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The Threat of Disease Increases as Species Move Toward Extinction

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Abstract: *At local scales, infectious disease is a common driver of population declines, but globally it is an infrequent contributor to species extinction and endangerment. For species at risk of extinction from disease important questions remain unanswered, including when does disease become a threat to species and does it co-occur, predictably, with other threats? Using newly compiled data from the International Union for Conservation of Nature (IUCN) Red List, we examined the relative role and co-occurrence of threats associated with amphibians, birds, and mammals at 6 levels of extinction risk (i.e., Red List status categories: least concern, near threatened, vulnerable, endangered, critically endangered, and extinct in the wild/extinct). We tested the null hypothesis that the proportion of species threatened by disease is the same in all 6 Red List status categories. Our approach revealed a new method for determining when disease most frequently threatens species at risk of extinction. The proportion of species threatened by disease varied significantly between IUCN status categories and linearly increased for amphibians, birds, and all species combined as these taxa move from move from least concern to critically endangered. Disease was infrequently the single contributing threat. However, when a species was negatively affected by a major threat other than disease (e.g., invasive species, land-use change) that species was more likely to be simultaneously threatened by disease than species that had no other threats. Potential drivers of these trends include ecological factors, clustering of phylogenetically related species in Red List status categories, discovery bias among species at greater risk of extinction, and availability of data. We echo earlier calls for baseline data on the presence of parasites and pathogens in species when they show the first signs of extinction risk and arguably before.*

Keywords: endangered, infectious disease, IUCN, parasite, pathogen, threatened species

La Amenaza de Enfermedades Incrementa a Medida que las Especies se Aproximan a la Extinción

Resumen: *En escalas locales, las enfermedades infecciosas son un factor común en la declinación de poblaciones, pero a nivel global no contribuyen frecuentemente a la extinción de especies. Para especies en riesgo de extinción por enfermedad preguntas importantes permanecen si respuesta, incluyendo ¿cuándo se convierte una enfermedad en amenaza para las especies? y ¿ocurre al mismo tiempo, predeciblemente, con otras amenazas? Utilizando datos recientemente compilados por la Lista Roja de la Unión Internacional para la Conservación de la Naturaleza (UICN), examinamos el papel relativo y la co-ocurrencia de amenazas asociadas con anfibios, aves y mamíferos en 6 niveles de riesgo de extinción (i.e., categorías de estatus de la Lista Roja: menor preocupación, casi amenazada, vulnerable, en peligro, en peligro crítico y extintas en la naturaleza/extinta). Probamos la hipótesis nula de que la proporción de especies amenazadas por enfermedades es la misma en las 6 categorías de estatus de la Lista Roja. Nuestro enfoque reveló un método nuevo para determinar cuando las enfermedades amenazan más frecuentemente a especies en riesgo de extinción. La proporción de especies amenazadas por enfermedades varió significativamente entre categorías de estatus de la UICN y decreció linealmente para anfibios, aves y todas las especies combinadas a medida*

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que estos taxa se mueven de menos preocupación a en peligro crítico. Las enfermedades no fueron la única amenaza involucrada. Sin embargo, cuando una especie era afectada negativamente por una amenaza mayor diferente a una enfermedad (e.g., especies invasoras, cambio de uso de suelo) fue más probable que esa especie estuviera amenazada simultáneamente por una enfermedad que especies que no tenían otras amenazas. Los factores potenciales de estas tendencias incluyen aspectos ecológicos, agrupamiento de especies relacionadas filogenéticamente en categorías de estatus de la Lista Roja, sesgo de descubrimiento entre especies con mayor riesgo de extinción y la disponibilidad y limitaciones de los datos. Hacemos eco en los llamados anteriores de datos de base sobre la presencia de parásitos y patógenos en especies cuando muestran las primeras señales de riesgo de extinción, incluso antes.

Palabras Clave: enfermedad infecciosa, en peligro, especies amenazadas, parásito, patógeno, UICN

Introduction

Despite imperfect and relatively few data on the diversity and abundance of pathogens and parasites (we use these terms interchangeably) in wild populations, recent strides have been made to quantify the role of infectious disease in species extinction. At local scales infectious disease is a common driver of temporary or permanent population declines (de Castro & Bolker 2005; Pedersen et al. 2007; Smith et al. 2009*a*). Globally, however, infectious disease (hereafter disease) appears to be an infrequent driver of species extinction or endangerment (Smith et al. 2006). A 2004 analysis of the International Union for Conservation of Nature (IUCN) Red List showed that disease was a contributing threat in <4% of known species extinctions since 1500, and <8% of critically endangered species (Smith et al. 2006). The minor role of disease as a driver of species extinction is in sharp contrast to the roles of invasive species, habitat destruction, and overexploitation in driving extinction, each of which are cited (alone and in combination with other threats) as causing 45–54% of well-documented animal extinctions (Clavero & Garcia-Berthou 2005; Hoffmann et al. 2010; IUCN 2011). Nevertheless, some diseases pose substantial threats to certain taxonomic groups: chytridiomycosis in amphibian species worldwide (Daszak et al. 1999; Schloegel et al. 2006; Hof et al. 2011), avian pox and avian malaria in Hawaii's native avifauna (Atkinson et al. 1995), facial tumor disease in the Tasmanian devil (*Sarcophilus harrisii*) (Jones et al. 2007), fibropapillomatosis in green sea turtles (*Chelonia mydas*) (Van Houtan et al. 2010), and white-nose syndrome in 6 species of North American bats (Blehert et al. 2009; Foley et al. 2011).

Basic theory predicts diseases should drive species to extinction when pre-epidemic population size is small, transmission is frequency dependent, reservoir hosts are available, or the pathogen can survive in the environment for long periods or under a range of abiotic conditions (de Castro & Bolker 2005; Smith et al. 2009*b*). The latter is an especially concerning characteristic of a growing number of pathogenic fungi that currently threaten wildlife and domesticated species worldwide (Fisher et al. 2012). For many pathogens, transmission rates decline with decreasing host population size to the extent that directly transmitted parasites and pathogens may be lost if a host population drops below a particular threshold density (Anderson & May 1986; McCallum & Dobson 1995). Following this logic, species on the verge of extinction should harbor relatively few pathogenic species, a situation consistent with a study of Red Listed primates, the results of which show total parasite species richness is significantly lower among threatened compared with nonthreatened species (Altizer et al. 2007). Although this study did not distinguish between parasites that are known threats to primates and those simply identified as present in a population, the results, in combination with those described above, suggest the effect of a single pathogenic species may be all that is required to tip a host toward extinction. Therefore, 2 questions arise: when does disease become a threat to species on the road to extinction and does it co-occur predictably with other threats?

On the one hand, one might expect diseases to more commonly threaten host species early in the extinction process (i.e., least concern or near threatened species), when populations are still large enough to sustain transmission and encounter a greater pool of potential pathogens (Anderson & May 1986; McCallum & Dobson 1995). On the other hand, disease may be a more common threat among endangered species whose populations are reduced in terms of genetic diversity and absolute abundance and are likely stressed from other threats that predispose them to infection (O'Brien & Evermann 1988; Aguirre & Tabor 2008). For example, amphibians affected by land-use change and climate change may be more likely to face threats from disease (Hof et al. 2011). Disease may also become a substantial threat to a species following the onset of other threats. For example, invasive animals are predators on a large number of Red Listed species but also have the potential to harbor parasites and pathogens that could spread to and establish in native animal populations (Gurevitch & Padilla 2004; de Castro & Bolker 2005; Smith & Carpenter 2006).

It is difficult to determine the onset and sequence of events that drive species towards extinction. In part, this is due to a lack of long-term data on the changing conditions in the native ranges of species and on the pool of parasites and pathogens species harbor (Plowright et al.

2008). Preliminary insight may be gained, however, by examining the relative role and co-occurrence of threats associated with groups of species at varying levels of extinction risk (e.g., least concern vs. near threatened vs. vulnerable vs. endangered vs. critically endangered species). We used Red List data on amphibians, birds, and mammals to gain new insight into global trends in disease threats to wildlife. First, we examined whether the proportion of species threatened by disease varies among 7 Red List status categories (least concern to extinct). We used this proportion to consider when in the process of extinction disease becomes a contributing threat. We then determined the other threats that co-occur with disease and which of these threats increased the likelihood that a species would be threatened by disease.

Methods

The IUCN Red List does not provide a simple means of assessing temporal trends in disease, or other threats, for individual species over time. However, Red List data can be used to calculate variation in the relative occurrence of a given threat between status categories for groups of species. We searched the Red List for amphibian, bird, and mammal species listed in the following status categories: least concern, near threatened, vulnerable, endangered, critically endangered, extinct in the wild, and extinct for assessment years 1996–2011 (n = 19,378 species). We selected amphibians, birds, and mammals as our focal taxa because they are the most represented classes in the IUCN Red List and arguably the best studied taxonomic groups (Baillie et al. 2004). Following established methods (Smith et al. 2006), we read each species account in full to identify those for which disease is a purported threat. We considered disease a threat if the species account included one or more of the following terms (or related variations): *pathogen, parasite, disease, virus, bacteria, malaria, pox, infection, helminth, protozoa, protista, endoparasite, ectoparasite*, *fungus* or *fungi*. We identified 917 Red List species as potentially threated by disease (554 amphibians, 190 birds, and 173 mammals) (Supporting Information).

Because the Red List does not categorize threats on the basis of strength of supporting evidence (Smith et al. 2006; Heard et al. 2011), each species account must be read in full to determine which threats are based on evidence and which are hypothesized to be current or future threats (Smith et al. 2006). We classified each of the 917 species purportedly threatened by disease into the following 2 groups: evidence-based threat of disease (disease is a confirmed historical or present threat) or hypothesized threat of disease (disease is hypothesized to be a current threat but there is no evidence to support the claim, ongoing research is attempting to discern the threat of disease, or disease may pose a threat in the future). Of the 19,378 Red Listed species we examined, 1.2% (240 species including 83 amphibians, 43 birds, and 114 mammals) were in the evidenced-based threat category (26% of 917 disease-threatened species) and 3.5% (677 species including 471 amphibians, 147 birds, and 49 mammals) were in the hypothesized-threat category (74% of 917 disease-threatened species). Analyses were initially conducted for all species (evidence + hypothesized threat of disease) and those with just evidence of a disease threat. However, results for both groupings were quantitatively and qualitatively similar, so we present only results from the group for which there was an evidence-based threat of disease (240 species). See Supporting Information for analyses including the hypothesized species.

We tested the null hypothesis that the proportion of species threatened by disease is the same in each Red List status category. We used ordinal chi-square analyses to test this hypothesis (Agresti et al. 1990; Agresti 1996). This approach is ideal because Red List categories represent a directional increase in threat level as species move toward being critically endangered. We determined the number of species threatened and not threatened by disease in each Red List status category to determine whether the proportion of species affected by disease differs among status categories. Least concern species are not considered at risk of extinction, but have not been assessed at the same level as those that are (near threatened, vulnerable, endangered, critically endangered). Because they are qualitatively different from the other status categories, we ran all analyses with and without least-concern species. We also excluded extinct species and those extinct in the wild from analyses because these categories are also qualitatively different from other status categories in several ways. First, these categories are unique in that they do not reflect a specific intermediate stage in the extinction process, but rather a temporal endpoint. Second, threats reported in the Red List for extinct species include all threats ever known to the species and do not specify when they affected the species or whether threats were removed between assessments. Although threats can differ between assessments, either by being added or deleted (making threats specific to the current status category [Butchart et al. 2005]), this is not so for extinct species. There were too few extinct species and species extinct in the wild with actual evidence of disease being a threat to warrant including them in analyses.

To contextualize our findings for disease, we also examined whether the proportion of species affected by other threats varied between Red List status categories. Currently, there are more than 12 potential threats listed in the Red List, each has at minimum 3 additional subcategories. For ease of investigation, because our Red List research was done manually, we created 6 general categories of threats from the original 12: (1) land-use change, (2) overexploitation, (3) invasive or problematic species, (4) pollution, (5) geological events, and (6) climate change or severe weather. We collectively defined IUCN Red List threat categories 1–4, 6–7, and 5.2 and 5.3 as land-use change (5.2 and 5.3 because we did not assess plants in this study, but these threats, gathering plants and logging, may affect animal species). Our categories for invasive or problematic species, pollution, geological events, climate change, or severe weather paralleled IUCN established categories. Disease is sometimes considered an invasive or problematic threat, although this determination is not predictable. For species threatened by invasive or problematic species, we removed those from analyses if the only threat identified under the invasive or problematic listing was disease. The IUCN threat categories 5.1 and 5.4 refer to animal exploitation either as intentional or accidental. We grouped these categories together as overexploitation. On the basis of the IUCN accounts, we identified which of the 6 threats most frequently co-occurred with disease. We calculated the proportion of the 240 species with evidence of a disease threat that were also threatened by each of the 6 additional threats. The Red List does not determine the order in which threats manifest. However, it is possible to determine the correlative strength of co-occurring threats. We examined whether being affected by any of the 6 nondisease threats increased the probability of a species being threatened by disease.

We used odds ratios, common to epidemiological studies (Woodward 2005; Merrill 2010), to estimate the strength of association between a categorical outcome, in this case the occurrence of a disease threat, and factors suspected of contributing to the odds of the outcome, in this case the 6 nondisease threats. This method has been recently used in other conservation biology and ecology studies to evaluate the effects of multiple stressors on threatened species (Davidson & Knapp 2007; Johnson et al. 2008; Witte et al. 2008). We used the odds ratio to determine whether being threatened by any of the 6 major threats in the Red List increased the likelihood of also being threatened by disease. Odds ratios were calculated for each of the 6 threats using the following example formula for land-use change: (number of species threatened by disease and land-use change divided by number of species not threatened by disease, but threatened by land-use change) divided by (number of species threatened by disease, but not by land-use change divided by number of species not threatened by disease or land-use change). Statistical evaluations of odds ratios incorporated Fisher's Exact Test. Analyses were conducted separately for amphibians, birds, mammals, and all species.

Results

The proportion of species affected by disease varied significantly between Red List status categories for amphibians ($\chi^2 = 56.7$, $P < 0.0001$), birds ($\chi^2 = 137.0$, $P < 0.0001$), mammals ($\chi^2 = 61.2$, $P < 0.0001$), and all species ($\chi^2 = 188.2$, $P < 0.0001$) (Fig. 1). For amphibians, birds, and all species, the proportion of species threatened by disease increased linearly and significantly as status category increased from near threatened to critically endangered (Fig. 1). For mammals, the relation between disease threat and status category was nonlinear; the highest proportion of mammals affected by disease was in the endangered category (Fig. 1). Exclusion of species in the least concern category from our analyses did not change the statistical trends we observed.

The proportion of species affected by the 6 other major threats differed among Red List categories for all species: land-use change ($\chi^2 = 8199.7$, $P < 0.0001$), overexploitation ($\chi^2 = 1802.1$, $P < 0.0001$), invasive or problematic species ($\chi^2 = 2720.4$, $P < 0.0001$), pollution ($\chi^2 = 832.6$, $P < 0.0001$), geological events ($\chi^2 = 258.4$, $P < 0.0001$), and climate change or severe weather ($\chi^2 = 776.1$ $P < 0.0001$) (Fig. 2). The proportion of species threatened by invasive or problematic species, pollution, geological events, and climate change or severe weather, increased linearly as status category increased from near threatened to critically endangered (Fig. 2). Land-use change and overexploitation showed no clear directional trends (Fig. 2). Again, exclusion of species of least concern did not change our statistical results.

Disease was infrequently the sole threat to Red List species (1.3% of all species with disease) (Table 1). Land-use change was the most common threat that co-occurred with disease; it threatened amphibians, birds, and mammals nearly equally. The second most common co-occurring threat was unique to each taxonomic group (Table 1). For amphibians, birds, mammals and all species combined, the occurrence of any major threat increased the likelihood of also being threatened by disease (Fig. 3). However, no single threat appeared to uniformly increase the likelihood of disease also being a threat (for individual taxonomic groups or all species combined) (Fig. 3).

Discussion

Despite recent updates to the IUCN Red List, evidence for the role of disease as a major threat to species at risk of extinction remains scant. Earlier work revealed supporting evidence in less than half of the critically endangered species, with disease listed as a threat in the 2004 Red List (Smith et al. 2006). Results of our analyses suggest little progress has been made to acquire evidence for many hypothesized disease-induced species declines because only 26% (240 species) of the 917 species we examined had disease listed as a driver of extinction and contained evidence of an actual disease threat (Supporting Information). The listing of hypothesized, ongoing,

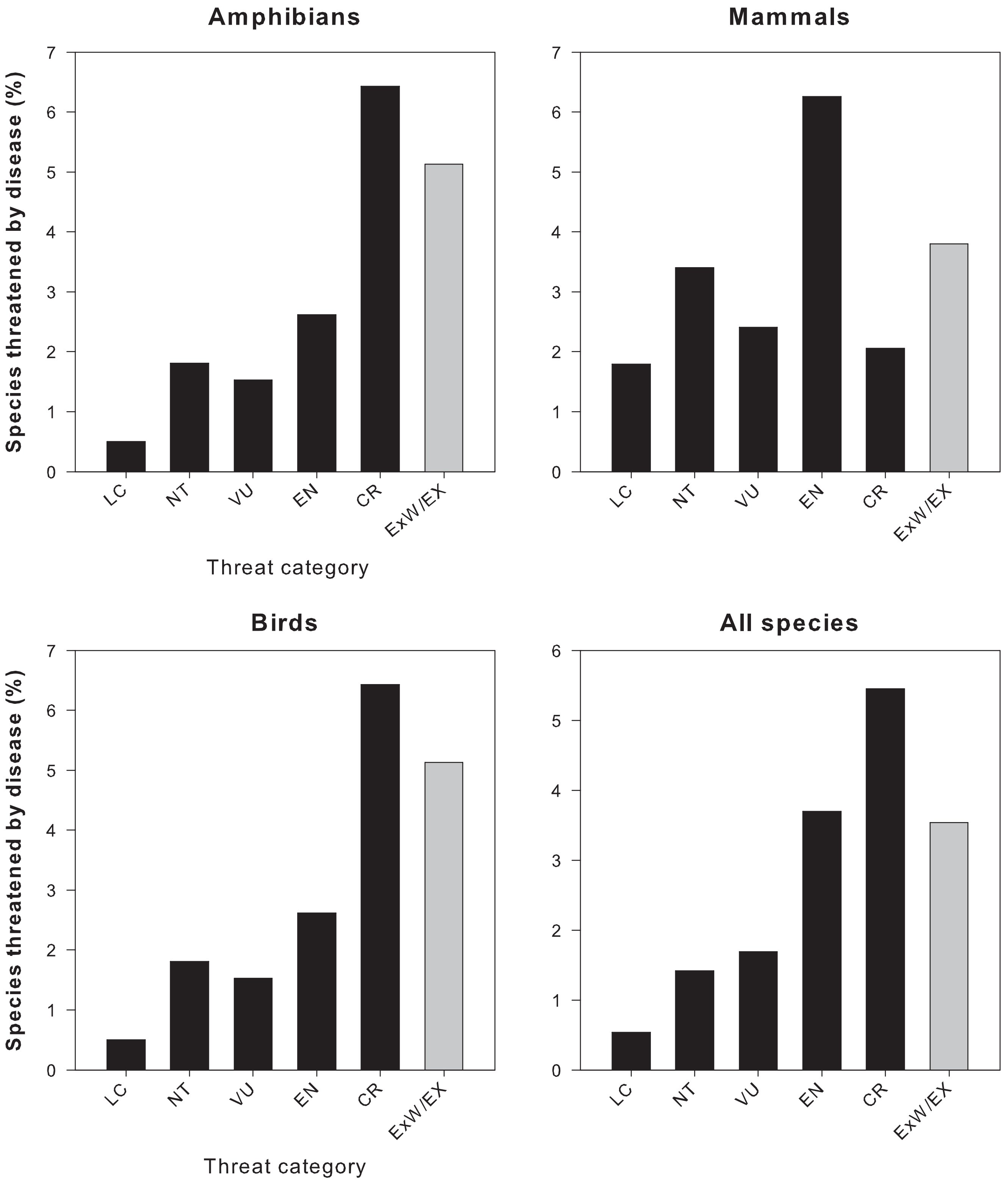

Figure 1. Percentage of species with evidence of a disease threat by status category (LC, least concern; NT, near threatened; VU, vulnerable; EN, endangered; CR, critically endangered; ExW/Ex, extinct in the wild or extinct). Extinct species (shaded) were excluded from statistical analyses (see Methods).

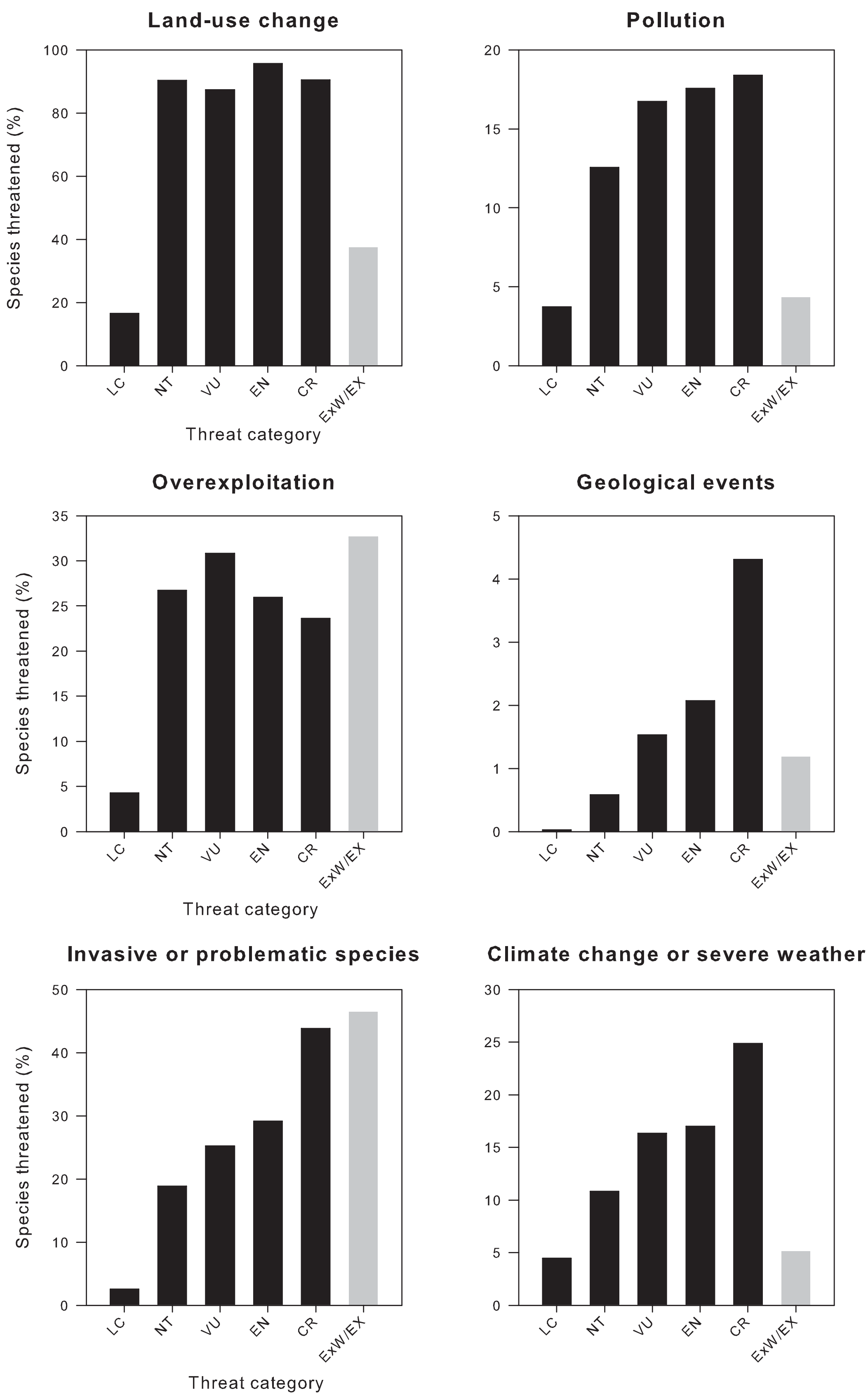

Figure 2. Percentage of species impacted by 6 major threats by status category. Extinct species are shaded because they are excluded from statistical analyses (see Methods).

Table 1. Percentage of 240 species with an evidence-based disease threat that are also threatened by the 6 other major threats.

Threats	*Amphibians*	*Birds*	*Mammals*	*All species*
No other threats	0.0	0.0	2.7	1.3
Land-use change	73.5	76.7	82.9	78.5
Overexploitation	13.3	37.2	71.2	44.7
Invasive or problematic	37.4	60.5	33.3	39.7
Pollution	39.8	20.9	18.9	26.6
Geological events	4.8	4.7	0.0	2.5
Climate change or severe weather	20.5	30.2	25.2	24.5

and future predicted threats to Red List species is the result of a precautionary approach adopted by assessment teams. Precaution is justified, but the sheer number of nonevidence-based threats to species at risk of extinction implies a major lack of on-the-ground surveillance systems, or basic research, critical for providing the data necessary to design effective conservation strategies (Heard et al. 2011).

The proportion of species threatened by disease differed between IUCN status categories and increased significantly for amphibians, birds, and all species combined as status category increased from near threatened to critically endangered (Fig. 1). We found that disease was infrequently a single contributing threat (Table 1) and that being affected by any of the other 6 major threats increased the likelihood of a species being simultaneously threatened by disease (Fig. 3). Our results may have been affected by the relative lack of evidence for disease-threatened animals in the IUCN Red List and the paucity of parasites and pathogens associated with these species. Our findings may also have been affected by the clustering of phylogenetically close relatives in Red List status categories, which have inherently similar disease threats; discovery bias (an artifact of increasing resources and accumulation of knowledge about the threats to species as their extinction risk increases), or ecological drivers associated with relatively high threat levels that predispose species to infection with parasites and pathogens.

Because host relatedness is often considered the best predictor of whether a taxonomic group is likely to share pathogens, parasites, and therefore diseases (Davies & Pedersen 2008), phylogenetic clustering of species affected by disease within IUCN Red List categories may bias our findings. For example, if all critically endangered amphibians were closely related and exhibited similar susceptibilities to chytridiomycosis while amphibians of least concern were closely related but not susceptible to the fungus, then our findings may not be robust. However, closer examination of the species with evidence of a disease threat (Supporting Information) suggests this is not the case. Of the 41 genera with multiple species threatened by disease, 75.6% (n = 31) of the genera had species listed in multiple Red List status categories (e.g., frogs in the genus *Eleutherodactylus* had species in least concern, endangered, and critically endangered status categories; birds in the genus *Hemignathus* had species in vulnerable and endangered status categories; and mammals in the genus *Eliurus* have species in least concern, vulnerable, and endangered status categories) (Supporting Information).

Discovery bias may be especially plausible for disease given the difficulties associated with studying parasites and pathogens in wild populations (Plowright et al. 2008). A case in point is the recently extinct Polynesian tree snail (*Partula turgida*). The last 5 individuals were diagnosed with a parasitic infection only after they were taken into captivity in hopes of curtailing extinction (Cunningham & Daszak 1998). Disease was considered the final threat that drove the species to extinction, but the causal parasites may never have been discovered if the few remaining individuals had not been studied so thoroughly. If discovery bias is the sole driving mechanism behind the accumulation of threats to species threatened with extinction, then the same pattern should hold for other threats, many of which also become increasingly apparent when extinction risk increases and species are more thoroughly studied. However, a preliminary look at the nondisease threats revealed that this trend occurred some (for invasive or problematic species, pollution, geological events, and climate change or severe weather), but not all (in the case of land-use change and overexploitation), the time (Fig. 2).

Collectively, land-use change, overexploitation, invasive or problematic species, pollution, geological events, and climate change or severe weather exhibit a wide range of variation in relative importance to extinction risk among status categories. Given that threats in the Red List are status specific (i.e., they may be deleted when a species is moved to another category), this variation implies that ecological drivers, in addition to scientific effort, affect the timing of threats to species as they become increasingly at risk of extinction (Fig. 2). For example, most species (except those of least concern) are threatened by land-use change (Vitousek et al. 1997; Wilcove et al. 1998; Hoffmann et al. 2010), whereas climate change or severe weather, a frequently hypothesized future threat to species on the Red List, is more likely to be documented for species in higher threat categories (Hoegh-Guldberg et al. 2008; Araujo et al. 2011) (Fig. 2). The potential ecological reasons

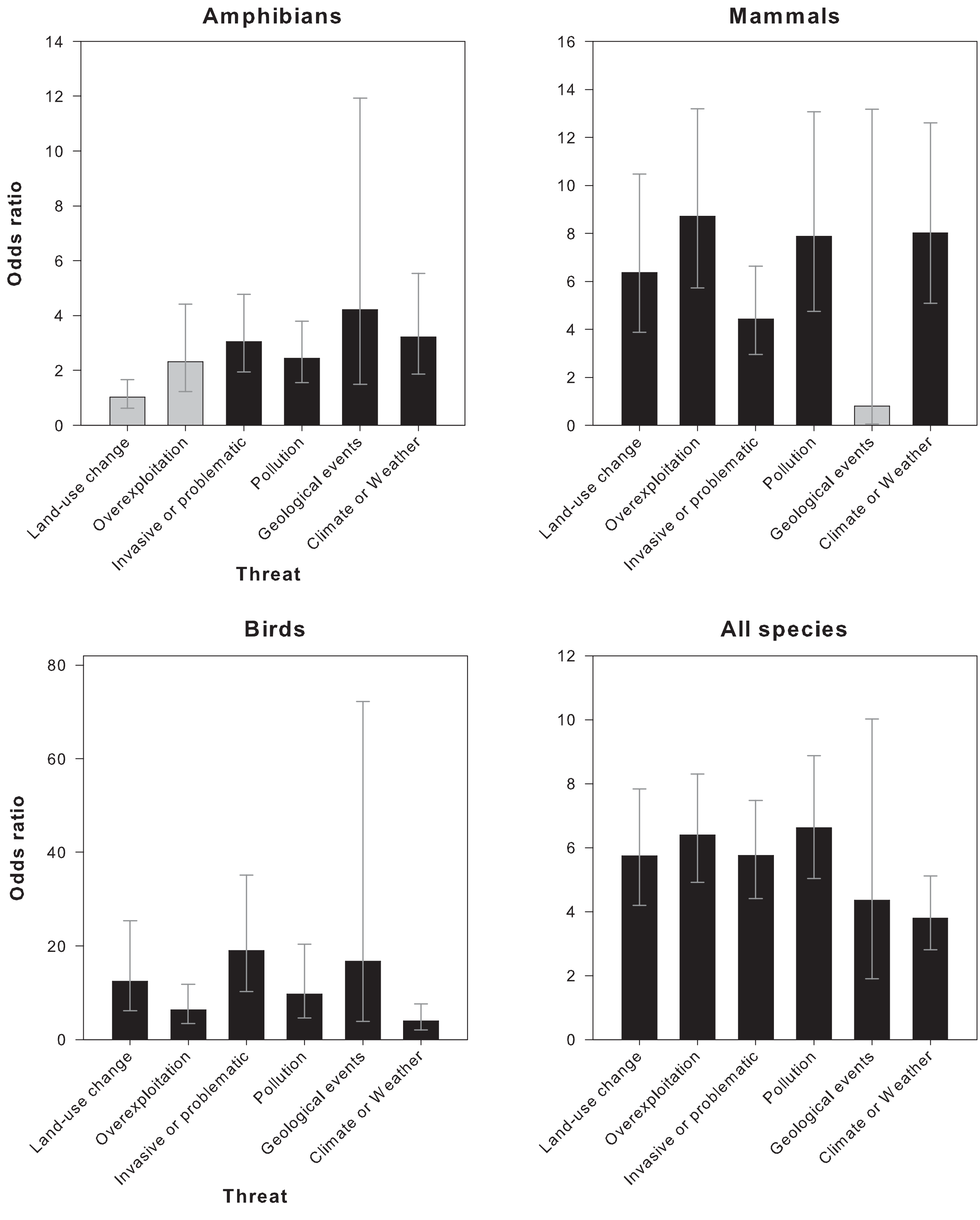

Figure 3. Odds ratios and confidence intervals (CIs) showing the increase in likelihood of having disease co-occur with each of 6 additional threats for 240 species with evidence of a disease threat (Supporting Information). Odds ratios greater than one indicate there is a higher likelihood of having disease occur as a threat when another threat is present (black bars, statistically significant odds ratios with CIs, ($P < 0.05$) as determined by Fisher's exact test; gray bars, nonsignificant results).

for why disease would be a more common threat to species on the verge of extinction may be explained by differences in the characteristics of the parasites and pathogens associated with species in different status categories or the interaction between disease and other threats. Theory predicts an increasing representation of frequency-dependent host-generalist pathogens that use reservoir hosts or that can survive in the abiotic environment species closer to extinction (Smith et al. 2006; Pedersen et al. 2007). Unfortunately, a paucity of information on parasite and pathogen diversity associated with threatened species prevented us from quantitatively assessing such a trend (Supporting Information). Similarly, because there was limited statistical variation among the odds ratios of each of our major threats for amphibians, birds, and mammals (Fig. 3), we could not infer which specific threats most increased the likelihood of species also being threatened by disease. Nevertheless, some discussion of parasite or pathogen characteristics and their interaction with nondisease threats is warranted.

Common diseases associated with birds in our data set included avian influenza, botulism, cholera, pox, and malaria (Supporting Information). Each of these diseases is caused by a host generalist parasite or pathogen, many of which have had substantial impacts on island species following either their introduction via importing of domestic birds (e.g., avian pox in Hawaii) or the accidental introduction of vector hosts that promoted their transmission (e.g., avian malaria in Hawaii) (Warner 1968). In the case of birds, a number of other extinction threats likely occurred long before infectious disease played a role in population declines. The endemic avifauna of the worlds' islands arguably were overexploitated (e.g., for food and feathers) and affected by predation from introduced species (e.g., cats and rats) long before pathogens, parasites, and vectors established and facilitated a disease threat (Blackburn et al. 2004).

In the case of amphibians, the fungus, *Batrachochytrium dendrobatidis*, that causes chytridiomycosis has a large host range, can persist for long periods in the ambient environment, and is asymptomatic in some species (e.g., North American Bullfrogs [*Lithobates catesbeianus*]) (Dobson & Foufopoulos 2001; Johnson & Speare 2005). Numerous reports link the global spread of chytrid to the international trade in amphibians for food and pets (Gratwicke et al. 2010), climate change (Pounds et al. 2006; Bosch et al. 2007), and alterations in land-use trends (Becker et al. 2007). The complexity of interactions between these threats are a matter of continued research, but recent work suggests that although land-use and climate change appear to be spatially overlapping threats, chytrid is often the sole driver of extinction for many species (Hof et al. 2011). Chytrid is one of few diseases that seem capable of driving species to extinction in the complete absence of other threats.

For mammals, the highest proportion of disease threats occurs in endangered species (Fig. 1). Many of the diseases (e.g., rinderpest and canine and phocine distemper viruses) threatening mammals are caused by density-dependent pathogens that originate in domestic or feral animals (Pedersen et al. 2007; IUCN 2011; Supporting Information). The spillover of density-dependent pathogens such as these, between human-associated livestock and pets and wild mammals, has arguably occurred since humans first began domesticating animals (Pearce-Duvet 2006). Close phylogenetic relatedness between pathogen-swapping wild and domestic hosts should increase the likelihood of establishment and potentially disease (Pedersen et al. 2007). Plague is another disease threat of note among mammals, specifically rodents. Although a number of rodent species in the genus *Rattus* are reservoir hosts for the bacterium and do not suffer disease, many others are amplification hosts that have low resistance to infection, high mortality due to disease, and can have rapid spread of disease throughout their populations (Witmer 2004). North American prairie dogs (*Cynomys*) are susceptible to plague and have been affected by, for example, persecution by ranchers, habitat loss for development, and El Nino Southern Oscillation events that cause booms in both the flea vector and prairie dog populations that fuel outbreaks of plague in prairie dog colonies (Stapp et al. 2004).

Assessments to update threats and status categories for species on the Red List occur intermittently; thus, there are undoubtedly disease (and other) threats not yet accounted for. For example, there has been a seemingly sudden increase in the number of fungal pathogens threatening wildlife worldwide, many of which have not been mentioned in the IUCN Red List. White-nose syndrome (WNS), the disease caused by the ascomycete fungus *Geomyces destructans*, has been decimating North American bat populations since approximately 2006 (Frick et al. 2010). Three species have been particularly hard hit by the disease, which has reduced affected populations by >70%. Scientists believe the little brown bat (*Myotis lucifugus*) has a 99% chance of becoming locally extirpated form the northeastern United States by 2025 (Frick et al. 2010). On the Red List, however, *M. lucifugus* is still listed as a species of least concern, and there is no mention of WNS in the assessment. *M. septentrionalis* (least concern) and *M. sodalist* (endangered) are also threatened by WNS, and this threat is not accounted for on the IUCN Red List. The loggerhead turtle (*Caretta caretta*) is susceptible to the ascomycete fungus (*Fusarium solani*), which is a soil-dwelling saprotroph that can cause hatch failure and juvenile suboptimality (Sarmiento-Ramírez et al. 2010; Fisher et al. 2012). *C. caretta* was last assessed as endangered in the mid 1990s, so this new fungal threat has not yet been incorporated to the Red List record. Evidence suggests that fungal threats are on the rise in human, plant, and animal populations worldwide and are of special concern to biodiversity given their resilient dispersal stages, ability to survive for prolonged periods in the ambient environment, typically high virulence, and often broad host ranges (Fisher et al. 2012). Fungal pathogens other than *B. dendrobatidis* appear to be underreported in the Red List, although this is expected to change as species assessments are updated.

Despite potential data gaps, we hope our work sparks more examination of the timing of disease, and interactions between threats, as species become increasingly threatened with extinction. The creation of such timelines may benefit conservation biologists trying to predict what the next threat may be for Red Listed species they are tying to protect. Most critical to the study of disease as a threat to species is the compilation of baseline data on the presence of parasites and potential pathogens in species populations when they show the first signs of extinction risk and if possible before they become threatened. Such data would benefit wildlife conservation and potentially help detect zoonotic infectious agents of concern to humans.

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Supporting Information

Species threatened with disease in the IUCN Red List (Table S1) and the analysis of the proportion of species affected by disease in each IUCN Red List status category (Fig. S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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