova, H., Novotný, L., Meteyer, C.U., Zukal, J., Irwin, N.R., Zima, J. & Martínková, N. (2012) Histopathology confirms white-nose syndrome in bats in Europe. *Journal of Wildlife Diseases*, **48**, 207–211.
- Puechmaile, S.J., Verdeyroux, P., Fuller, H., Ar Gouilh, M., Bekaert, M. & Teeling, E.C. (2010) White-nose syndrome fungus (*Geomyces destructans*) in bat, France. *Emerging Infectious Diseases*, **16**, 290–293.

- Puechmaile, S.J., Wibbelt, G., Korn, V. *et al.* (2011a) Pan-European distribution of white-nose syndrome fungus (*Geomyces destructans*) not associated with mass mortality. *PLoS ONE*, **6**, e19167.
- Puechmaile, S.J., Frick, W.F., Kunz, T.H., Racey, P.A., Voigt, C.C., Wibbelt, G. & Teeling, E.C. (2011b) White-nose syndrome: is this emerging disease a threat to European bats? *Trends in Ecology and Evolution*, **26**, 570–576.
- Purvis, A., Gittleman, J.L., Cowlshaw, G. & Mace, G.M. (2000) Predicting extinction risk in declining species. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 1947–1952.
- R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
- Ramsey, F.L. & Schafer, D.W. (2002) *The statistical sleuth: a course in methods of data analysis*, 2nd edn. Duxbury Thomson Learning, Pacific Grove, CA.
- Skerratt, L.F., Berger, L., Speare, R., Cashins, S., McDonald, K.R., Phillott, A.D., Hines, H.B. & Kenyon, N. (2007) Spread of chytridiomycosis has caused the rapid global decline and extinction of frogs. *EcoHealth*, **4**, 125–134.
- Smith, F.A., Lyons, S.K., Ernest, S.K.M. & Brown, J.H. (2008) Macroecology: more than the division of food and space among species on continents. *Progress in Physical Geography*, **32**, 115–138.
- Tompkins, D.M., Dunn, A.M., Smith, M.J. & Telfer, S. (2011) Wildlife diseases: from individuals to ecosystems. *Journal of Animal Ecology*, **80**, 19–38.
- Torchin, M.E., Lafferty, K.D., Dobson, A.P., McKenzie, V.J. & Kuris, A.M. (2003) Introduced species and their missing parasites. *Nature*, **421**, 628–630.
- Travis, J. (1996) The significance of geographical variation in species interactions. *The American Naturalist*, **148**, S1–S8.
- Walsh, A.L. & Harris, S. (1996) Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. *Journal of Applied Ecology*, **33**, 519–529.
- Warnecke, L., Turner, J.M., Bollinger, T.K., Lorch, J.M., Misra, V., Cryan, P.M., Wibbelt, G., Blehert, D.S. & 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 USA*, **109**, 6999–7003.
- Wibbelt, G., Puechmaile, S.J., Ohlendorf, B., Mühldorfer, K., Bosch, T., Görföl, T., Passior, K., Kurth, A., Lacreman, D. & Forget, F. (2013) Skin lesions in European hibernating bats associated with *Geomyces destructans*, the etiologic agent of white-nose syndrome. *PLoS ONE*, **8**, e74105.
- Zukal, J., Bandouchova, H., Bartonička, T., Berkova, H., Brack, V., Brichta, J., Dolinay, M., Jaron, K.S., Kovacova, V., Kovarik, M., Martínková, N., Ondracek, K., Reháček, Z., Turner, G.G. & Pikula, J. (2014) White-nose syndrome fungus: a generalist pathogen of hibernating bats. *PLoS ONE*, **9**, e97224.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Phylogeny of European and North American bat species.

Figure S2 Three methods used to estimate winter colony size in bat populations.

Figure S3 Comparison of mean winter colony sizes for restricted and full datasets.

Figure S4 Ecological variables associated with variation in winter colony size.

Table S1 Ecological variables used in analysing local abundances.

BIOSKETCH

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