PATTERNS OF THREATENED VERTEBRATES BASED ON TROPHIC LEVEL, DIET, AND BIOGEOGRAPHY

by

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ABSTRACT

Patterns of threatened vertebrates based on trophic level, diet, and biogeography

by

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Earth is experiencing a biodiversity crisis exemplified by increasing rates of extinction. To reduce species loss, understanding what makes species more prone to extinction is crucial. Past studies show that species extinction risk varies with biological characteristics like trophic level. There is a pervasive assumption based on theory and anecdotal evidence that predators have the highest extinction risk. However, the relationship between extinction risk and trophic level has not been tested explicitly. Understanding this relationship can help us predict what ecological consequences may occur in the future as trophic level and ecosystem function are linked.

We explicitly compared the extinction risks of species in different trophic levels. We classified all mammals, birds, and reptile diet, trophic level, and body size. Furthermore, we investigated whether the systems, habitats, geographic regions, and anthropogenic threats associated with each species influenced patterns of extinction risk across trophic levels. We used bootstrapping to simulate the observed proportions of
threatened species and compared them to expected proportions within each trophic level or diet group.

In contrast to conventional thinking, herbivores were consistently more threatened than expected. Within herbivores, frugivores and plant eaters were more threatened than expected. Only a few predator groups including scavengers and piscivorous birds had higher proportions of threatened species than expected. In addition, all large-bodied species except predatory reptiles were more threatened than expected. Regionally, herbivores were more threatened than expected in Oceania, south and Southeast Asia, and sub-Saharan Africa while predatory birds were more threatened in Oceania and predatory reptiles in sub-Saharan Africa. Within habitats, herbivores were more threatened than expected in tropical forests and marine coastal habitats and predatory birds in marine habitats. These extinction risk patterns may derive from the disproportionate impacts on herbivores and omnivores through anthropogenic disturbances including biological resource use, habitat alteration, and pollution. Conservation should shift its focus from an emphasis on predators to hone in on select predatory groups and herbivores in general. By conserving these highly threatened species, we can protect their associated ecosystem functions—seed dispersal, vegetation structure, disease control, and nutrient transfer—and curb the biodiversity crisis.
PUBLIC ABSTRACT

Patterns of threatened vertebrates based on trophic level, diet, and biogeography

Shaley A. Valentine

Humans have indirectly and directly contributed to the extinction of over 500 species within the past 500 years, a rate far higher than we have seen in the past. The high extinction rate and the fact that 18% of vertebrates may become extinct within the next century have pushed Earth into a biodiversity crisis. Understanding what makes species more at risk of extinction is needed to protect Earth’s biodiversity.

Generally, it is expected that predators have greater extinction risk than omnivores and herbivores because predators are larger in body size, depend on other animal species for food, need large home ranges, and have fewer individuals within their populations. However, no study to date has actually tested the assumption that predators have the highest extinction risk. This question is important to understand because diet is associated with the ecological role a species plays in an ecosystem.

We compared the extinction risk of species with different diets to determine species in which trophic level are proportionately more at risk of extinction. We classified each species’ diet, trophic level (i.e., predator, omnivore, and herbivore), body size, habitat, geographic region, system, and associated threats. We focused our analyses on all mammals, birds, and reptiles assessed by the International Union for the Conservation of Nature. We then compared the expected and observed proportions of threatened species within each trophic level and diet group at global, system, habitat, and regional scales.
We found that predators, except scavengers, fish-eating birds, and obligate mammal and bird eaters, were not more threatened than expected. On the other hand, herbivores consistently had greater proportions of threatened species than expected. Specifically within herbivores, fruit, grass, and leaf-eating species had high proportions of threatened species. When we separated large-bodied and small-bodied species, we found that most large-bodied species, regardless of their trophic level, had greater proportions of threatened species. When we looked at the regions and habitats where species were more often threatened, we found that herbivores were highly threatened in south and Southeast Asia, sub-Saharan Africa, and Oceania. In addition, herbivores were highly threatened in tropical forests, marine coasts, and sometimes grasslands. Overall, terrestrial herbivores and marine predatory birds were highly threatened. We found that these patterns may have resulted from overexploitation, habitat alteration, and pollution targeting herbivores and sometimes omnivores.

These findings suggest that we should shift conservation focus from predators to include herbivores. The most threatened species, tropical herbivores, scavengers, and mammal, bird, and fish eaters should be of highest conservation priority.
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CHAPTER I
INTRODUCTION

Species extinction is a natural phenomenon, but high rates of extinction can lead to dramatic changes in the course of evolution. For most of Earth’s history, species have become extinct at a steady rate of one in every 1,000,000 species each year (i.e., the background rate; Ceballos et al. 2010). However, sometimes widespread biological or environmental changes occur such as global cooling or alterations in atmospheric composition that few species are physiologically able to survive (Knoll et al. 2007). These changes have led to five mass extinction events (Jablonski 1986). In each mass extinction, approximately 75% of all species became extinct in a relatively short geologic time span (e.g., < 2 million years), shifting the trajectory of species evolution (Barnosky et al. 2011). Today, Earth is at the precipice of its sixth mass extinction (McCauley et al. 2015, Young et al. 2016, Ceballos et al. 2017).

Humans have indirectly and directly caused species to become extinct or decline to such an extent that they are threatened with extinction (Dirzo et al. 2014, McCauley et al. 2015). These losses have created a new extinction wave that began around 500 years ago with the expansion of the human population (Dirzo et al. 2014). In this extinction wave, humans have partially contributed to the extinction of at least 363 vertebrate species: 83 mammals (1.5% of mammals), 156 birds (1.4%), 27 reptiles (0.5%), 33 amphibians (0.5%), and 64 fish (0.4%; “The IUCN Red List of Threatened Species” 2016). The current rate at which vertebrate species have gone extinct is up to 1,000 times faster than the background extinction rate (Ceballos et al. 2010, Pimm et al. 2014). More concerning than the number of extinctions to date is the percentages of threatened
species, which are the species most likely to become extinct in the near future. According to the International Union for Conservation of Nature’s (IUCN) Red List of Threatened Species, birds are the least threatened vertebrate group (13.4% of species are threatened), followed by fish (15.3%), reptiles (19.3%), and mammals (21.9%), although not all fish and reptiles have been evaluated. Amphibians are the most threatened taxa with 32% of species currently assessed as threatened by the IUCN (“The IUCN Red List of Threatened Species” 2016). If these threatened species become extinct in the near future, the species extinction rate may quickly exceed rates experienced during the past five mass extinction events (Barnosky et al. 2011, but see McCallum 2015), ensuring this new extinction wave is one of the largest mass extinctions in Earth’s history.

Extinction not only influences biodiversity on Earth, it also has consequences for fundamental ecosystem processes and services (Ceballos et al. 2010, Stork 2010). Loss of ecosystem processes may be caused by the extirpation of species with an irreplaceable functional role (i.e., a non-functionally redundant species; Pimiento et al. 2017) or a shift in the dominant species group (Mcelwain et al. 2007). A review by Estes et al. (2011), found that functional loss of apex predators in many ecosystems have led to increases in the number and intensity of wildfires, outbreaks of diseases, soil and water chemical changes, and loss of storm protection. Moreover, major species declines, as seen with historical mass extinctions, yield more serious ecosystem alterations at a global scale. For example, declines in species during the Cretaceous-Paleogene extinction in part led to significant changes in primary production and biogeochemical cycles that did not return to pre-extinction levels until 2 million years later (Hondt 2005). To impede the sixth mass
extinction event and prevent widespread environmental changes, we must determine patterns in species loss.

Extinction is not random: specific biological and environmental traits can alter a species’ susceptibility to extinction. Biological traits measure a species’ inherent susceptibility to disturbance (Davidson et al. 2012), and several biological traits have been associated with increased susceptibility to extinction. These traits include geographic range size (Purvis et al. 2000b, Böhm et al. 2016, Verde Arregoitia 2016), body size (Olden et al. 2007, Sodhi et al. 2008, Anderson et al. 2011, Tingley et al. 2013), litter size (Purvis et al. 2000b, Anderson et al. 2011), and to some extent trophic level (Purvis et al. 2000b, Dobson et al. 2006, Anderson et al. 2011). With the exception of trophic level, these characteristics do not provide information on ecological consequences of extinction (Duffy 2003, Dobson et al. 2006, Duffy et al. 2007). Quantifying the association between trophic level and extinction susceptibility may help us predict the far-reaching consequences of species loss on ecosystem processes and services.

Trophic level is an ecological characteristic that is associated with a species’ functional role in its ecosystem (Duffy 2003, Duffy et al. 2007, Barnosky et al. 2015). Specifically, herbivores create and maintain vegetation structure within their ecosystems (Şekercioğlu et al. 2004, Barnosky et al. 2015). For example, declines in ungulate herbivore populations have caused vegetation community structures to change, leading to bottom-up effects on other animal species (Staver et al. 2011), and pollination and seed dispersal have decreased due to declines in frugivorous birds (Sekercioğlu 2011, Galetti et al. 2013). Predators control their prey populations through direct predation and reduce
the chance of disease outbreaks by scavenging carrion and removing sick prey from populations (Estes et al. 2011, Buechley and Şekercioğlu 2016). Apex predators also control mesopredator populations which stabilizes species’ populations throughout the entire food web (Crooks and Soulé 1999). Omnivores, being more generalist, serve similar functions to both herbivores and predators as well as influence decomposition (Zhang et al. 2004). Species in each trophic level provide fundamental ecosystem functions and services; thus, overrepresentation of threatened species in a trophic group could have dire consequences for the ecosystem functions supported by species within a trophic level (Duffy 2003, Atwood et al. 2015).

Several ecological relationships predict that predators are more sensitive to extinction than species in lower trophic levels (Duffy 2003, Estes et al. 2011). First, predators are perceived to be large-bodied species (Henle et al. 2004). Large-bodied species require more resources to maintain metabolic function and expansive geographic ranges to obtain necessary resources (Cagnolo et al. 2009). Second, predators rely on species in lower trophic levels as resources. As a result, predators experience the cumulative effects of resource depletion if basal resources are altered by disturbance or if a food web is disrupted (Holt et al. 1999, Vázquez and Simberloff 2002). Third, predators are associated with low fecundity and high longevity (i.e., slow life history traits) compared to species in other trophic levels. Species with these traits are less able to recover after a disturbance compared to species with fast life history traits (Purvis et al. 2000b). Finally, predators may be disproportionately affected by human-targeted actions (e.g., overexploitation and persecution) due to their large size or human fear of the
species (Duffy 2003). These relationships derived from theory suggest predatory species are likely to have higher extinction risk than species in lower trophic levels.

Evidence to support the hypothesis that predators are at a high risk of extinction has had mixed support from several regional or family-specific studies. In these studies, both non-predatory and predatory species had similar extinction risks (Hilbers et al. 2016), omnivorous birds had the greatest extinction risk (Şekercioğlu et al. 2004), or a subset of predatory mammals had greater extinction risk than non-predatory ones (Hilbers et al. 2016). These inconclusive results, which are based on spatially and phylogenetically small-scale studies, suggest that a large-scale quantification of extinction risk that directly compares species in different trophic levels is needed. Both global and regional quantification is crucial to determine whether patterns in extinction risk with regards to trophic level are ubiquitous or context dependent.

Global patterns of trait-related extinction risk give us an idea of what biological traits may affect a species’ susceptibility to extinction, but a species’ natural history varies among habitats and by region (Fritz et al. 2009). Therefore, looking at regional patterns in extinction risk can yield a sense of where conservation action is most urgent and if regional patterns corroborate or differ from the global pattern (Ricketts et al. 2005). In addition to regional patterns, understanding what anthropogenic disturbances are more often associated with certain species groups may yield insights into the major causes of species declines within a trophic level. Anthropogenic disturbances are the major proximate causes of species loss and may differentially affect species in one system, habitat, geographic region, or trophic level compared to another, contributing to species extinction (Vamosi and Vamosi 2008, Ducatez and Shine 2017).
Our overall goal was to quantify extinction risks of species in different trophic levels at global and regional scales for mammals, birds, and reptiles. Our proxy for extinction risk was the proportion of threatened species. In Chapter 2 of this study, our goal was to determine species in which trophic level(s) are overrepresented in threatened species compared to an expected proportion of threatened species. To accomplish this goal, we addressed three objectives. First, we compared proportions of threatened vertebrate species among the trophic levels of predator, omnivore, and herbivore. These proportions were measured within each trophic level across all species combined and within the classes of mammals, birds, and reptiles. Second, we refined the trophic level comparisons by comparing proportions of threatened species as a function of diet group. Third, we analyzed the interaction between body size and trophic level by analyzing the proportions of large-bodied and small-bodied threatened species in each trophic level. In Chapter 3 of this study, our goal was to determine the biogeography of threatened species patterns across trophic levels. To accomplish this goal, we addressed four objectives. First, we quantified the proportion of threatened species within each trophic level across systems (i.e., freshwater, marine, and terrestrial). Second, we refined the first objective by measuring the proportion of threatened species within each trophic level across habitat types. Third, we measured the proportion of threatened species within each trophic level across geographic regions. Fourth, to determine which anthropogenic disturbances influence the proportions of threatened species in each trophic level, we analyzed the proportions of threatened species across five major anthropogenic threats affecting species (i.e., habitat alteration, biological resource use, climate change, invasive species, and pollution).
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CHAPTER II
PATTERNS OF THREATENED SPECIES ACROSS TROPHIC LEVEL AND DIET

ABSTRACT

Earth is in the midst of the sixth mass extinction event, resulting from extensive anthropogenic disturbance. Understanding what characteristics make over 18% of vertebrates currently threatened with extinction is critical for conservation action. Biological characteristics like body size and perhaps trophic level are associated with extinction risk of a species. Trophic level and diet more specifically can tell us what role a species plays in an ecosystem while body size can tell us the magnitude of that role. For example, frugivores disperse seeds, promoting recruitment of trees, and large frugivores can disperse seeds for longer distances than small frugivores. In the literature, predators are assumed to have greater extinction risk than omnivores and herbivores. However, no study has explicitly compared the extinction risks of species in different trophic levels at a global scale.

Here, we classified the diet and trophic level of all mammals, birds, and reptiles on the International Union for the Conservation of Nature’s Red List of Threatened Species. Then we compared the observed and expected proportions of threatened species in each trophic level and diet group using 95% confidence intervals of bootstrapped numerical simulations. In addition, because body size is a prominent predictor of extinction risk, we combined body size and trophic level variables.

We found that contrary to assumption, herbivores, not predators, had greater proportions of threatened species than expected. When we specifically analyzed across
diet groups, we found that frugivores and plant eaters in each class as well as scavengers, obligate endotherm eaters, piscivorous birds, and granivorous reptiles had greater proportions of threatened species than expected. When we analyzed using body size, we found that all large-bodied species, except predatory reptiles, had higher proportions of threatened species than expected. These results indicate that ecosystem services like vegetation structuring, seed dispersal, pollination, disease prevention, and transfer of marine nutrients to land may decrease in the future due to the high proportions of threatened species associated with these functions.

INTRODUCTION

Humans have affected Earth to such an extent that a new geological epoch has begun: the Anthropocene (Williams et al. 2016). Thus far in the Anthropocene, humans have directly (e.g., hunting) and indirectly (e.g., climate change) caused extensive vertebrate species loss including population declines, local extirpations, and global extinctions (Collen et al. 2014, Dirzo et al. 2014, McCauley et al. 2015). At least 363 vertebrate species have become extinct over the past 500 years in this newest wave of extinctions (Young et al. 2016, Ceballos et al. 2017). However, this number of extinctions pales in comparison to the percentage of species currently threatened with extinction (i.e., those that are most likely to become extinct in the near future). To curb future species losses, determining what characteristics make species more prone to extinction is critical.

Specific biological characteristics inherently make species more susceptible to extinction. Large body size (Reynolds et al. 2005a, Cardillo et al. 2006, Anderson et al. 2011, Verde Arregoitia 2016) and slow life history characteristics (e.g., high longevity
and low fecundity; Purvis et al. 2000b, Cardillo et al. 2006) are usually associated with high extinction risk. Large, less fecund species are disproportionately affected by human disturbances as populations cannot recover as quickly as smaller, more fecund species. To a less consistent extent than body size and life history characteristics, the size of the geographic range a species occupies can influence extinction risk. Species with large geographic ranges (i.e., multiple populations) tend to be less prone to global extinction than species with small ranges (i.e., fewer populations; Purvis et al. 2000a, Cardillo et al. 2004, Tingley et al. 2013). If a disturbance occurs within a large geographic area, a population may be extirpated, but other populations can still persist. However, for species with a small geographic range, a disturbance may occur across the entirety of its range (Henle et al. 2004, Keinath et al. 2017), wiping out the entire species. While evidence exists for these associations between characteristics and extinction risk, quantification for other associations is lacking.

Throughout the literature, species in higher trophic levels are assumed to have greater extinction risk than species in lower trophic levels. Extinction risk might be expected to correlate with trophic position for a number of reasons. First, body size generally increases with trophic position, and larger-bodied species have greater metabolic demands (Cagnolo et al. 2009), so these species must consume more resources that may not necessarily be available. Second, trophic transfer of nutrients dictates that fewer individuals exist at higher trophic levels, so populations are more easily decimated by disturbances (Purvis et al. 2000b). Third, species in higher trophic levels rely on those in lower trophic levels for food. Disturbances that affect species in lower trophic levels
can reverberate up the food chain to affect species in higher trophic levels (Holt et al. 1999, Vázquez and Simberloff 2002).

The hypothesis that foraging ecology is associated with extinction risk is supported by evidence from past mass extinctions (Hondt 2005, Payne et al. 2016) and ancillary evidence from studies not focused specifically on extinction risk. For example, Pauly et al.’s (1998) notion of “fishing down the food web” and Ripple et al.’s (2014) paper on the status of the world’s largest carnivores have instilled the belief that predators are more susceptible to extinction than species in other trophic levels. Yet, no study to date has compared extinction risk quantitatively across multiple trophic levels. It therefore remains unknown if predators are at a greater risk of extinction than species lower in the food chain.

In this study, our overall goal was to determine the relative proportions of threatened species, a proxy for extinction risk, across different trophic levels (i.e., herbivore, omnivore, and predator). We used all of the mammals, birds, and reptiles assessed on the International Union for the Conservation of Nature’s (IUCN) Red List of Threatened Species. To accomplish this goal we had three objectives. First, we quantified the proportions of threatened species within each trophic level for all taxa, as well as within each class (i.e., mammal, bird, and reptile). Second, we refined the trophic level analyses by quantifying the proportions of threatened species by diet group (i.e., endotherm, herptile, fish, invertebrate, carrion, egg, plant, fruit, nectar, and grain) and reanalyzed extinction risk across all species, and again within each class. Third, we quantified the proportions of threatened species within each trophic level and accounted
for body size, which has been found to be intricately linked to extinction susceptibility (Reynolds et al. 2005a, Fritz et al. 2009).

METHODS

Overview

We created a database containing biological data (i.e., body size, diet, and trophic level) on all extant mammal (5,567), bird (11,121), and reptile (5,338) species assessed on the 2017 IUCN Red List of Threatened Species (current as of February 23, 2017). First, we assigned binary threat assessments to each species. Second, we characterized the diets of each species based on available information. Third, we classified the trophic levels of each species based on our diet characterization. We used the completed database to quantify the observed proportions of threatened species in specific trophic levels in relation to the expected proportions of threatened species.

Binary Threat Classification

For each species assessed by the IUCN, we assigned a binary threat classification of “threatened” or “non-threatened”. Species with IUCN assessments of “critically endangered”, “endangered”, and “vulnerable” were considered threatened with extinction, and species with “near threatened”, “least concern”, and “lower risk” assessments were considered non-threatened (Baillie et al. 2004, González-Suárez et al. 2013). This binary classification system represents the two potential outcomes in an extinction event (i.e., extinction or survival; Davidson et al. 2009, González-Suárez et al. 2013, Hilbers et al. 2016, Payne et al. 2016). Species assessed as “extinct” (EX) or
“extinct in the wild” (EW) were not included as they are neither threatened nor non-threatened and are no longer found in the wild.

A large proportion of species are assessed as “data deficient” (DD; Table 2-1) by the IUCN, and the literature suggests that DD species may proportionately have high extinction risk (Collen et al. 2014a, Bland and Böhm 2016). We accounted for DD species in two ways. First, we analyzed data excluding all DD species. We then analyzed data including DD species using three classification scenario: relaxed, precautionary, and intermediate (Purvis et al. 2000a, González-Suárez et al. 2013, Collen et al. 2014, Payne et al. 2016). For the relaxed scenario, all DD species were classified as non-threatened. In contrast, for the precautionary scenario all DD species were classified as threatened. These two scenarios represent the lower and upper boundaries of the true model if DD species were to be assessed (González-Suárez et al. 2013, Payne et al. 2016). For the intermediate scenario, DD species were randomly classified based on current threatened species proportions using the following equation from Collen et al. (2014): threatened / (non-threatened – DD – EX – EW). Results for when DD species were included in analyses are provided in Appendix A, Figures A-1-A-12.

**Diet Categories**

We classified the diet and diet breadth for all extant mammal, bird, and reptile species assessed by the IUCN using published literature, reference texts, databases, or extrapolation from related taxa. Species’ diets were determined from various data types (i.e., percent, ranked presence-absence, and unranked presence-absence of specific diet items). We classified diets using a binary response of present or absent. Only adult diet information from wild populations was used. The primary diet items (with subcategories
in parentheses) were endotherm (mammal and bird), herptile (amphibian and reptile), fish, invertebrate (insect), carrion, egg, plant (foliage, root, wood), fruit, nectar, and grain (Kissling et al. 2014, Wilman et al. 2014). A carrion eater (i.e., scavenger) was defined as a species that consumes animal-based carrion. An egg eater was a species that consumed bird or reptile eggs; amphibian and fish eggs were excluded from this category (Andreone and Luiselli 2000, Allen et al. 2013). A plant eater was defined as a species that consumed algae, fungus, leaves, shoots, roots, wood, flowers, pollen, sepals, or other miscellaneous plant material (e.g., vegetable matter; Wilman et al. 2014). Dietary breadth was calculated as the number of main diet categories a species consumed food from and was used as a measure of dietary specialization. A diet breadth of one indicated a high dietary specialization (Buechley and Sekercioglu 2016).

For diets described in the literature as percentages, we used specific percentage cut-offs to classify diet items as either present or absent (69.1% of all species). Percentage cut-offs were adjusted based on the number of unique diet items included in a species’ diet, because as the number of diet items increases, the weight of a diet item in the species’ total diet increased. Specifically, if a species only consumed two diet items and one diet item comprised ≤ 20% of the diet, that item was classified as absent. However, if the species’ diet had more than two diet items, any item with a ≥ 20% contribution was classified as present.

For diets described as ranked presence-absence data, diet items were classified according to keywords (9.4% of species). We included diet items associated with the following keywords: “primary”, “secondary”, “mostly”, “also”, “frequently”, “regularly”, “usually”, and “fair amount”. We excluded diet items associated with the keywords
“tertiary”, “sometimes”, “occasionally”, “rarely”, “small quantities”, “and even”,
“opportunistically”, and “at times supplemented with”. If a diet item was associated with
uncertainty statements of “probably”, “possibly”, “may”, or “presumably” it was excluded unless no other diet information was available. For diets described using
unranked presence-absence data (e.g., “eats fruit, insects, and seeds”), all listed diet items were classified as present (3.8% of species).

When diet information could not be found for a species, we extrapolated diets from former classifications or sister taxa. Here, diet information was averaged from related species to classify the species of interest’s diet profile. If a species was formerly classified as another species or a subspecies, then diet data from the former classification was used (5.1% of species). If the species was not formerly classified as another species or a subspecies, then diet data was extrapolated from the closest living congener (10.8% of species) or comfamiliar (1.6% of species) using previously published phylogenies (Allen et al. 2013, Kissling et al. 2014, Wilman et al. 2014). If a phylogeny of a species was not resolved, we extrapolated from all congeners or comfamiliars based on the most common diet items across all species.

We assessed data quality based on the following rankings. Rank 1: Quantitative assessments of diet information (i.e., as percentage diet) represented the highest quality data. Rank 2: Presence-absence data. Rank 3: Unranked presence-absence data. Rank 4: Extrapolation from a former classification. Rank 5: Extrapolation from a congener. Rank 6: Extrapolated from a comfamiliar. Extrapolations from a former classification were further sub-ranked based on whether the original diet data was presented as percent data (4.1), ranked presence-absence data (4.2), or unranked presence-absence data (4.3).
**Trophic Level**

Using dietary information, we classified species into three trophic levels: predator, omnivore, and herbivore. For data that was described from percent data, predators were defined as having a > 90% animal-based diet, herbivores as having > 90% plant-based, and omnivores as having a more evenly distributed diet. For ranked presence-absence data, predators were defined as animals that primarily consumed animal-based diet items and could consume plant-based diet items in small amounts; herbivores primarily consumed plant-based diet items and could consume animal-based diet items in small amounts, and omnivores primarily or secondarily consumed a mixture of both animal and plant diet items. For unranked presence-absence data, predators consumed only animal-based diet items, herbivores only plant-based diet items, and omnivore included diet items from both categories.

To explore the sensitivity of results to trophic level classification, trophic level was classified three times: 70% cutoff, 80% cutoff, and 90% cutoff. The previously described trophic level classification of > 90% was the 90% cutoff classification. For the 80% cutoff classification, we set the percentage cutoff to 80%, and for the 70% cutoff classification we set the cutoff to 70%. For diet data categorized from presence-absence data, the three trophic level classifications were classified equivalently.

**Body Size**

We classified mammal, bird, and reptile species into two body size categories: small-bodied and large-bodied. Mammals with a body mass of ≥ 5.5 kg (Davidson et al. 2009) and birds with a body mass of ≥ 60 g were classified as large-bodied (Boyer and Jetz 2010). For reptiles, we used the mode of log10 body mass (~1.16 = 14.5 g) as the
threshold between large and small body size (Boyer and Jetz 2010). In all cases, we used adult body size for classification. When male and female body sizes were given, we used the geometric mean of the two values. When a range of body sizes were given we used the geometric mean of the smallest and largest value (Wilman et al. 2014).

Body mass was most readily available for birds and mammals. However, body size measurements for different reptiles were not standardized across taxa. Body size for Squamata was commonly reported as total length or snout-vent length, while body size for Testudines was reported as standard carapace length. To overcome non-standardization methods for measuring body size, we converted all length measurements to body mass using previously published family-level length-mass regressions. If previously published regressions were not available, we developed regressions from data collected in our dataset.

For species with missing body size data, we extrapolated body size using the average of all congeners (excluding congeners that had been previously extrapolated this way; 8.8% of species). If no congeners existed, we only classified the body size category (i.e., small-bodied or large-bodied) based on the majority classification of all conm familiars (.7% of species).

**Analyses**

We used bootstrapping to numerically simulate observed proportions of threatened species in each group. We compared expected versus observed proportions of threatened species for 1) trophic levels across all species combined, 2) diets groups across all species combined, and 3) trophic level binned by body size across all species combined. We then re-tested the above scenarios within each individual class (i.e., Aves,
Mammalia, and Reptilia). To compare expected and observed proportions of threatened species, we first calculated the expected proportion of threatened species for all species combined and for each class. The expected value was the total proportion of threatened species within the focal species group. To generate the observed proportion of threatened species, we used bootstrapping. The sample size for each bootstrap was the sample size of the focal group. Bootstrapping was repeated for 10,000 iterations per comparison (Collen et al. 2009). The observed proportion of threatened species for each trophic level or diet category was calculated as a range of the median and 2.5% and 97.5% quantile proportions of the 10,000 bootstrapping iterations (Loh et al. 2005, Collen et al. 2009). A significant difference in the expected and observed proportions of threatened species was indicated by whether the expected proportion fell outside of the range of observed proportions. All analyses were run in R v 3.3.3 (R Core Team 2017).

RESULTS

Trophic Level

All comparisons of the proportions of threatened species resulting from bootstrapping are relative to the expected proportion of threatened species. Proportions of threatened species for less than 10 individuals are not discussed, but are still shown in figures. Patterns of threatened species across trophic levels were similar across all species combined and within classes (Figure 2-1). Surprisingly, predators did not have a greater proportion of threatened species; instead predators had proportions of threatened species as expected or lower. In contrast, herbivores had greater proportions of threatened species for each class. Omnivores had lower proportions of threatened species, except for reptiles where omnivores had a greater proportion of threatened species.
Our sensitivity analyses for trophic level classification cutoff and DD classification revealed some differences in models (Figure 2-2 for all species combined, Appendix A, Figures A-1, A-2, and A-3 for individual classes). The stricter an herbivore or predator diet, the higher its observed proportion of threatened species was. Specifically, the proportion of threatened herbivorous birds was as expected in the 80% and 70% cutoff trophic level classifications while the proportion was higher in the 90% trophic level classification. The way DD species were classified also affected some results (Appendix A, Figures A-1, A-2, and A-3). Herbivores consistently had greater proportions of threatened species in all of the DD classification scenarios. The observed proportions of threatened omnivores decreased while the observed proportions of threatened predators increased going from the relaxed (DD species classified as non-threatened) to precautionary (DD species classified as threatened) scenarios. This pattern resulted from the high percentages of DD classified predators, and the low percentages of DD classified herbivores and omnivores (Table 2-1).

**Diet**

Patterns of threatened species in different diet groups differed (Figure 2-3). When all species were combined, plant eaters, frugivores, scavengers, and piscivores had greater proportions of threatened species while nectarivores and granivores had lower proportions. When these patterns were analyzed for each class, the higher proportions of threatened plant eaters and frugivores were seen in all classes. The higher proportion of threatened piscivores and the lower proportion of threatened nectarivores were driven by birds only. The higher proportion of threatened scavengers was driven by both birds and reptiles. The lower proportion of threatened granivores was driven by mammals. Other
patterns at individual classes included nectivorous mammals and granivorous reptiles with greater proportions of threatened species while scavenger and invertebrate eating mammals, invertebrate eating birds, and herptile and egg eating reptiles with lower proportions of threatened species. When DD species were included in analyses, some results differed (Appendix A, Figures A-4, A-5, and A-6).

Some patterns of threatened species with high dietary specialization (i.e., a diet breadth of one) differed from the original diet group analysis (Figures 2-4, A-7, A-8, and A-9). Across all species combined, obligate endotherm eaters had a greater proportion of threatened species, while obligate invertebrate eaters had a lower proportion. The higher proportion of threatened obligate endotherm eaters was not observed at individual classes. The lower proportion of threatened obligate invertebrate eaters was driven by mammals and birds. At individual classes, granivorous birds and piscivorous reptiles had lower proportions of threatened species.

*Body Size and Trophic Level*

Including body size in analyses altered trophic level results. Across all species combined, large-bodied species in each trophic level had a higher proportion of threatened species (Figures 2-5, A-10, A-11, and A-12). Contrarily, small-bodied omnivores and predators had a lower proportion of threatened species. At individual classes, all large-bodied species in each class and trophic level, except predatory reptiles, had greater proportions of threatened species. For small-bodied species, birds had lower proportions of threatened species regardless of trophic level and reptiles had as expected proportions of threatened species in each trophic level. Furthermore, in mammals, small-
bodied omnivores and predators had lower proportions of threatened species while herbivores had an as expected proportion of threatened species.

**DISCUSSION**

This study is the first global analysis to quantify the proportions of threatened species in different trophic levels across all IUCN assessed birds, mammals, and reptiles. In quantifying the proportions of threatened species, we tested the assumption that predators have greater extinction risk than other species. This assumption has been assumed from theory, models, and smaller scale studies. In this large-scale study, only a few results corroborated this long-held assumption. We found that on the whole, herbivores, specifically frugivores and plant eaters, consistently were more threatened than expected. Thus, ecosystem services associated with herbivores including seed dispersal, vegetation structuring, and pollination may be negatively affected in the future if the threatened herbivores become extinct.

Contrary to some anecdotal evidence and theory, at the trophic level scale herbivores consistently had greater proportions of threatened species than expected. Our finding corroborates evidence that some herbivores are declining (Stoner et al. 2006), that herbivores tend to have high extinction risk in birds (Şekercioğlu et al. 2004), and that the world’s largest herbivores are at risk of population collapse (Ripple et al. 2015). This global herbivore crisis should be the focus of more conservation attention as it has already led to changes in some ecosystem functions (Galetti et al. 2013, Barnosky et al. 2015, Pérez-Méndez et al. 2016). Our results do not suggest that predators and omnivores are not critical to ecosystem functioning, nor that species in these trophic levels are not at risk of extinction. It is well established that loss of predators can trigger extinction
cascades (Donohue et al. 2017) and both predators and omnivores provide crucial ecosystem functions (Zhang et al. 2004, Estes et al. 2011) as well as ecosystem stability (Schmitz et al. 2000, Jonsson et al. 2006).

Our results show that within the broad classification of herbivores, plant eaters and frugivores are facing an extinction crisis. Plant eaters such as folivores, browsers, and grazers have experienced population declines, especially in sub-Saharan Africa (Stoner et al. 2006, Collen et al. 2009). Consequences of past extinctions of plant eaters have resulted in entire ecosystem shifts where savannas and grasslands became woodier habitats (Barnosky et al. 2015). With the high proportion of currently threatened plant eaters, more vegetation shifts may occur. Declines in frugivores in general and the extinction of large-bodied frugivores have been documented in several studies (Galetti et al. 2013, Pérez-Méndez et al. 2016). These extinctions have led to loss of seed dispersal (Cordeiro and Howe 2001) as extant frugivores are typically too small or specialized to feed on larger fruits that were dispersed by now extinct species (Malhi et al. 2016, Pérez-Méndez et al. 2016, Heinen et al. 2017). In addition, most frugivores are tropical (Cordeiro and Howe 2001, Kissling et al. 2009, Heinen et al. 2017) which is where the majority of threatened species occur (Vamosi and Vamosi 2008, Fritz et al. 2009), so geographic region may heavily influence the observed threatened species patterns.

The focus on predators having greater extinction risk typically concerns apex predators (Myers and Worm 2003, Ripple et al. 2014a). Our study did not explicitly define the difference between apex predators and other predators. However, our separation of vertebrate eaters from invertebrate eaters in the diet analyses was a crude approximation for apex predators. We found that only obligate endotherm eaters and
piscivorous birds were more threatened, and invertebrate eaters were generally less threatened than expected. Even predators that are highly specialized in their diet (e.g., vertebrate eaters) were still not proportionately more threatened than expected. Therefore, the notion that predators have the greatest extinction risk may be inaccurate.

Obligate endotherm eaters and piscivorous birds were two predatory groups that had greater proportions of threatened species. The pattern in obligate endotherm eaters was not supported at individual classes, but this difference in pattern may be due to smaller sample sizes or different expected proportions of threatened species within classes. Some of the classic examples of apex predators—wolves, big cats, raptors, and snakes—are endotherm eaters. These species tend to be large-bodied and are known to be highly threatened with extinction (Ripple et al. 2014). The other threatened predator group, piscivorous birds, are typically seabirds which have experienced large declines in population sizes (Spatz et al. 2014, Paleczny et al. 2015), causing many of these species to be classified as threatened by the IUCN. Piscivorous birds provide important links between marine and terrestrial nutrients, so the loss of these species may lead to dramatic shifts in nutrient transfer between aquatic and terrestrial systems (Young et al. 2017).

Scavengers, specifically avian and reptilian scavengers also had high proportions of threatened species. This result corroborates the idea of the avian scavenger crisis occurring across the globe (Schindler et al. 2013, Buechley and Şekercioğlu 2016) where many scavengers, particularly vultures, are at the brink of extinction because of human persecution and poisoning. Scavengers provide a crucial ecosystem service of removing dead animals, preventing the spread of disease (Donázar et al. 2016). With the extreme population declines of avian scavengers, disease outbreaks such as anthrax and rabies
may become more frequent (Buechley and Sekercioglu 2016). The majority of scavenging reptiles are turtles, which have high proportions of threatened species in general (Baillie et al. 2004) which most likely drives the pattern in this diet group.

Body size plays a major role in species extinction risk. Almost all large-bodied species regardless of trophic level were more threatened than expected. Our results corroborate the overwhelming evidence that large body size is related to high extinction risk (Purvis et al. 2000b, Reynolds et al. 2005b, Anderson et al. 2011). Interestingly, we found that large-bodied predatory reptiles had a lower than expected proportion of threatened species. This anomaly could be due to metabolic differences between endotherm and ectotherms. Ectotherms have lower metabolisms than endotherms (Gillooly and Charnov 2001), so they do not require as many resources and may not be as susceptible to resource altering disturbances as endothermic species. Despite this difference, the higher extinction risk of large-bodied species may have detrimental ecosystem consequences. Large-bodied species tend to have larger impacts on their environments compared to small-bodied species (Malhi et al. 2016). For example, elephants trample vegetation and remove woody debris, while smaller herbivores like mice cannot. In addition, when large-bodied species have become extinct, typically there have been no functionally equivalent species to replace the roles of that large-bodied species, so ecosystem functions may be lost (Pérez-Méndez et al. 2016).

The disparity in the percentages of DD species in each trophic level affected results. Considerably higher percentages of predators than herbivores and omnivores are classified as DD by the IUCN. When all DD species were classified as threatened, vertebrate predators had a greater proportion of threatened species than expected (Figure
This result was only found in one of 12 trophic level and DD classification scenarios, but it may indicate that if DD species are more often threatened than non-threatened as is suggested by the literature (Böhm et al. 2013), then at least across all vertebrate species, predators may also be highly threatened with extinction. If DD species were to be classified by the IUCN, we could know if this one scenario may accurately represent the extinction risk of predators. Therefore, more effort should be focused on assessing predators as they have the greatest percentages of DD species, so better estimates of species extinction risk across all trophic levels can be quantified.

Several limitations to these data and analyses are evident. First, the most prominent limitation is the lack of IUCN assessment of the majority of reptile species. Only ~50% of reptiles are on the IUCN Red List of Threatened Species (Uetz et al. 2017), compared to all mammals and birds. The majority of assessed reptiles are either well known species or ones thought to be highly threatened with extinction (Roll et al. 2017), so the results for reptiles may be biased by available data. Second, these data and analyses only include three major vertebrate species groups. It is unknown whether amphibians and fishes show the same patterns in extinction risk. Third, these data are mean trait values for species: they do not fully account for intraspecific variability. However, interspecific variability should be greater than intraspecific, so our results should not be greatly affected (Liu and Olden 2017). Fourth, these patterns in threatened species are not independent from patterns in species families and orders. Typically, species within the same family share life history and ecological traits, so they may have similar susceptibility to extinction (Reif and Štěpánková 2016). This clumping of species is especially noticeable in the reptiles where many of the herbivores and omnivores
happen to be Testudines. Testudines in general has a high proportion of threatened species, so the pattern in reptilian species may be heavily influenced by Testudines.

In conclusion, herbivores, specifically plant eaters and frugivores in mammals, birds, and reptiles as well as obligate endotherm eaters, scavenger reptiles, and piscivorous and scavenger birds are highly threatened with extinction. This finding is in stark contrast to the pervasive notion that predators in general are more susceptible to extinction. The results for diet group analyses corroborated evidence of population declines and extirpations in frugivores, plant eaters, scavengers, large apex predators, and piscivores across the globe. We suggest that more conservation attention should focus on the species groups with the greatest proportions of threatened species: herbivores in general along with the select predatory groups. A shift in conservation attention may prevent future species extinctions and subsequent loss of the ecosystem functions supported by species in different trophic levels.

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TABLES

Table 2-1. Percent of data deficient species in each trophic level by species clade.

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</tbody>
</table>
FIG. 2-1. Patterns of threatened species across trophic levels. The proportions of threatened species within each trophic level across all species (All) and within classes (mammals, birds, and reptiles). Dashed horizontal lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.
FIG. 2-2. Sensitivity analyses for patterns of threatened species across trophic levels. The proportions of threatened species within each trophic level across all species for each model scenario of data deficient (DD) classification (i.e., No DD species, Relaxed, Intermediate, and Precautionary) and each trophic level cutoff classification (i.e., 90, 80, and 70). For the DD classification either no DD species were included, all DD species were classified as non-threatened (relaxed), DD species were classified in proportion as threatened and non-threatened (Intermediate), or DD species were classified as threatened (Precautionary). Dashed horizontal lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.
FIG. 2-3. Patterns of threatened species across diet groups. The proportions of threatened species within each diet group across all species and within classes. Some species may be classified in multiple diet groups. Dashed horizontal lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.
FIG. 2-4. Patterns of threatened species across diet groups for species with high dietary specialization. The proportions of threatened species within each diet group across all species and within classes for species with a dietary breadth of one. Dashed horizontal lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.
FIG. 2-5. Patterns of threatened species across trophic levels and body size. The proportions of threatened species within each trophic level for large-bodied and small-bodied species separated across all species and within classes. Large-bodied species are those with a body mass of 5.5 kg, 60 g, and 15.5 g or greater for mammals, birds, and reptiles, respectively. Dashed horizontal lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.
CHAPTER III

BIOGEOGRAPHY OF THREATENED PREDATORS, OMNIVORES, AND HERBIVORES

ABSTRACT

Humans have affected Earth through numerous anthropogenic disturbances including pollution, deforestation, and overhunting. The magnitudes of these anthropogenic disturbances vary by region and habitat and may affect species with certain biological traits, including trophic level, more than others. Trophic level is an important characteristic as it is associated with a species’ ecological role. As more species become threatened with extinction, it is critical to determine patterns in threatened species to understand potential ecosystem consequences of extinction. If the patterns of threatened species in specific trophic levels can be quantified across regions, habitats, and associated anthropogenic threats, then we can determine region-specific, ecosystem-level consequences of potential extinctions.

We used bootstrapping with comparisons against a null model to determine whether proportions of threatened mammals, birds, and reptiles in each trophic level (i.e., predator, omnivore, and herbivore) differ from the expected proportion of threatened species across systems, habitats, and regions classified by the International Union for the Conservation of Nature. We then used binomial generalized linear models with a logit-link function to determine if anthropogenic disturbances differentially affect threatened species in different trophic levels. We found that terrestrial herbivores in tropical forests and some grassland habitats (reptiles) and marine predatory birds were more threatened than expected. Regionally, herbivores in sub-Saharan Africa, south and Southeast Asia,
and Oceania as well as predatory birds in Oceania and predatory reptiles in sub-Saharan Africa were highly threatened. Biological resource use, habitat alteration, and pollution were the most prominent anthropogenic threats affecting more threatened herbivores and sometimes omnivores than predators. Based on these results, we may expect to find decreases in ecosystem functions supported by herbivores in tropical regions including pollination, seed dispersal, and vegetation structuring. Due to the highly threatened nature of marine predatory birds, we may also see a decrease in the transfer of marine nutrients to land, which are important subsidies on islands.

INTRODUCTION

Earth has entered a new geologic epoch, the Anthropocene, marked by a human-caused biodiversity crisis (Williams et al. 2016). Thus far in the Anthropocene, humans have extensively altered environments through nutrient additions, deforestation, dredging oceans, impounding rivers, and changing climate variables as a result of the release of CO₂ from burning fossil fuels (as reviewed by Vitousek et al. 1997). Human-induced changes to landscapes have resulted in the extinction of numerous island species and altered the species compositions in other regions (Boivin et al. 2016). The extent of landscape alterations will continue to increase in the future as the human population and the need for resources increase, perpetuating the potential for more species extinctions (Vitousek et al. 1997). Due to the domination of humans on Earth’s ecosystems, 18% of vertebrates are currently threatened with extinction ("The IUCN Red List of Threatened Species" 2016; Young et al. 2016). The magnitude of this biodiversity crisis varies across species due to each taxon’s biological traits (Cardillo et al. 2008, Anderson et al. 2011) as

Biological traits determine a species’ inherent susceptibility to anthropogenic disturbances (Cardillo et al. 2004). Traits such as large body size (Reynolds et al. 2005b, Anderson et al. 2011) and high age to maturity (Anderson et al. 2011) are linked to higher susceptibility to disturbances, because populations of species with these traits cannot recover from disturbances quickly. Although many biological traits are used to predict which species may become extinct in the future (Dulvy and Reynolds 2002, Ribeiro et al. 2016), they cannot tell us what ecosystem consequences will result from those extinctions. However, trophic level is related to extinction risk of species (Valentine, unpublished data; Duffy 2003; Myers & Worm 2003) and is directly related to each species’ ecological role (Dobson et al. 2006, Duffy et al. 2007, Estes et al. 2011). Therefore, patterns in extinction risk based on trophic level can provide insight into what ecosystem consequences may occur in the future.

A species’ natural history varies across habitats, regions, and taxa due to evolutionary selective pressures (Cardillo et al. 2008, Fritz et al. 2009). For example, species found at high elevations are physiologically constrained by abiotic factors such as lower temperatures compared to species at lower elevations. Species within different regions have varying natural histories due to evolving with different environmental factors. Due to this fact, when anthropogenic disturbances occur in various environments, these disturbances may interact in differential ways to influence species extinction risk (Cardillo 2003, Cardillo et al. 2006, 2008). Because of this interaction, quantifying the extinction risks of species in different trophic levels and taxonomic groups across
biogeographic areas yields important information on how humans and other disturbances
have affected species extinction risk.

Across geopolitical regions, humans have differentially altered environments
(Yackulic et al. 2011). The highest intensity of anthropogenic disturbance has occurred in
resource-rich regions like the tropics (Rapacciuolo et al. 2017) and along coasts (Lotze et
al. 2006). These resource-rich regions also harbor high numbers of species. The
combination of high anthropogenic disturbance and high species richness has led to
resource-rich areas to be classified as hotspots of threatened species (Brooks et al. 1997,
Vamosi and Vamosi 2008). Many resource-rich areas occur in developing regions, such
as the Amazon, sub-Saharan Africa, and Southeast Asia where there tends to be an
overabundance of highly threatened species due to the large magnitude of anthropogenic
disturbances occurring (Cardillo et al. 2006, Lotze et al. 2006). Contrarily, developed,
westernized regions like Europe and North America tend to have fewer threatened
species as the species most affected by anthropogenic disturbances have adapted or have
already been extirpated (Cardillo et al. 2006, Lee and Jetz 2011).

Similar to geographic regions, extinction risk also differs across systems and
habitats. Terrestrial systems have been extensively influenced by humans for far longer
than marine systems. The pervasive effects of humans on land is thought to have
contributed to over 500 terrestrial species extinctions occurring within the past ~500
years (Baillie et al. 2004, Dirzo et al. 2014, McCauley et al. 2015). In marine systems, far
fewer known species extinctions have occurred. The lower number of extinctions may be
due to greater connectivity in marine systems, a shorter duration of anthropogenic
disturbance, or less knowledge about marine species (McCauley et al. 2015). However, in
freshwater systems, the proportion of threatened species is exceptionally high (Angermeier 1995, Reynolds et al. 2005b, Wake and Vredenburg 2008). As human modification to aquatic ecosystems intensifies, it may be expected that more species will soon become threatened or extinct in aquatic systems (McCauley et al. 2015).

Much of the difference in threatened species biogeography is thought to stem from the magnitude and type of disturbances occurring within a region or habitat (Ducatez and Shine 2017). Anthropogenic disturbances including habitat alteration, biological resource use, pollution, invasive species, and climate change are the major proximate causes of species loss (Young et al. 2016). Because of the nature of these different disturbances, the susceptibility of species in different trophic levels to these disturbances may vary. Habitat alteration is currently the leading cause of species loss (Young et al. 2016, Ducatez and Shine 2017), and habitat alteration occurs extensively near large human population centers, in tropical forests, and along large rivers (Lotze et al. 2006, Rapacciuolo et al. 2017). Habitat alteration may more heavily affect herbivores as they rely directly on their habitat’s vegetation as a food resource. Biological resource use, including overexploitation, is the direct exploitation of species for consumption, pets, or other applications like medicine. This anthropogenic threat occurs heavily in areas of high biodiversity such as the tropics where species, especially herbivores, are hunted for bushmeat (Peres and Palacios 2007). Pollution is a more latent driver of extinction risk (Dudgeon et al. 2006, Collen et al. 2014b) as it stems from exceptionally long-lasting chemicals (e.g., methylmercury) that can persist in the environment for decades while species accumulate toxins within their tissues (Sergio et al. 2008). Predatory species may be affected more than species in lower trophic levels by pollution.
due to bioaccumulation or through consuming highly polluted prey items (Cai et al. 2007). Invasive species heavily decimate island-dwelling species, especially flightless birds and those without natural predators (Boyer 2008, Young et al. 2016). Invasive species tend to be generalists, outcompeting large, slow-growing or specialist native species (Reynolds et al. 2005b). Climate change, an indirect anthropogenic disturbance, affects species globally, but especially in the polar and tropical regions (Carpenter et al. 2008, Maclean and Wilson 2011, Young et al. 2016). As temperature and precipitation patterns change, species adapted to their formerly stable climates will be most affected (Carpenter et al. 2008). These five disturbances may differentially act on the inherent biological characteristics of species in different trophic levels and across regions, affecting patterns of species extinction risk.

Our main goal was to understand the biogeography of threatened species through quantifying the proportions of threatened predators, omnivores, and herbivores across systems, habitats, geographic regions, and anthropogenic threats to which species are exposed. To accomplish this goal we had four objectives. First, we quantified the proportions of threatened species in freshwater, marine, and terrestrial systems as a function of trophic level. Second, we quantified the proportions of threatened species in different habitats (e.g., marine coastal, tropical forest, savanna), a refinement of system, as a function of trophic level. Third, we quantified the proportions of threatened species in different geographic regions (e.g., South and Southeast Asia, North America, Oceania) as a function of trophic level. Fourth, we quantified the proportions of threatened species affected by the five main anthropogenic threats to determine if specific threats
differentially affect species in different trophic levels. Our dataset included all bird, mammal, and reptile species assessed by the IUCN.

METHODS

Overview

We created a dataset containing biological and geographical data on all extant mammal (5,567), bird (11,121), and reptile (5,338) species assessed on the 2017 IUCN Red List of Threatened Species (current as of February 23, 2017). First, we assigned binary threat assessments to each species. Second, we classified the trophic levels of each species. Third, we combined this data with species-specific geographic region, habitat, system, and threat information from the IUCN Red List of Threatened Species. We used the completed dataset to quantify the observed proportions of threatened species in specific trophic levels (i.e., predator, omnivore, and herbivore) in relation to the expected proportions of threatened species.

Binary Threat Classification

For each species assessed by the IUCN, we assigned a binary threat classification of “threatened” or “non-threatened”. Species with IUCN assessments of “critically endangered”, “endangered”, and “vulnerable” were considered threatened with extinction, and species with “near threatened”, “least concern”, and “lower risk” assessments were considered non-threatened (Baillie et al. 2004, González-Suárez et al. 2013). This binary classification system represents the two potential outcomes in an extinction event (i.e., extinction or survival; Davidson et al. 2009, González-Suárez et al.
2013, Hilbers et al. 2016, Payne et al. 2016). Species assessed as “extinct” (EX) or “extinct in the wild” (EW) were not included in analyses.

A large proportion of species assessed by the IUCN are listed as “data deficient” (DD). We accounted for DD species in two ways. First, we analyzed proportions of threatened species excluding all DD species. Second, we analyzed proportion of threatened species including DD species using three classification scenarios: relaxed, precautionary, and intermediate (Purvis et al. 2000a, González-Suárez et al. 2013, Collen et al. 2014b, Payne et al. 2016). For the relaxed scenario, all DD species were classified as non-threatened. In contrast, for the precautionary scenario, all DD species were classified as threatened. These two scenarios represent the lower and upper boundaries of the true model if DD species were to be assessed by the IUCN (González-Suárez et al. 2013, Payne et al. 2016). For the intermediate scenario, DD species were randomly classified based on current proportions using the following equation from Collen et al. (2014): threatened / (non-threatened – DD – EX – EW). Results for when DD species were included in analyses are provided in Appendix B, Figures B-1-B-12.

**Trophic Level**

Using dietary information, we classified species into three trophic levels: predator, omnivore, and herbivore. For data that described diet using percentages, predators were defined as having a > 90% animal-based diet, herbivores as having > 90% plant-based, and omnivores a more even distribution of diet. For ranked presence-absence data, predators were defined as animals that primarily consumed animal-based diet items and could consume plant-based diet items in small amounts; herbivores primarily consumed plant-based diet items and could consume animal-based diet items in small
amounts, and omnivores primarily or secondarily consumed a mixture of both types of
diet items. For unranked presence-absence data, predators consumed only animal-based
diet items, herbivores only plant-based diet items, and omnivores diet items from both
categories.

 Systems, Habitats, Regions, and Threats

To look at anthropogenic effects on trophic level patterns, all species-specific
extrinsic variables (i.e., systems, habitats, regions, and associated anthropogenic threats)
were downloaded from the IUCN Red List of Threatened Species. Major systems,
habitats, geographic regions (locations on the IUCN Red List of Threatened Species), and
anthropogenic threats were classified as either present or absent for each species.

The major habitats classified by the IUCN included multiple marine, terrestrial,
and artificial habitats, other habitats, and one freshwater habitat. Of the marine habitats,
no mammals, birds, or reptiles occurred in the marine deep benthic habitat, so this habitat
type was excluded from analyses. Of the terrestrial habitats, we subset the forest habitat
category into tropical and temperate forests. We did not include artificial (i.e., introduced
vegetation, artificial aquatic, and artificial terrestrial) or other habitats (i.e., other and
unknown) in analyses.

The major threats classified by the IUCN were reduced to only include the five
major anthropogenic threats affecting vertebrates (i.e., habitat alteration, biological
resource use, climate change, pollution, and invasive species) in analyses (Young et al.
2016). We combined several IUCN threats into habitat alteration: residential and
commercial development, agriculture and aquaculture, energy production and mining,
transportation and service corridors, human intrusions and disturbance, and natural
system modifications (Ducatez and Shine 2017, Young et al. 2016). Species could be associated with multiple anthropogenic threats.

The geographic regions on the IUCN Red List of Threatened Species included the oceanic regions and major terrestrial geopolitical regions. Due to small sample sizes, the oceanic regions (e.g., western central Atlantic Ocean, Atlantic-Antarctic Ocean), encompassing the Atlantic, Pacific, and Indian oceans were combined into their respective major ocean (Atlantic, Pacific, or Indian). All other ocean, sea, and terrestrial regions remained as defined on the IUCN Red List of Threatened Species.

Analyses

We used bootstrapping to numerically simulate the proportions of threatened species in each group. We compared expected versus observed proportions of threatened species for 1) trophic levels across systems, 2) trophic levels across habitat types, and 3) trophic levels across geographic regions. We then retested the above four questions within each class (i.e., Aves, Mammalia, and Reptilia). To conduct analyses, we first calculated the expected proportion of threatened species for all species combined and for each class. The expected value was the total proportion of threatened species across all species combined or within a class. To generate the observed proportion of threatened species, we used bootstrapping. For each bootstrap, the sample size was the number of focal species (e.g., number of terrestrial mammalian herbivores). Bootstrapping was repeated for 10,000 iterations per comparison (Collen et al. 2009). The observed proportion of threatened species for each trophic level or diet category was calculated as a range of the median and 2.5% and 97.5% quantile proportions of the 10,000 bootstrapping iterations (Loh et al. 2005, Collen et al. 2009). A significant difference in
the expected and observed proportions of threatened species was indicated by whether the expected value fell outside of the range of observed bootstrapped values. To test whether anthropogenic disturbances differentially affect the proportions of threatened species in different trophic levels, we used generalized linear models with logit-link function and Tukey honest significant difference post-hoc analyses to compare the proportions of threatened species affected by each anthropogenic threat. Comparisons of the proportions of threatened species were only made within one anthropogenic threat type and within a class. All analyses were run in R v 3.3.3 (R Core Team 2017). All comparisons of the proportions of threatened species resulting from bootstrapping are relative to the expected proportion of threatened species. Proportions of threatened species for less than five individuals are not discussed due to small sample size but are still shown in figures.

RESULTS

Systems

When all species were combined, proportions of threatened species within each trophic level varied across systems (Figure 3-1). Including DD species altered some results (Appendix B, Figures B-1, B-2, and B-3). Across all species, marine herbivores, marine predators, and terrestrial herbivores had greater proportions of threatened species. At individual classes, the higher proportion of threatened marine herbivores was largely driven by mammals and reptiles, and the higher proportion of marine predators was driven by birds.

In freshwater systems across all species combined, predators had a lower proportion of threatened species. At individual classes, this lower proportion of threatened predators was driven by birds. In addition, herbivorous and omnivorous birds
also had lower proportions of threatened species while herbivorous mammals and reptiles and omnivorous reptiles had greater proportions of threatened species.

In terrestrial systems across all species combined, herbivores had a greater proportion while omnivores and predators had lower proportions of threatened species. At individual classes, the greater proportion of threatened herbivores was driven by all classes, the lower proportion of threatened omnivores was driven by mammals and birds, and the lower proportion of threatened predators was driven by mammals and reptiles.

*Habitats*

Habitats represent a subset of ecosystems within marine, freshwater, and terrestrial systems. When all species were combined, proportions of threatened species varied across habitat types (Figure 3-2). When DD species were included in analyses, some results differed (Appendix B, Figures B-4, B-5, and B-6). In marine habitats, herbivores in the four habitats as well as coastal, neritic, and oceanic predators had greater proportions of threatened species. At individual classes, the high proportions of threatened marine herbivores were driven by mammals and reptiles and this same trend was observed in marine predatory birds. In addition, omnivorous marine oceanic birds and omnivorous marine intertidal reptiles had greater proportions of threatened species.

In freshwater habitats (i.e., wetlands) across all species combined, predators and omnivores had lower proportions of threatened species. At individual classes, the lower proportion of threatened predators was driven by reptiles and birds, and the lower proportion of threatened omnivores was driven by mammals and birds. Furthermore, reptilian omnivores had a greater proportion, while avian herbivores had a lower proportion of threatened species.
In terrestrial habitats across all species combined, herbivores in tropical forests had a greater proportion of threatened species, a pattern that was observed in all classes. Species in all trophic levels within shrublands, savannas, and grasslands, predators and omnivores in rocky areas, deserts, and temperate forests, and omnivores in tropical forests had lower proportions of threatened species. At individual classes, the lower proportions of threatened species in all trophic levels within shrublands, savannas, and grasslands were seen in all classes except herbivorous reptiles. Herbivorous reptiles had an as expected proportion in savannas and higher proportions of threatened species in shrublands and grasslands. The lower proportions of threatened species in all trophic levels within rocky areas and deserts were driven by all classes except predatory birds which had as expected proportion of threatened species. The lower proportion of threatened species in all trophic levels within temperate forests was seen in all three classes except predatory birds and omnivorous reptiles which had as expected proportions of threatened species. The trend of a lower proportion of threatened omnivores in tropical forests was driven by birds. Other patterns at individual classes included lower proportions of threatened predatory mammals in tropical forests and caves and herbivorous birds in rocky areas. There was a higher proportion of threatened omnivorous reptiles in tropical forests.

**Geographic Locations**

When all species were combined, proportions of threatened species varied across geographic regions (Figure 3-3). When DD species were included some results differed (Appendix B, Figures B-7, B-8, and B-9). In the oceans, across all species, predators in the Atlantic Ocean had a greater proportion of threatened species. At individual classes,
this higher proportion of threatened Atlantic Ocean predators was not supported. Reptilian predators (e.g., sea snakes) in the Pacific and Indian oceans had lower proportions of threatened species.

In the Americas, the majority of species in different trophic levels had lower proportions of threatened species. Across all species, species in all trophic levels in North America and Mesoamerica and predatory and omnivorous species in South America had lower proportions of threatened species. In individual classes, the lower proportions of threatened species in each trophic level within North America were driven by all mammals, omnivorous and herbivorous birds, and predatory reptiles. In Mesoamerica the lower proportions of threatened species in each trophic level were driven by predatory and herbivorous mammals, predatory and omnivorous birds, and predatory reptiles. In South America the lower proportions of threatened predators and omnivores were seen in all classes. In addition, avian herbivores in the Caribbean Islands had a lower proportion of threatened species. Reptilian omnivores in Mesoamerica were the only species group that had a higher proportion of threatened species in the Americas.

In Eurasia, the majority of species in different trophic levels had lower proportions of threatened species. Across all species combined, species in all trophic levels in West and Central Asia and North Asia along with omnivores and predators in East Asia, South and southeast Asia, and Europe had lower proportions of threatened species. Contrarily, herbivores in South and southeast Asia had a higher proportion of threatened species. At individual classes, the lower proportions of threatened species in West and Central Asia were primarily driven by all mammals and birds as well as predatory reptiles. The lower proportions of threatened species in North Asia were driven
by all mammals and omnivorous birds. The lower proportions of threatened omnivores and predators in East Asia were driven by all classes, except for omnivorous reptiles which had a greater proportion of threatened species. The lower proportions of threatened omnivores and predators in South and southeast Asia were driven by predators in all classes and omnivorous birds. The higher proportion of threatened herbivores in South and southeast Asia was driven by mammals and reptiles. Additionally, in South and southeast Asia, omnivorous reptiles had a greater proportion of threatened species.

In Africa across all species combined, omnivores and predators had lower proportions of threatened species in North Africa. Omnivores had a lower proportion and herbivores a higher proportion of threatened species in sub-Saharan Africa. At individual classes, the lower proportions of threatened predators and omnivores in North Africa were seen in all classes, except reptilian omnivores. The lower proportion of threatened omnivores in sub-Saharan Africa was driven by mammals and birds, while the higher proportion of threatened herbivores in this region was driven by mammals and reptiles. Furthermore, reptilian predators and omnivores had higher proportions while mammalian predators and avian herbivores had lower proportions of threatened species in sub-Saharan Africa.

In Oceania across all species combined, omnivores had a lower proportion, while herbivores had a higher proportion of threatened species. The lower proportion of threatened omnivores was not supported in individual classes. The higher proportion of threatened herbivores was driven by mammals. Additionally, mammalian predators had a lower proportion, while avian predators and reptilian omnivores had higher proportions of threatened species.
**Threats**

Proportions of threatened species affected by the five major threat types differed across trophic levels (Figure 3-4). When DD species were included in analyses, some results differed (Appendix B, Figures B-10, B-11, and B-12). The proportions of threatened species affected by habitat alteration differed across trophic levels ($\chi^2 = 43.036, \text{DF} = 2, P < 0.001$). Greater proportions of threatened herbivores ($P < 0.001$) and omnivores ($P < 0.001$) were affected by habitat alteration than predators. At individual classes, some results differed from when all species were combined. Mammals showed similar differences in proportions of threatened species in each trophic level affected by habitat alteration ($\chi^2 = 22.955, \text{DF} = 2, P < 0.001$) as the combined species analysis. The proportions of threatened birds ($\chi^2 = 6.907, \text{DF} = 2, P = 0.032$) and reptiles ($\chi^2 = 6.9177, \text{DF}=2, P = 0.031$) affected by habitat alteration were higher for herbivores than predators ($P = 0.024$ for birds, $P = 0.036$ for reptiles).

The proportions of threatened species affected by biological resource use differed across trophic levels ($\chi^2 = 86.808, \text{DF} = 2, P < 0.001$). A greater proportion of threatened herbivores was affected by biological resource use than omnivores ($P = 0.012$) and predators ($P < 0.001$), and a greater proportion of threatened omnivores were affected by biological resource use compared to predators ($P < 0.001$). At individual classes, mammals showed similar patterns in proportions of threatened species in each trophic level affected by biological resource use ($\chi^2 = 54.371, \text{DF} = 2, P < 0.001$) as when all species were combined. In birds, the proportions of threatened species affected by biological resource use were similar across species in all trophic levels ($\chi^2 = 4.214, \text{DF} = 2, P = 0.122$). In reptiles, the proportions of threatened species affected by biological
resource use differed across trophic levels ($\chi^2 = 43.073$, DF = 2, $P < 0.001$) and were higher in herbivores ($P < 0.001$) and omnivores ($P < 0.001$) than predators.

The proportion of threatened species affected by climate change differed across trophic levels ($\chi^2 = 12.226$, DF = 2, $P = 0.002$). Across all species, only a greater proportion of threatened herbivores were affected by climate change than omnivores ($P = 0.002$). In mammals, the proportions of threatened species in each trophic level were affected similarly by climate change ($\chi^2 = 3.1991$, DF = 2, $P = 0.202$). The proportion of threatened birds affected by climate change differed across trophic levels ($\chi^2 = 7.1151$, DF = 2, $P = 0.029$), with a greater proportion of predators affected than omnivores ($P = 0.044$). The proportions of threatened reptiles affected by climate change were similar across trophic levels ($\chi^2 = 0.506$, DF = 2, $P = 0.777$).

The proportions of threatened species affected by pollution differed across trophic levels ($\chi^2 = 20.375$, DF = 2, $P < 0.001$). Greater proportions of threatened herbivores ($P = 0.005$) and omnivores ($P < 0.001$) were affected by pollution than predators. The proportions of threatened mammals in each trophic level were similarly affected by pollution ($\chi^2 = 4.6671$, DF = 2, $P = 0.097$). The proportions of threatened birds ($\chi^2 = 8.7202$, DF = 2, $P = 0.013$) and reptiles ($\chi^2 = 8.3754$, DF = 2, $P = 0.015$) affected by pollution differed across trophic levels, and a greater proportion of threatened omnivores were affected by pollution than predators ($P = 0.044$ for birds, $P = 0.168$ for reptiles).

The proportions of threatened species affected by invasive species were similar across trophic levels ($\chi^2 = 1.9$, DF = 2, $P = 0.387$). All mammals, birds, and reptiles in different trophic levels were similarly affected by invasive species as well.
DISCUSSION

These analyses are the first to quantify the proportions of all IUCN assessed threatened mammals, birds, and reptiles in different trophic levels across systems, habitats, geographic regions, and associated threats. In this large-scale study, we found that the proportions of threatened species in different trophic levels varied across biogeographic regions and habitats. In general, terrestrial herbivores, mainly in tropical forests, marine predatory birds, and marine and freshwater herbivorous mammals and reptiles had higher proportions of threatened species than expected. These patterns may be caused by differential targeting of species in trophic levels by anthropogenic threats, socio-political, cultural, or economic factors associated with specific regions (Karanth et al. 2010). Furthermore, our results suggest that the provisioning of ecosystem functions such as seed dispersal and pollination in the tropics as well as the transfer of marine nutrients to land may decline.

Higher than expected proportions of threatened herbivores was a relatively consistent pattern across terrestrial, freshwater, and marine systems. This pattern was most prominent in terrestrial ecosystems where herbivores in each class were more threatened than expected. In addition, herbivorous mammals and reptiles were more threatened than expected in freshwater and marine systems. In contrast to freshwater and terrestrial systems, predatory birds had a higher proportion of threatened species in marine systems. Terrestrial herbivores may be consistently highly threatened due to the large cumulative anthropogenic impact on terrestrial systems compared to aquatic systems (Dirzo et al. 2014, McCauley et al. 2015). Anthropogenic disturbances such as habitat alteration and biological resource use may impact herbivores and sometimes
omnivores more than predators as our results concerning anthropogenic disturbances suggest, contributing to this pattern of herbivores being more threatened than expected in systems. Freshwater mammalian herbivores and predators include threatened species such as hippos, tapirs, manatees, river dolphins, and otters. Marine predatory birds may be more threatened than expected due to declines in seabirds (Spatz et al. 2014, Paleczny et al. 2015) which are mostly predatory species.

Within terrestrial habitats, herbivores in each class inhabiting tropical forests and herbivorous reptiles inhabiting grasslands and shrublands were proportionately more threatened than expected. Tropical forest herbivores may be disproportionately threatened because anthropogenic disturbances like habitat alteration and biological resource, the anthropogenic threats that proportionately affect more herbivores in our results, are concentrated in tropical regions (Peres and Palacios 2007, Hansen et al. 2013).

Declines in tropical herbivores may have large ecological consequences. For example, Galetti et al. (2013) found that declines in native frugivores in tropical forests have led to a reduction in seed dispersal of many plant species. Our results suggest that future declines in tropical herbivores are likely. Such a decline will likely influence future vegetation structure by possibly shifting the ecosystem type (Barnosky et al. 2015), decreasing pollination (Sekercioğlu 2011), or reducing seed dispersal (Galetti et al. 2013, Pérez-Méndez et al. 2016). Furthermore, secondary extinctions of tropical plants that have symbiotic relationships with herbivores are likely to occur (Brodie and Aslan 2012).

Evidence suggests that in general freshwater and wetland species are some of the most threatened species due to impoundments, nutrients, and pollution (Angermeier 1995, Reynolds et al. 2005b, Cumberlidge et al. 2009, Junk et al. 2013, Collen et al.)
2014a, Kopf et al. 2016). However, for wetland habitats we found that only omnivorous reptiles had a greater proportion of threatened species than expected. The majority of the freshwater omnivorous reptiles are turtles which are one of the most threatened species groups (Baillie et al. 2004), potentially driving this result. The lack of higher proportions of threatened species in wetland habitats from our analyses may differ from other studies because fishes, amphibians, and invertebrates are not included in our analyses, which are the taxa that are often cited as highly threatened in wetland habitats.

Within marine systems, predatory birds and herbivorous mammals and reptiles are highly threatened. These results correspond with previously published evidence of large population declines in seabirds (Paleczny et al. 2015) and the degradation of coastal areas that are important seabird habitats (Lotze et al. 2006). Although we found invasive species to equally affect species in all trophic levels, it is supported in the literature that invasive species have led to population declines in many seabirds that nest on islands (Spatz et al. 2014) or coastal regions (Jones et al. 2008). Not only are most seabirds predators, but we also found that predatory birds were highly threatened in Oceania, which is mainly comprised of island nations. Marine herbivorous reptiles (e.g., marine iguanas) are also known to be highly threatened species (Baillie et al. 2004) due to invasive species and development on islands. The marine classified herbivorous mammals included mostly coastal lagomorphs and rodents. These marine herbivores may be highly threatened because of the large magnitude of urbanization and development (i.e., habitat alteration) that occurs in coastal regions (Lotze et al. 2006). Based on our results, habitat alteration disproportionately affects threatened mammalian herbivores compared to predators, which may in part explain why mammalian herbivores are
overrepresented in threatened species along coasts. However, we are unsure why marine coastal herbivores may be more threatened than omnivores in this habitat as threatened omnivores were similarly affected by habitat alteration. With the likely extinctions of marine predatory birds and herbivorous mammals and reptiles, the transfer of important marine nutrients to land will likely decrease, with consequences for soil and plant nutrient compositions (Young et al. 2017).

Based on our analyses, herbivores in Oceania, South and Southeast Asia, and sub-Saharan Africa are overrepresented in threatened species. Additionally, predatory birds in Oceania as well as predatory and omnivorous reptiles in sub-Saharan Africa were more threatened than expected. Oceania, South and Southeast Asia, and sub-Saharan Africa contain many developing countries, which likely puts more anthropogenic pressure on the species living within them. Reptiles in general are highly threatened in sub-Saharan Africa (Tingley et al. 2016), and anthropogenic pressures in sub-Saharan Africa may not target species in one trophic level over another, contributing to our finding that reptiles in all trophic levels had greater proportions of threatened species. Surprisingly, species in no specific trophic level were overrepresented in threatened species in South America and Mesoamerica, except omnivorous reptiles in Mesoamerica. It would be expected that areas with high rates of deforestation and other habitat alterations as seen in the Amazon and Atlantic rainforests and Pampas would influence species in multiple trophic levels (Hansen et al. 2013). For example, frugivorous species have declined greatly in South America (Galetti et al. 2013), yet based on our results herbivores are not overrepresented in threatened species in this region.
We found that threatened herbivores and omnivores are impacted by habitat alteration, biological resource use, and pollution in greater proportions than predators. Habitat alteration may target omnivores and herbivores more than predators because these species rely directly on vegetation for food and the vegetation structure is generally the first aspect of a landscape to be altered (Cordeiro and Howe 2001). In addition, more plant-eating species live in tropical forests, where habitat alteration is the most severe (Hansen et al. 2013). Thus, herbivores and omnivores (i.e., plant-eating species) may be disproportionately affected by habitat alteration in the tropics. Biological resource use, especially hunting for human consumption, often targets large species or herbivores (Peres and Palacios 2007), which may explain why we found more threatened herbivores affected by this threat compared to omnivores and predators. In addition, tropical sub-Saharan Africa has exceptionally high bushmeat hunting and exportation rates (Fa et al. 2002), potentially contributing to our result of high proportions of threatened herbivores in this region. Although we predicted that pollution would affect predators more than species in other trophic levels due to bioaccumulation (Nakamaru et al. 2003), we did not find this pattern. Rather, we found that pollution proportionately affected more omnivores and in a few cases, herbivores (mammals and reptiles), compared to predators. Whether through direct or indirect targeting, it is clear that humans are having a large impact on threatened herbivores and omnivores through habitat alteration, biological resource use, and pollution.

Invasive species and climate change did not consistently target species in any particular trophic level. Invasive species affected similar proportions of threatened species across all trophic levels and classes while climate change differentially affected
threatened species in each vertebrate class. Invasive species tend to heavily affect native prey species that do not have natural predators or are flightless (Ducatez and Shine 2017); however, these “prey” species are not necessarily species of lower trophic levels. For example, many of the most heavily affected species by invasion are seabirds (Jones et al. 2008) which tend to be predators. Furthermore, invasive species can outcompete and displace other species in the same trophic level (Snyder and Evans 2006). The fact that invasive species can influence native fauna through both predation and competition may contribute to our finding that invasive species similarly affected threatened species in all trophic levels. Climate change is a global phenomenon that can affect all species. Climate change may not differentially affect species in different trophic levels because it affects regions more than individual species (Deutsch et al. 2008). Even though invasive species and climate change do not appear to differentially affect threatened species within certain trophic levels, they remain major drivers of extinction, and may target species in specific trophic levels in the future.

Extinction filters may play a role in current threatened species patterns. Humans have influenced species extinctions for thousands of years from overhunting large megafauna in the Pleistocene (Barnosky et al. 2004) to over 2,000 island birds being decimated by invasive species, hunting, and habitat alteration (Steadman 1995). These past extinctions have filtered the pool of species that may be threatened with extinction today. Because current species have already gone through an extinction filter, current patterns of extinction risk may not reflect long-term patterns of extinction vulnerability (Balmford 1996). Extinction filters may explain our general trophic level patterns of omnivores and predators having as expected or lower than expected proportions of
threatened species in many systems, habitats, and geographic regions. To answer whether extinction filters play a major role in current threatened species patterns, future research should conduct analyses on the biogeography of extinct species, particularly predators and omnivores.

Our study has several limitations regarding the data and analyses. First, the IUCN data is lacking for reptiles. Only about 50% of reptiles are assessed by the IUCN (Uetz et al. 2017), so patterns of threatened species may be different if all reptiles were to be assessed. Many of these unassessed species are located in developing regions (Tingley et al. 2016), so the patterns of threatened species in developing regions may be most affected. Second, the IUCN is lacking system (3.74% of assessed mammals, birds, and reptiles), habitat (2.68%), region (2.81%), and associated threat (58.5%) information for species. Location, system, and habitat information seems to be well covered on the IUCN Red List of Threatened Species. However, the larger percentage of species without associated threat information is concerning for our analyses. We do not know whether the species with associated threat information are representative of all species (i.e., species with and without classified associated threats). Thus, if all species were to have their associated threats identified, our results may differ. Third, our results discuss trophic level patterns in mammals, birds, and reptiles. Biogeographic trophic level patterns may be different for other species groups like amphibians and fishes. Further analyses, should include more vertebrate and invertebrate groups if possible.

In conclusion, terrestrial herbivores, specifically in tropical forests, as well as marine predatory birds, marine herbivorous mammals and reptiles, and shrubland and grassland herbivorous reptiles are highly threatened with extinction. In addition to these
habitat patterns, hotspots of threatened herbivores, predatory birds, and omnivorous reptiles exist in the tropics, especially in Oceania, sub-Saharan Africa, and south and Southeast Asia. Within developed, westernized regions like North America and Europe, there were lower proportions of threatened species within all trophic levels which may be due to extinction filters like extirpations that already removed vulnerable species. In general, our patterns in threatened species may be heavily affected by anthropogenic disturbances as habitat alteration, biological resource use, and pollution tend to affect threatened herbivores and sometimes omnivores more than predators. These most highly threatened species groups and regions should be the main focus of future conservation efforts to preserve species as well as the ecosystem functions they support.

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FIG. 3-1. Patterns of threatened herbivores, omnivores, and predators across systems. The proportion of threatened species within each trophic level for species in the three major system types (marine, freshwater, terrestrial). Some species may be classified into multiple systems. Dashed horizontal lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.
FIG. 3-2. Patterns of threatened herbivores, omnivores, and predators across habitats. The proportion of threatened species within each trophic level for species in the major habitat types classified by the IUCN. Some species may be classified into multiple habitats. Dashed vertical lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.
FIG. 3-3. Patterns of threatened herbivores, omnivores, and predators across geographic regions. The proportions of threatened species within each trophic level for species in the major geographic regions classified by the IUCN. Some species may be classified into multiple geographic regions. Dashed vertical lines represent the expected values (i.e., null model). Groups with median ± 95% confidence above the dashed line are proportionally more threatened than expected, while groups with median ± 95% confidence below the dashed line are proportionally less threatened than expected. Asterisks denote significant differences from the expected value.

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FIG. 3-4. Proportions of threatened herbivores, omnivores, and predators affected by five anthropogenic threats. The mean proportions ± SE of threatened species within each trophic level for species associated with the five major threat types (habitat alteration, biological resource use, climate change, pollution, and invasive species). Some species may have multiple associated threats. Letters denote significant differences ($P < 0.05$) between proportions of threatened species in each trophic level within an anthropogenic threat.
CHAPTER IV
SUMMARY AND CONCLUSIONS

The overall goal of our research was to quantify the extinction risks of species in different trophic levels across multiple spatial scales for mammals, birds, and reptiles. In Chapter 2 of this research, we investigated whether proportions of threatened species varied across trophic levels, diet groups, and body sizes. To our knowledge, this is the first study to quantify the proportions of threatened species in each trophic level, testing the long-held assumption that predators have greater extinction risk than species in other trophic levels. Contrary to this assumption, we found that herbivores, not predators, were the most threatened species group. In diet analyses, plant eaters and frugivores consistently had greater proportions of threatened species, consistent with literature indicating population declines in these groups (Stoner et al. 2006, Galetti et al. 2013). Although in general herbivores had higher proportions of threatened species, species in some predatory diet groups were also overrepresented in threatened species. These diet groups included scavengers, obligate endotherm eaters, and piscivorous birds. In the literature it is often suggested that apex predators are the most threatened species. However, we found that even species in most vertebrate-eater groups were not proportionally overrepresented as threatened. Trophic level differences in proportions of threatened species were not apparent when body size was included. All large species except predatory reptiles had greater proportions of threatened species than expected, supporting the evidence that large bodied species are the most prone to extinction (Myers and Worm 2003, Reynolds et al. 2005b, Anderson et al. 2011). The result that herbivores consistently had greater proportions of threatened species while only a handful of
predatory species groups were more threatened than expected suggests that the emphasis on predators having greater extinction risk than species in lower trophic levels may be unwarranted.

In Chapter 3 of this research, we investigated whether proportions of threatened species in different trophic levels varied with biogeographic factors and if humans have targeted certain species groups through specific anthropogenic disturbances. We found that mostly herbivores and some predators and omnivores are overrepresented in threatened species in tropical regions and tropical forests. Specifically, herbivores in Oceania, sub-Saharan Africa, South and Southeast Asia, reptilian omnivores in Mesoamerica and sub-Saharan Africa, and some predators in Oceania and sub-Saharan Africa had higher proportions of threatened species than expected. These regions tend to be developing, underfunded (Waldron et al. 2013), and are currently exposed to high magnitudes of anthropogenic disturbances (Vamosi and Vamosi 2008). We also found that species in each trophic level located in developed regions such as the Americas and Europe tended to be less threatened than expected. This pattern in developed regions may be due to past species extinctions (Balmford 1996) that altered current extinction risk patterns or species adapted to live with high rates of anthropogenic disturbances (Cardillo et al. 2006). Anthropogenic disturbances including deforestation (Hansen et al. 2013), climate change (Deutsch et al. 2008), and hunting for bushmeat (Peres and Palacios 2007) are major threats affecting tropical regions. In our results, the effects of habitat alteration, biological resource use, and pollution were some of the most pronounced anthropogenic threats (Ducatez and Shine 2017, Young et al. 2016) on herbivores and omnivores. This targeting of herbivores and omnivores by humans most likely
contributes to the overall pattern of herbivores and sometimes omnivores being more threatened than expected in multiple regions. More care should be taken to reduce the magnitude of anthropogenic disturbances and to conserve the high proportions of threatened herbivores and other select species groups, especially in tropical regions.

The combined results of this research suggest that the results are robust to differences in spatial scales. We found that herbivores and marine predatory birds were consistently more threatened than expected at global, regional, system, and habitat scales. Therefore, the consistent results of our research can be used to inform conservation decisions at multiple spatial scales (Boyd et al. 2008).

Because our results are consistent we can pinpoint what areas or species in certain diet groups and trophic levels are in need of conservation action. Furthermore, we can predict how ecosystem functions may be affected by future extinctions. Herbivores, which we identified as a highly threatened group, are associated with vegetation structuring, seed dispersal, and pollination. Marine, piscivorous birds provide links between marine and terrestrial nutrients while scavengers reduce disease outbreaks. Our results suggest that these services are likely to decline in tropical regions, especially in forests and most marine habitats (Chapter 3). Furthermore, the magnitude of ecosystem function change may be exceptionally high as large-bodied species are highly threatened (Chapter 2), and it has been shown that large-bodied species have the greatest effects on their environments (Barnosky et al. 2015, Malhi et al. 2016, Heinen et al. 2017). Overall, our study suggests that herbivores, omnivorous reptiles, scavengers, and predatory birds in tropical regions should be the focus of conservation attention to protect the high
proportions of threatened species associated with each trophic level and reduce the risk of altered ecosystem services.

This research has several limitations based on the methods we used. Some data were not available for all species. First, the diet and body sizes of some species, mostly reptiles, were not available at the species level. As a result, this information was extrapolated from congeners and comfamiliars. Data from congeners and comfamiliars may be similar to other species within the same taxon (Reif and Štěpánková 2016), but sometimes related species have different diets (e.g., Rodentia) or body sizes (e.g., Bovidae). Second, the diets and body sizes of each species were based on average available diet information for species. Average available data does not account for the large variation that can occur in diets across a species. However, the variation within a species should be less than the variation between species (Liu and Olden 2017), so using the average diet of a species in analyses should not greatly affect our results. Third, the IUCN has not assessed all species. Reptiles in general (Tingley et al. 2016, Roll et al. 2017) along with predators are lacking threat assessments compared to herbivores and omnivores (Chapter 2; Table 2-1). Fourth, not all animal species are included in our analyses. We did not include fishes, amphibians, or invertebrates. Including these species will most likely alter results as these other two vertebrate groups are mostly aquatic, so they are subject to different evolutionary pressures and anthropogenic disturbances compared to the majority of terrestrial species in this study. Finally, we did not specifically create a classification for apex predators. Apex predators are assumed to have the highest extinction risk compared to species in other trophic levels (Myers and Worm 2003, Ripple et al. 2014b). We separated apex from lesser predators by separately
comparing vertebrate- and invertebrate-eating predators, but this comparison was only a crude approximation of relative risk. Creating a rigorous classification of apex predator may yield different results from what we found for predators in general (Chapter 2).

This research should be expanded in the future to include more classes and look at extinction filter effects. First, the trophic level and diet classification of fishes and amphibians must be included to complete a vertebrate dataset. Most adult amphibians are predators, so they may not have interesting trophic level or diet results, but are important to understanding the global patterns in vertebrate species extinction risk. Fishes have a wider variety of diets than amphibians, are completely aquatic, and some predatory species have experienced population collapse (Myers and Worm 2003). Second, current patterns of extinction risk (i.e., our results) may be influenced by past extirpations and global extinctions (i.e., extinctions since 1500 which are species assessed as extinct by the IUCN or extinctions before 1500; Balmford 1996). In the past, predators may have been more prone to extinction than other species (Woodroffe 2000), but due to extinctions, this pattern is not evident anymore. Therefore, further research should look at changes in trophic level and/or diet patterns of extinction risk due to recent extinctions to see if humans have altered current extinction risk patterns.

Despite the limitations in our research, our results suggest that a different approach to conservation is needed. First, the colloquial definition of predator may be skewed. Predators are often thought of as large-bodied, vertebrate-eating species. In fact, the majority of predators are insect predators, not the conventional idea of predator. Therefore, a shift in the idea of what a predators is defined as may be warranted. Second, conservation biology has focused on predators and large-bodied charismatic megafauna
as having the greatest extinction risk. We found that large-bodied species were more threatened than expected, so conservation efforts should continue for large-bodied species. However, our results show that herbivores, seabirds, and reptilian omnivores have high risk. As conservation efforts have not been successful in slowing the rate of defaunation (Dirzo et al. 2014), these results should be used to inform future conservation decisions. Numerous species continue to decline in population size, become extirpated, and sometimes become globally extinct. This defaunation may be due to lack of preventative action as conservation is reactive rather than proactive (Soulé 1985) or lack of conservation at the appropriate spatial scale (Boyd et al. 2008). Conservation initiatives must consider both regional-specific information along with broad-scale spatial patterns to be effective (Boyd et al. 2008), which these two chapter provide. Our past focus on charismatic species and predators should be shifted to accommodate the patterns found within these two chapters: herbivores and select omnivorous and predatory species groups in tropical regions and forests are more threatened than expected. With our results concerning trophic level patterns of extinction risk, we may be able to rework how conservation acts to better protect species and their associated ecosystem functions, eventually slowing the rate of defaunation.

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APPENDICES
Appendix A

Supplementary Material to Chapter 2
FIG. A-1. Trophic level and data deficient classified species sensitivity analysis for all mammals.
FIG. A-2. Trophic level and data deficient classified species sensitivity analysis for all birds.
FIG. A-3. Trophic level and data deficient classified species sensitivity analysis for all reptiles.
FIG. A-4. Relaxed scenario sensitivity analysis of data deficient classified species for species in different diet groups across species clades. In the relaxed scenario, all data deficient species were classified as non-threatened.
FIG. A-5. Intermediate scenario sensitivity analysis of data deficient classified species for species in different diet groups across species clades. In the intermediate scenario, data deficient species were classified as either threatened or non-threatened in proportion to non-data deficient species threat assessments.
FIG. A-6. Precautionary scenario sensitivity analysis of data deficient classified species for species in different diet groups across species clades. In the precautionary scenario, all data deficient species were classified as threatened.
FIG. A-7. Relaxed scenario sensitivity analysis of data deficient classified species for species in different diet groups with a high dietary specialization across species clades. In the relaxed scenario, all data deficient species were classified as non-threatened.
FIG. A-8. Intermediate scenario sensitivity analysis of data deficient classified species for species in different diet groups with a high dietary specialization across species clades. In the intermediate scenario, data deficient species were classified as either threatened or non-threatened in proportion to non-data deficient species threat assessments.
FIG. A-9. Precautionary scenario sensitivity analysis of data deficient classified species for species in different diet groups with a high dietary specialization across species clades. In the precautionary scenario, all data deficient species were classified as threatened.
FIG. A-10. Trophic level and body mass sensitivity analysis for data deficient classified species for the relaxed scenario. In the relaxed scenario all data deficient species were classified as non-threatened.
FIG. A-11. Trophic level and body mass sensitivity analysis for data deficient classified species for the intermediate scenario. In the intermediate scenario data deficient species as either threatened or non-threatened in proportion to non-data deficient species threat assessments.
FIG. A-12. Trophic level and body mass sensitivity analysis for data deficient classified species for the precautionary scenario. In the precautionary scenario all data deficient species were classified as threatened.
Appendix B
Supplementary Material to Chapter 3
FIG. B-1. Relaxed scenario sensitivity analysis of data deficient classified species for species in different systems within a trophic level across species clades. In the relaxed scenario, all data deficient species were classified as non-threatened.
FIG. B-2. Intermediate scenario sensitivity analysis of data deficient classified species for species in different systems within a trophic level across species clades. In the intermediate scenario, data deficient species as either threatened or non-threatened in proportion to non-data deficient species threat assessments.
FIG. B-3. Precautionary scenario sensitivity analysis of data deficient classified species for species in different systems within a trophic level across species clades. In the precautionary scenario, all data deficient species were classified as threatened.
FIG. B-4. Relaxed scenario sensitivity analysis of data deficient classified species for species in different habitats within a trophic level across species clades. In the relaxed scenario, all data deficient species were classified as non-threatened.
FIG. B-5. Intermediate scenario sensitivity analysis of data deficient classified species for species in different habitats within a trophic level across species clades. In the intermediate scenario, data deficient species as either threatened or non-threatened in proportion to non-data deficient species threat assessments.
**FIG. B-6.** Precautionary scenario sensitivity analysis of data deficient classified species for species in different habitats within a trophic level across species clades. In the precautionary scenario, all data deficient species were classified as threatened.
FIG. B-7. Relaxed scenario sensitivity analysis of data deficient classified species for species in different geographic regions within a trophic level across species clades. In the relaxed scenario, all data deficient species were classified as non-threatened.
FIG. B-8. Intermediate scenario sensitivity analysis of data deficient classified species for species in different geographic regions within a trophic level across species clades. In the intermediate scenario, data deficient species as either threatened or non-threatened in proportion to non-data deficient species threat assessments.
FIG. B-9. Precautionary scenario sensitivity analysis of data deficient classified species for species in different geographic regions within a trophic level across species clades. In the precautionary scenario, all data deficient species were classified as threatened.
FIG. B-10. Relaxed scenario sensitivity analysis of data deficient classified species for species in different trophic levels associated with five major anthropogenic threats. In the relaxed scenario, all data deficient species were classified as non-threatened.
FIG. B-11. Intermediate scenario sensitivity analysis of data deficient classified species for species in different trophic levels associated with five major anthropogenic threats. In the intermediate scenario, data deficient species as either threatened or non-threatened in proportion to non-data deficient species threat assessments.
FIG. B-12. Precautionary scenario sensitivity analysis of data deficient classified species for species in different trophic levels associated with five major anthropogenic threats. In the precautionary scenario, all data deficient species were classified as threatened.