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LETTER

# Simultaneously operating threats cannot predict extinction risk

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**Abstract**

Species afflicted by multiple threats are thought to face greater extinction risk. However, it is not known whether multiple threats operate antagonistically, additively, or synergistically, or whether they vary across different taxonomic and spatial scales. We addressed these questions by analyzing threats to 10,378 species in six vertebrate classes at global and regional spatial scales using network analysis. The total number of threats was a poor predictor of extinction risk, and particular combinations of threats did not predict extinction risk in the same way at different spatial scales. The exception was cartilaginous fishes, which faced increased extinction risk with increasing numbers of threats. Except for cartilaginous fishes, our findings indicate that species facing more threats than others do not face a higher risk of extinction and suggest that effective conservation will require more investment in identifying how threats and different ecosystem stressors operate together at local scales.

**KEYWORDS**
conservation, extinction, IUCN, multiple threats, networks

## 1 | INTRODUCTION

To help resolve the Earths' biodiversity crisis (Ceballos et al., 2015; Pimm et al., 2014), there is an urgent need to understand which species are at greatest risk of extinction, which regions they occupy, and why levels of risk vary. A potential first step in gaining such understanding is to utilize cumulative threat maps and focus on species or regions that are affected by the greatest numbers of threats (Brown, Saunders, Possingham, Richardson, & Essl, 2014; Di Marco & Santini, 2015; Evans et al., 2011; Halpern et al., 2008; Tulloch et al., 2015; Venter et al., 2016). For example, maps of cumulative human pressures have been used to predict changes in range sizes of species (Di Marco & Santini, 2015; Venter et al., 2016; Yackulic, Sanderson, & Uriarte, 2011), quantify species population sizes (Hand, Cushman, Landguth, & Lucotch, 2014), and investigate extinction risk to carnivores in close proximity to areas of high human density (Safi & Pettorelli, 2010). Maps of cumulative threats have also been used to suggest regions to direct conservation efforts in terrestrial, marine, and freshwater ecosystems (Allan et al., 2013; Halpern et al., 2008; Veach, Moilanen, & Di Minin, 2017) and identify threat "hotspots" at global and regional scales to prioritize conservation efforts (Brooks et al., 2006; Moran & Kanemoto, 2017). However, it is not known whether species afflicted by multiple threats actually have an elevated risk of extinction, or whether multiple threats operate antagonistically, additively, or synergistically at different spatial scales. Identifying which combinations of threats are associated with elevated extinction risk should therefore allow more effective conservation planning and decision-making (Brook, Sodhi, & Bradshaw, 2008).

Here, we employ network analysis to determine how multiple threats operate to drive extinction risk in vertebrates at global, regional, and taxonomic scales by developing a threat-extinction risk network. Specifically, using data from the IUCN Red List v3.2 (IUCN, 2017), we test two predictions. First, extinction risk will be higher for species exposed to a greater number of threats; that is, when the network becomes more connected as threats accumulate across threat classes (weighted mean number of shared threats). Our study considered 39 individual threats from exploitation, agriculture, overdevelopment, and resource use, to invasive species, pollution, and climate change (Table S1 in the Supporting Information). Second, we predicted that combinations of particular threats will operate together or consistently within different taxonomic groups to produce modular structure or groupings within the network. Finally, using our threat-extinction risk network, we identify the combinations of threats that affect the largest numbers of at-risk vertebrates and assess whether there are any consistent global or regional scale patterns for each vertebrate class (see Supplementary Table S1 for more details); consistent patterns would indicate that conservation policy at the global scale is likely to be relevant to policy that is applied regionally.

# 2 | METHODS

## 2.1 | Data

Data on extinction risk and threats for each vertebrate species were obtained from the IUCN Red List (total 44,705 species) (IUCN, 2017). Vertebrate species classified as near threatened (NT), vulnerable (VU), endangered (EN), critically endangered (CR), extinct in the wild (EW), or extinct (EX) were then collated (total 11,137 species), along with their individual threats. This resulted in 10,378 species of vertebrates (23% of all vertebrate species) with identified threats on the IUCN Red List ($n$ = 1,546 mammals, 2,635 birds, 1,272 reptiles, 2,391 amphibians, 2,229 ray-finned fishes (actinopterygians), and 305 cartilaginous fishes (chondrichthians).

Threats followed the categories defined by the IUCN Red List Classification Scheme v 3.2, which identified 39 individual threats (Table S1 in the Supporting Information). The country of endemism of each threatened species was also obtained from the IUCN Red List. Data were obtained using the package rredlist 0.4.0 (Chamberlain, 2017) in R vs 3.0 (R Core Team, 2017).

To classify each country into a world region, we followed the classification scheme of the United Nations (1999), with five regions thus defined: Africa, Oceania, America, Asia, and Europe. Due to the lack of threatened species data for Antarctica, we did not calculate a network for this region. Data from the IUCN Red List provide one of the most comprehensive global datasets on threatened species, but do have some limitations. Data on the length of time and location of where each threat has been operating on threatened species populations are limited or aggregated across entire species distributions. Thus only global and regional-scale analyses can be conducted, which may miss finer-scale processes. In addition, the threats for some vertebrate groups may be better known than for others, and thus the number of shared threats may be underreported (Possingham et al., 2002).

## 2.2 | Network analysis

Global threat-extinction risk networks were calculated by summing the total number of species affected by each threat for each level of extinction risk. Threat-extinction risk networks were also calculated at the regional scale for each vertebrate class and then visualized using the package circlize 0.4.3 (Gu, Gu, Eils, Schlesner, & Brors, 2014) in R vs 3.0 (R Core Team, 2017). We represented each network as a quantitative bipartite network, where the nodes were either extinction risk category or threat type, and edges (interactions) were the total number of threatened species affected by each threat for each level of extinction risk. A bipartite network was chosen as threat or extinction risk represented two distinct levels that could interact with each other, but within levels (e.g., within extinction risk categories) they could not. Bipartite networks are commonly used in ecology to explore ecological interactions between multiple species across two trophic levels, such as in plant–pollinator (Campbell, Yang, Albert, & Shea, 2011; Popic, Wardle, & Davila, 2013) and predator–prey interactions (Wirta et al., 2015).

To investigate whether extinction risk increased with the number of threats, the number of effective partners, weighted for the number of threatened species, was calculated for each level of extinction risk at both global and regional scales for each vertebrate class. Effective partners are the weighted mean number of threats per extinction risk category, defined by Dormann, Fründ, Blüthgen, and Gruber (2009) as

$$G = \sum_{j=1}^{J} \frac{A_j}{m} 2^{H_j},$$

where $J$ is the number of threats, $A_j$ is the total number of interactions of threat $j$ and extinction risk category, $m$ is the total number of interactions, and $H_j$ is the Shannon diversity index; where

$$H_j = -\sum_{i=1}^{I} \left( \frac{a_{ij}}{A_j} \ln \frac{a_{ij}}{A_j} \right),$$

$a_{ij}$ is the number of interactions (species that share each threat within each extinction risk category) between extinction risk category $i$ and threat $j$

Network size (number of species and interactions) can influence connectance indices, and thus the effective partner index was used to account for networks with different number of species and aid comparisons (Dormann et al., 2009).

Effective partners were then regressed against extinction risk, where extinction risk was coded from 1 to 6 for near- threatened to extinct. One-tailed linear regressions were used to investigate whether extinction risk increased with the number of effective partners. Effective partners were calculated using the package bipartite 2.08 (Dormann, Gruber, & Fruend, 2008), with all analyses performed in R vs 3.0 (R Core Team, 2017). Inspection of diagnostic plots (fitted values vs. residuals, QQ plots, fitted values vs. standardized residuals, and leverage plots) indicated that all models met statistical assumptions of normality and homoscedasticity (Zuur, 2009).

To investigate whether particular combinations of threats operate together to increase extinction risk at global and regional scales for each vertebrate class, each network was investigated using fast greedy optimization of modularity to find groups of threats within each network (Clauset, Newman, & Moore, 2004). Modularity measures the structure of networks by assessing the strength of divisions between groups. The modularity index was thus used to assess whether there was support for more than one group structure. The index ranges from −1/2 to 1, with values closer to 1 indicating higher groupings of nodes within the network (Luke, 2015). Then, to test if the number of groups found was due to chance, Monte Carlo methods were used to generate approximations to the corresponding reference null network, with the same order, size, and degree sequence of the original network, using 1,000 simulations (Kolaczyk & Csárdi, 2014). Analysis was performed using the R package igraph 1.1.2 (Csardi & Nepusz, 2006).

# 3 | RESULTS

## 3.1 | Extinction risk is not higher for species exposed to greater numbers of threats

We found that, contrary to expectation, the weighted mean number of shared threats was a poor predictor of extinction risk for five of the six vertebrate classes (Figure 1a–e). The weighted mean number of shared threats (the number of effective partners) was weighted for the number of threatened species calculated for each level of extinction risk at both a global and regional scale for each vertebrate class. We chose the weighted mean number of shared threats as the connectance metric to avoid the influence of network size on the comparisons across threat categories extinction levels (see Methods). There was a significant increase at the global level in the number of shared threats (weighted mean number) and extinction risk only for cartilaginous fishes (chondrichthians) (Figure 1f; $t = 7.14$, $df = 2$, $p = .01$) and within Africa, Oceania, and Asia (Table 1). There was no relationship between the weighted mean number of threats and extinction risk at global or regional scales for mammals ($t = -3.27$, $df = 4$, $p = .98$), birds ($t = -1.99$, $df = 4$, $p = 0.94$), reptiles ($t = -1.92$, $df = 3$, $p = 0.92$), amphibians ($t = -0.68$, $df = 4$, $p = 0.73$), or ray-finned fishes (actinopterygians; $t = -2.57$, $df = 4$, $p = 0.97$; Figure 1; Table 1). Species listed as extinct and extinct in the wild had the fewest weighted mean numbers of shared threats for each vertebrate class and region (range: 1.00–11.07; Table S2).

## 3.2 | Particular combinations of threats are poor predictors of extinction risk

There was no network structure defined by groupings of particular threats within each extinction risk category and measured by modularity (see Methods) at either global (Figure 2) or regional scales (Figures 3 and 4), or within broad taxonomic classes (Figures S1–S4 in the Supporting Information). Modularity scores were low for each network at both global (Table S3; range 0.03–0.13) and regional scales (Table S4; range 0.03–0.22), indicating that no structure was identified within the network of threat categories or across spatial scales. In addition, the numbers of groups found were consistently lower than those predicted by Monte Carlo simulations for all vertebrate classes and regions (Figures S5–S11 in the Supporting Information), suggesting no groupings of threats for each extinction risk category.

The combined threats of cropping and logging had most impact on the largest number of terrestrial vertebrates

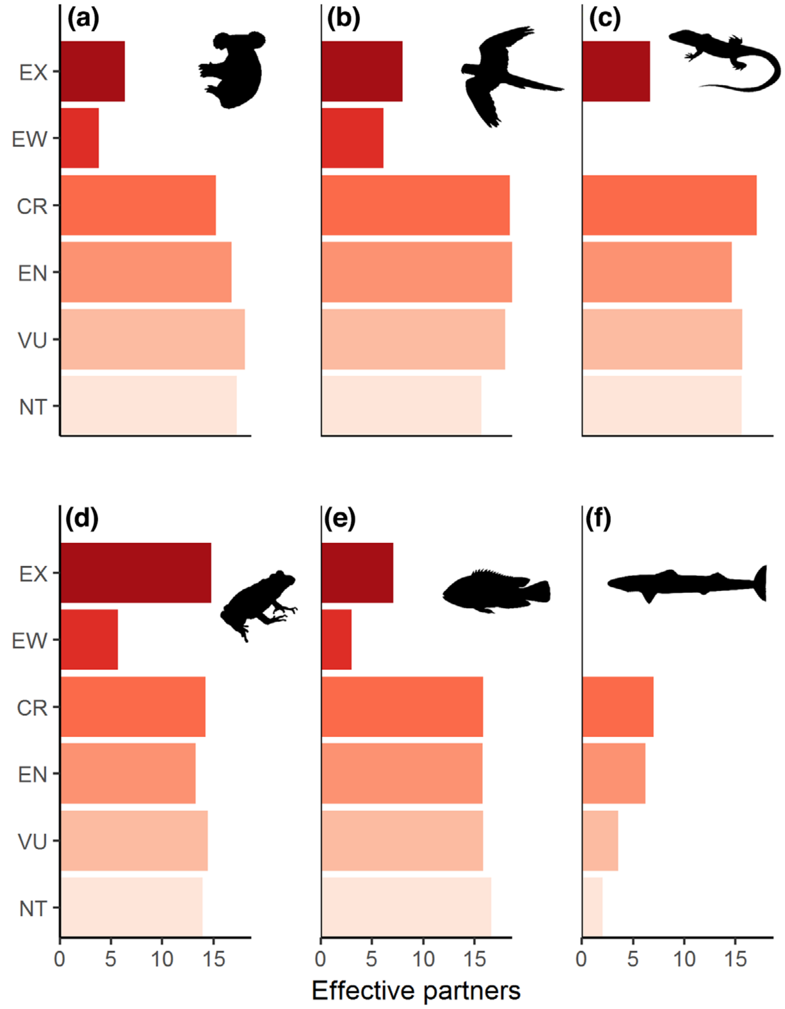


**FIGURE 1** Number of effective partners for each extinction risk class. Number of effective partners calculated from the global threat-extinction network for all threatened species of (A) mammals, (B) birds, (C) reptiles, (D), amphibians, (E) ray-finned fishes (actinopterygians), and (F) cartilaginous fishes (chondrichthians) on the IUCN Red List. "Effective partners" is a connectance metric weighted for the number of species that share each extinction risk and threat from the threat-extinction risk network. NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, EW = extinct in the wild, and EX = extinct

globally (cropping: IUCN subthreat 2.1; total species: 949 mammals, 1,746 birds, 724 reptiles, and 1,691 amphibians; Tables S2–S5; logging: subthreat 5.3; 829 mammals, 1,429 birds, 470 reptiles, and 1,565 amphibians; Figure 2; Tables S5–S8). Effluents from primary industry (subthreat 9.3; $n = 948$), building of dams (subthreat 7.2; $n = 865$) and overfishing (subthreat 5.4; $n = 806$) formed the greatest combined threat for species of ray-finned fishes (Figure 2; Table S9). Overfishing (subthreat 5.4; $n = 304$), urban development (subthreat 1.1; $n = 24$), and domestic waste water (subthreat 9.1; $n = 18$) were the greatest combined threats for species of cartilaginous fishes (Figure 2; Table S10 in the Supporting Information). Overexploitation and agriculture were the biggest threats to vertebrates overall (Table S11 in the Supporting Information), and our analyses also suggest that overishing, pollution, and the building of dams are important threats to freshwater and coastal marine species.

## 3.3 | Global patterns are not repeated at regional scales

Overall, global patterns were not repeated at regional scales (Figure 3; Figures S1–S4 in the Supporting Information), except for cartilaginous fishes (Figure 4). For example, invasive species (subthreat 8.1) were the major threat for most species of terrestrial vertebrates (including mammals, birds, reptiles, and amphibians) in Oceania (Figure 3; Figures S1–S3). Cropping (subthreat 2.1) was a major threat for mammals, birds, and reptiles in Africa, America, and Asia (Figure 3; Figures S1–S2), and for amphibians in Africa, America, and Europe (Figure S3). Dams (subthreat 7.2) were a major threat to ray-finned fishes in America, Asia, and Europe, whereas effluent from primary industry (subthreat 9.3) was a major threat to this group in Africa, as was overfishing (subthreat 5.4) in Oceania (Figure S4).

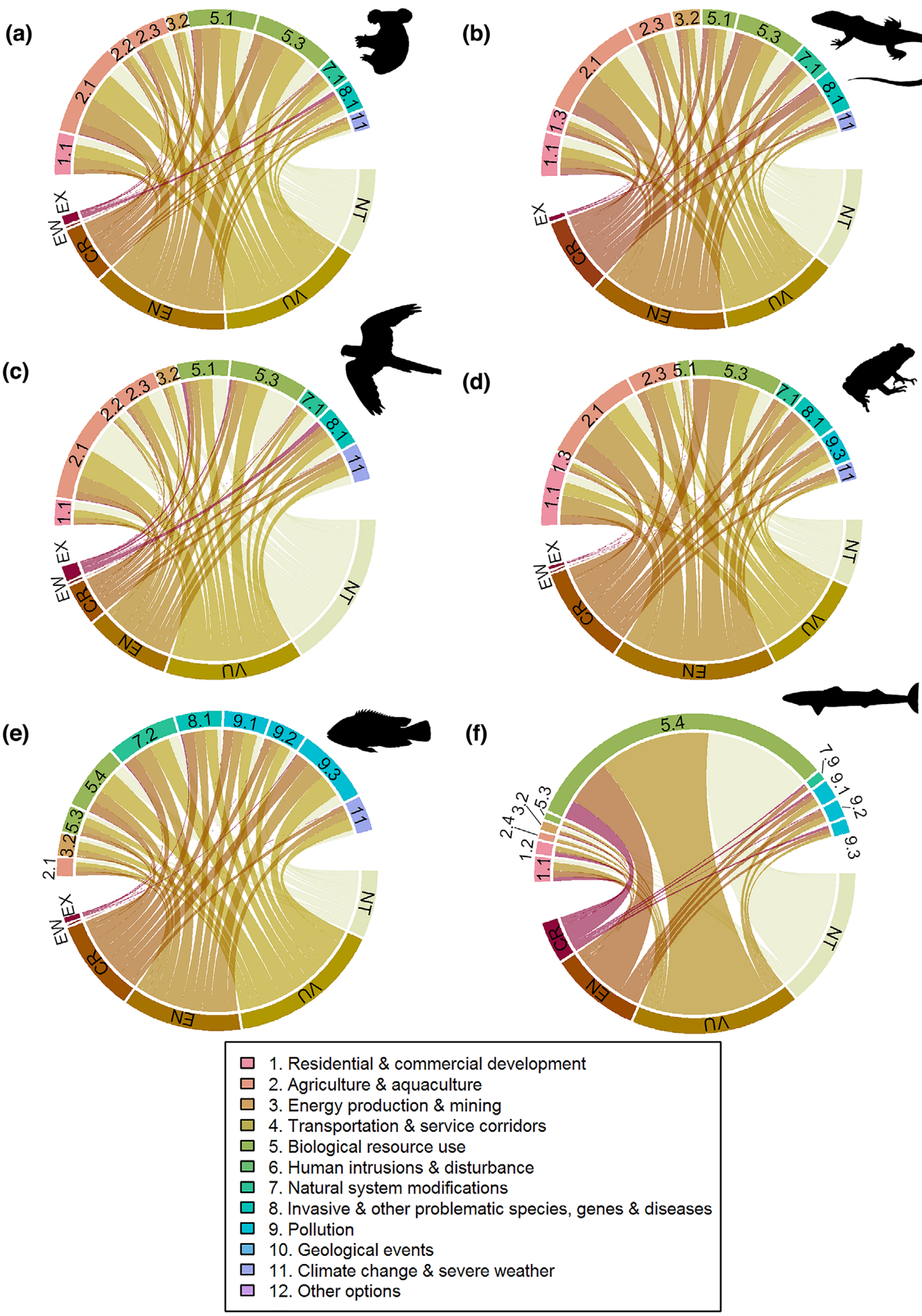


**FIGURE 2** Global threat-extinction risk networks illustrating the top 10 threats to threatened species. Networks illustrate the number of threatened species of (A) mammals, (B) reptiles, (C) birds, (D), amphibians, (E) ray-finned fishes (actinopterygians), and (F) cartilaginous fishes (chondrichthians) on the IUCN Red List that are impacted by each threat. Each node in the network is either an extinction risk category or threat class, and the size of the node, or length of each section around the circle, represents the number of species within that node. Widths of lines joining each extinction risk category and threat class (node) represent the number of threatened species (links or edges) affected by each threat, within each extinction risk category. NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, EW = extinct in the wild, and EX = extinct (see Table S1 for key to subthreat numbers and Tables S5–S10 for numbers of threatened species (links or edges))

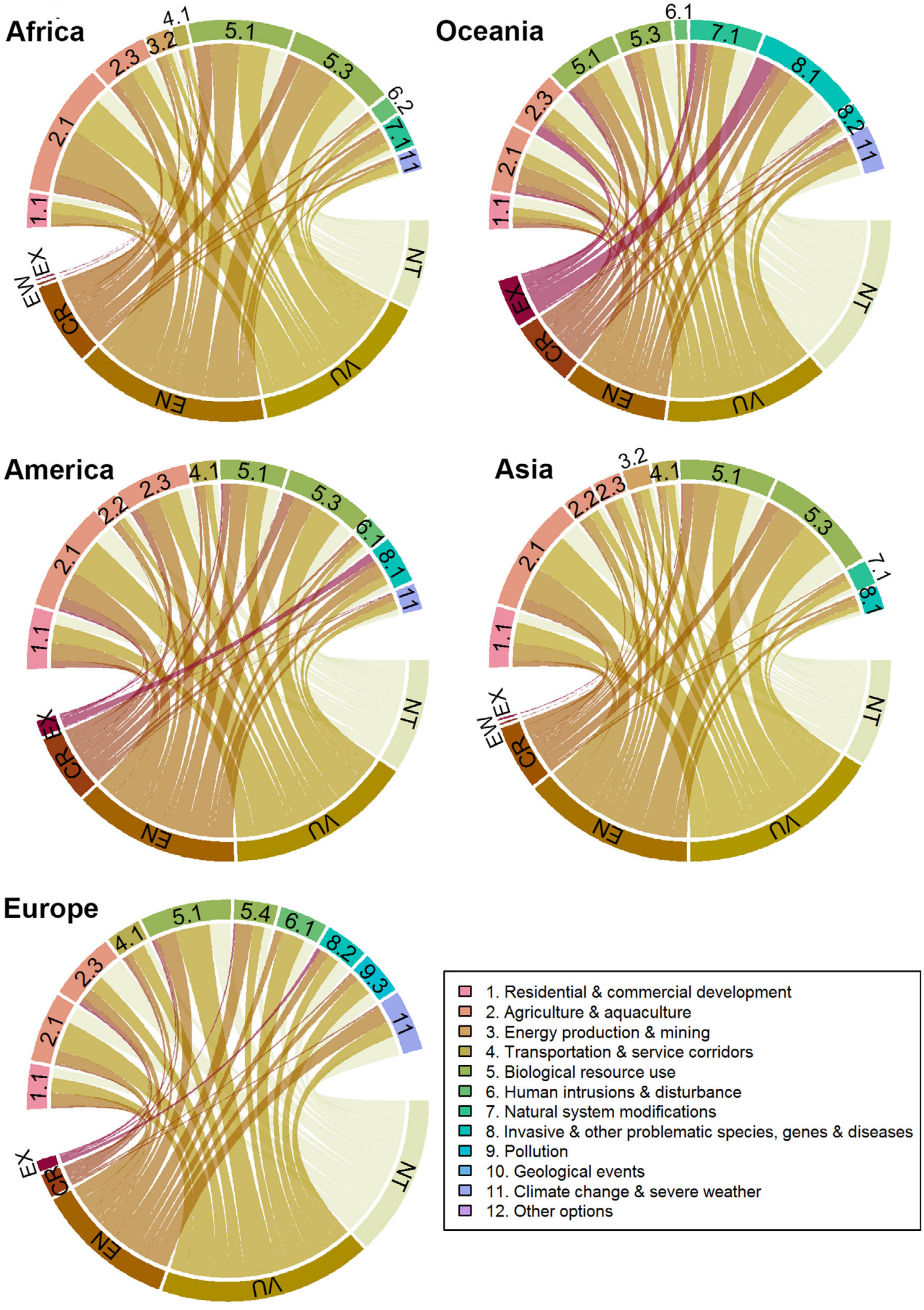


**FIGURE 3** Regional threat-extinction risk networks for mammals. The top 10 threats for threatened mammal species on the IUCN Red List. Each node in the network is either an extinction risk category or threat class, and the size of the node, or length of each section around the circle, represents the number of species within that node. Widths of lines joining each extinction risk category and threat class (node) represent the number of threatened species (links or edges) affected by each threat, within each extinction risk category. NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, EW = extinct in the wild, and EX = extinct (see Table S1 for key to subthreat numbers and Figures S1–S4 for other vertebrate classes)

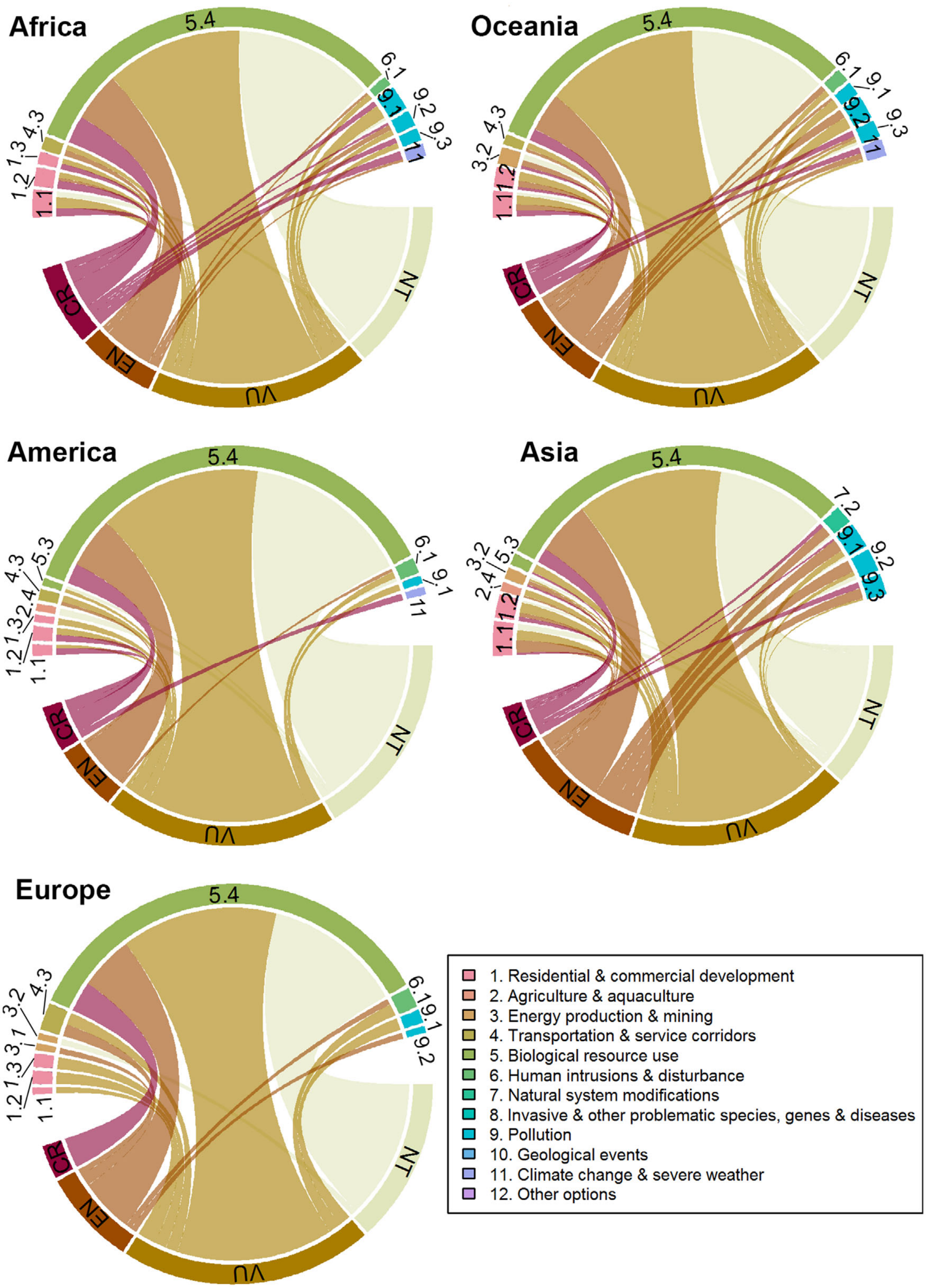


**FIGURE 4** Regional threat-extinction risk networks for cartilaginous fishes. Threat-extinction risk networks illustrating the top 10 threats affecting the number of threatened cartilaginous fishes (chondrichthians) species on the IUCN Red List for the regions. Each node in the network is either an extinction risk category or threat class, and the size of the node, or length of each section around the circle, represents the number of species within that node. Width of lines joining each extinction risk category and threat class (node) represent the number of threatened species (links or edges) affected by each threat, within each extinction risk category. NT = near threatened, VU = vulnerable, EN = endangered, CR = critically endangered, EW = extinct in the wild, and EX = extinct (see Table S1 for key to subthreat numbers and Figures S1– S4 for other vertebrate classes))

**TABLE 1** Regional one-tailed linear regression results for the number of effective partners and extinction risk for threatened vertebrates on the IUCN Red List. "Effective partners" is a connectance metric weighted for the number of species that share each extinction risk and threat from the threat-extinction risk network

| Extinction class | Africa | Oceania | America | Asia | Europe |
|---|---|---|---|---|---|
| Mammals | | | | | |
| *t* value | −5.54 | −2.23 | −3.00 | −3.65 | −3.35 |
| *df* | 4 | 3 | 3 | 4 | 3 |
| *p* | .997 | .94 | .97 | .99 | .98 |
| Birds | | | | | |
| *t* value | −2.90 | −2.64 | −2.96 | −1.64 | −4.41 |
| *df* | 3 | 4 | 4 | 3 | 3 |
| *p* | .97 | .97 | .98 | .90 | .99 |
| Reptiles | | | | | |
| *t* value | −0.91 | −2.57 | −4.26 | 1.91 | −1.38 |
| *df* | 3 | 3 | 3 | 2 | 2 |
| *p* | .78 | .96 | .99 | .10 | .85 |
| Amphibians | | | | | |
| *t* value | −1.35 | −0.85 | −2.06 | −1.06 | −1.86 |
| *df* | 3 | 3 | 4 | 23 | 2 |
| *p* | .87 | .77 | .95 | .0.82 | .90 |
| Ray-finned fishes | | | | | |
| *t* value | −2.38 | −1.03 | −2.95 | −2.13 | −1.03 |
| *df* | 3 | 3 | 3 | 4 | 4 |
| *p* | .95 | .81 | .97 | .95 | .82 |
| Cartilaginous fishes | | | | | |
| *t* value | 3.14 | 3.57 | 2.00 | 3.20 | −0.002 |
| *df* | 2 | 2 | 2 | 2 | 2 |
| *p* | .04 | .04 | .09 | .04 | .50 |

## 4 | DISCUSSION

Our analysis found that, when adjusted for the numbers of threatened species, an increasing tally of threats did not lead to increased extinction risk for most vertebrate assemblages at global, regional, or taxonomic scales. Thus, threats do not appear to be either additive or synergistic at the scales examined. In addition, there was no consistent pattern between shared threats at global and regional scales, suggesting that conservation policy targeted at multiple threats at the global scale is unlikely to be relevant to policy that is applied regionally. The clear exception was cartilaginous fishes, which showed elevated extinction risk with increasing numbers of threats. This finding may indicate that interactions between multiple threats and species in marine systems are largely synergistic (Crain, Kroeker, & Halpern, 2008). In addition, the Earth's oceans are entirely affected by humans, and 41% of the oceans experience multiple threats (Halpern et al., 2008). Cartilaginous fishes are often larger than ray-finned fishes and many terrestrial species and thus might range over larger distances, bringing them into contact with more threats. Alternatively, their larger body size makes them more at risk of overexploitation (Ripple et al., 2017), in addition to threats from coastal development, pollution, or habitat modification. Hence, managing multiple threats to coastal or inshore cartilaginous fishes, such as overfishing and development, should effectively reduce their extinction risk (Davidson & Dulvy, 2017; Halpern et al., 2008; Reynolds, Dulvy, & Roberts, 2002).

Species listed as extinct and extinct in the wild had the lowest numbers of shared threats. This may be because not all threats could be identified before these species became extinct and/or because extinct species are not at risk from new threats added to the IUCN list over time. The bias towards extinct species having fewer threats may obscure the relationship between increasing numbers of shared threats and extinction risk. However, even after exclusion of these categories there was still no increasing trend in extinction risk with increasing numbers of shared threats (see Figure 1 and Table S2).

Maps of cumulative human pressures have been used to investigate extinction risk in terrestrial and marine systems (Halpern et al., 2008; Safi & Pettorelli, 2010). Managers may assume that threats interact synergistically (Côté, Darling, & Brown, 2016) and prioritize threat management accordingly (Carwardine et al., 2012, 2018). However, our findings suggest that, for terrestrial species, there is no relationship between increasing extinction risk and number of threats at global or regional scales. This conclusion contrasts with that of Ducatez and Shine (2017) who found that extinction risk increased most in birds with increasing numbers of threats; however, the increase in extinction risk did vary across other taxonomic groups. At large spatial scales, we suggest that multiple threats may not be operating additively or synergistically and are dominated instead by widespread threats, such as overexploitation, agriculture, and land use changes (Ripple et al., 2015, 2016, 2017). For example, habitat loss is a major threat to large herbivores in parts of Latin America, Africa, and Southeast Asia (Ripple et al., 2015). Our analytical approach, which has not been used previously for assessing the severity and extent of individual threats on species populations, has allowed us to arrive at this initially surprising conclusion.

Indeed, the lack of consistent network structure or groups of threats in the reported threat-extinction networks suggests that there is no single important combination of threats that leads to an increase in vertebrate extinction risk. Thus, if multiple threats are operating additively or synergistically, they will be doing so at finer geographic and taxonomic scales than assessed herein. For example, within primates and amphibians, local extinction risk can be highly variable and dependent on both threat type and the biology of individual species (Grant et al., 2016; Isaac & Cowlishaw, 2004). Alternatively, synergistic threats may vary from population to population across space. For example, koala (*Phascolarctos cinereus*) populations across south-eastern Australia are subjected to multiple and synergistic threats, but the combinations of individual threats differ across these populations (Lunney, Gresser, O'Neill, Matthews, & Rhodes, 2007; Rhodes et al., 2011). Lastly, extinction risk may increase with the amount of time a species is exposed to a threat (Pimm & Raven, 2000). Thus, accounting for the role of time when determining whether shared threats increase extinction risk is suggested as an area for further research. Alternatively, communities may be more resilient to new threats if they have faced similar ones before, because past threats may act as "extinction filters" and remove vulnerable species from the community (Balmford, 1996; Paul Rodríguez, 2001).

## 5 | CONCLUSION

The IUCN Red List dataset is often used for regional and global assessments, and our interrogation of it here at these scales failed to confirm that species affected by more threats than others face a higher risk of extinction. Although associations between extinction risk and numbers of threats may emerge at local scales, use of cumulative threat mapping at global and regional scales clearly may not be effective on its own in prioritizing effective conservation action. Our findings show that basing conservation policy and action on cumulative threat maps or focusing on species that face multiple threats may not result in positive conservation gains at global or regional scales. Indeed, if two threats interact antagonistically rather than additively or synergistically, management of multiple threats to threatened species could even result in detrimental outcomes (Brown, Saunders, Possingham, & Richardson, 2013; Côté et al., 2016). We suggest, instead, that effective conservation will require a greater push for investment to identify how threats and different ecosystem stressors operate together at local scales. In particular, this will require a greater investment in local context-dependent research and management. Determining whether threats operate additively or synergistically may be achievable using meta-analysis, conservation-oriented experiments, adaptive monitoring, and local co-occurrence threat networks (Côté et al., 2016; Geary, Nimmo, Doherty, Ritchie, & Tulloch, 2019). Without such actions, we may not stem the tide of species extinctions and arrest the current biodiversity crisis.

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## AUTHOR CONTRIBUTIONS

A.G. designed the study and did the statistical modeling. The manuscript was written by A.G., with contributions from all coauthors.

## DATA ACCESSIBILITY STATEMENT

All data in the main text or the supplementary materials are available via the IUCN Red List web portal (IUCN, 2017).

## CONFLICT OF INTEREST

Authors declare no competing interests.

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## REFERENCES

Allan, J. D., McIntyre, P. B., Smith, S. D., Halpern, B. S., Boyer, G. L., Buchsbaum, A., … Steinman, A. D. (2013). Joint analysis of stressors and ecosystem services to enhance restoration effectiveness. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(1), 372–377. https://doi.org/10.1073/pnas.1213841110

Balmford, A. (1996). Extinction filters and current resilience: The significance of past selection pressures for conservation biology. *Trends in Ecology & Evolution*, *11*(5), 193–196. https://doi.org/10.1016/0169-5347(96)10026-4

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. *Trends in Ecology & Evolution*, *23*(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Brooks, T. M., Mittermeier, R. A., da Fonseca, G. A., Gerlach, J., Hoffmann, M., Lamoreux, J. F., … Rodrigues, A. S. (2006). Global biodiversity conservation priorities. *Science*, *313*(5783), 58–61. https://doi.org/10.1126/science.1127609

Brown, C. J., Saunders, M. I., Possingham, H. P., & Richardson, A. J. (2013). Managing for interactions between local and global stressors of ecosystems. *PLoS One*, *8*(6), e65765. https://doi.org/10.1371/journal.pone.0065765

Brown, C. J., Saunders, M. I., Possingham, H. P., Richardson, A. J., & Essl, F. (2014). Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Diversity and Distributions*, *20*(5), 538–546. https://doi.org/10.1111/ddi.12159

Campbell, C., Yang, S., Albert, R., & Shea, K. (2011). A network model for plant–pollinator community assembly. *Proceedings of the National Academy of Sciences*, *108*(1), 197–202. https://doi.org/10.1073/pnas.1008204108

Carwardine, J., Martin, T. G., Firn, J., Ponce Reyes, R., Nicol, S., Reeson, A., … Chadès, I. (2018). Priority threat management for biodiversity conservation: A handbook. *Journal of Applied Ecology*, *56*(2), 481–490. https://doi.org/10.1111/1365-2664.13268

Carwardine, J., O'Connor, T., Legge, S., Mackey, B., Possingham, H. P., & Martin, T. G. (2012). Prioritizing threat management for biodiversity conservation. *Conservation Letters*, *5*(3), 196–204. https://doi.org/10.1111/j.1755-263X.2012.00228.x

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Chamberlain, S. (2017). rredlist: 'IUCN' Red List Client. R package version 0.4.0. Retrieved from https://CRAN.R-project.org/package=rredlist

Clauset, A., Newman, M. E. J., & Moore, C. (2004). Finding community structure in very large networks. *Physical Review E*, *70*(6), https://doi.org/10.1103/physreve.70.066111.

Côté, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1824), 20152592. https://doi.org/10.1098/rspb.2015.2592

Crain, C. M., Kroeker, K., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, *11*(12), 1304–1315. https://doi.org/10.1111/j.1461-0248.2008.01253.x

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal Complex Systems*, *1695*, 1695. Retrieved from http://igraph.org

Davidson, L. N. K., & Dulvy, N. K. (2017). Global marine protected areas to prevent extinctions. *Nature Ecology & Evolution*, *1*(2), 40. https://doi.org/10.1038/s41559-016-0040

Di Marco, M., & Santini, L. (2015). Human pressures predict species' geographic range size better than biological traits. *Global Change Biology*, *21*(6), 2169–2178. https://doi.org/10.1111/gcb.12834

Dormann, C. F., Fründ, J., Blüthgen, N., & Gruber, B. (2009). Indices, graphs and null models: Analyzing bipartite ecological networks. *The Open Ecology Journal*, *2*(1), 7–24.

Dormann, C. F., Gruber, B., & Fruend, J. (2008). Introducing the bipartite package: Analysing ecological networks. *R News*, *8/2*, 8–11.

Ducatez, S., & Shine, R. (2017). Drivers of extinction risk in terrestrial vertebrates. *Conservation Letters*, *10*(2), 186–194. https://doi.org/10.1111/conl.12258

Evans, M. C., Watson, J. E. M., Fuller, R. A., Venter, O., Bennett, S. C., Marsack, P. R., & Possingham, H. P. (2011). The spatial distribution of threats to species in Australia. *Bioscience*, *61*(4), 281–289. https://doi.org/10.1525/bio.2011.61.4.8

Geary, W. L., Nimmo, D. G., Doherty, T. S., Ritchie, E. G., & Tulloch, A. I. T. (2019). Threat webs: Reframing the co-occurrence and interactions of threats to biodiversity. *Journal of Applied Ecology*, *56*, 1992–1997. https://doi.org/10.1111/1365-2664.13427

Grant, E. H., Miller, D. A., Schmidt, B. R., Adams, M. J., Amburgey, S. M., Chambert, T., … Muths, E. (2016). Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Scientific Reports*, *6*, 25625. https://doi.org/10.1038/srep25625

Gu, Z., Gu, L., Eils, R., Schlesner, M., & Brors, B. (2014). circlize implements and enhances circular visualization in R. *Bioinformatics*, *30*(19), 2811–2812. https://doi.org/10.1093/bioinformatics/btu393

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., … Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, *319*(5865), 948–952. https://doi.org/10.1126/science.1149345

Hand, B. K., Cushman, S. A., Landguth, E. L., & Lucotch, J. (2014). Assessing multi-taxa sensitivity to the human footprint, habitat fragmentation and loss by exploring alternative scenarios of dispersal ability and population size: A simulation approach. *Biodiversity and Conservation*, *23*(11), 2761–2779. https://doi.org/10.1007/s10531-014-0747-x

Isaac, N. J., & Cowlishaw, G. (2004). How species respond to multiple extinction threats. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *271*(1544), 1135–1141. https://doi.org/10.1098/rspb.2004.2724

IUCN. (2017). The IUCN Red List of Threatened Species. Version 2017.1. Retrieved from http://iucnRedList.org

Kolaczyk, E. D., & Csárdi, G. (2014). *Statistical Analysis of network data with R*. New York, NY: Springer.

Luke, D. (2015). *A user's guide to network analysis in R*. Cham: Switzerland: Springer International Publishing.

Lunney, D., Gresser, S., O'Neill, L., Matthews, A., & Rhodes, J. (2007). The impact of fire and dogs on koalas at Port Stephens, New South Wales, using population viability analysis. *Pacific Conservation Biology*, *13*(3), 189–201. https://doi.org/10.1071/pc070189

Moran, D., & Kanemoto, K. (2017). Identifying species threat hotspots from global supply chains. *Nature Ecology & Evolution*, *1*(1), 23. https://doi.org/10.1038/s41559-016-0023

Paul Rodríguez, J. (2001). Exotic species introductions into South America: An underestimated threat? *Biodiversity and Conservation*, *10*(11), 1983–1996. https://doi.org/10.1023/a:1013151722557

Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. L., Joppa, L. N., … Sexton, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, *344*(6187), 1246752. https://doi.org/10.1126/science.1246752

Pimm, S. L., & Raven, P. (2000). Biodiversity. Extinction by numbers. *Nature*, *403*(6772), 843–845. https://doi.org/10.1038/35002708

Popic, T. J., Wardle, G. M., & Davila, Y. C. (2013). Flower-visitor networks only partially predict the function of pollen transport by bees. *Austral Ecology*, *38*(1), 76–86. https://doi.org/10.1111/j.1442-9993.2012.02377.x

Possingham, H. P., Andelman, S. J., Burgman, M. A., Medellıń, R. A., Master, L. L., & Keith, D. A. (2002). Limits to the use of threatened species lists. *Trends in Ecology & Evolution*, *17*(11), 503–507. https://doi.org/10.1016/s0169-5347(02)02614-9

R Core Team. (2017). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from http://www.R-project.org/

Reynolds, J. D., Dulvy, N. K., & Roberts, C. M. (2002). Exploitation and other Threats to Fish Conservation. *Handbook of fish biology and fisheries*, *2*, 319.

Rhodes, J. R., Ng, C. F., de Villiers, D. L., Preece, H. J., McAlpine, C. A., & Possingham, H. P. (2011). Using integrated population modelling to quantify the implications of multiple threatening processes for a rapidly declining population. *Biological Conservation*, *144*(3), 1081–1088. https://doi.org/10.1016/j.biocon.2010.12.027

Ripple, W. J., Abernethy, K., Betts, M. G., Chapron, G., Dirzo, R., Galetti, M., … Young, H. (2016). Bushmeat hunting and extinction risk to the world's mammals. *Royal Society Open Science*, *3*(10), 160498. https://doi.org/10.1098/rsos.160498

Ripple, W. J., Newsome, T. M., Wolf, C., Dirzo, R., Everatt, K. T., Galetti, M., … Van Valkenburgh, B. (2015). Collapse of the world's largest herbivores. *Science Advances*, *1*(4), e1400103. https://doi.org/10.1126/sciadv.1400103

Ripple, W. J., Wolf, C., Newsome, T. M., Hoffmann, M., Wirsing, A. J., & McCauley, D. J. (2017). Extinction risk is most acute for the world's largest and smallest vertebrates. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(40), 10678–10683. https://doi.org/10.1073/pnas.1702078114

Safi, K., & Pettorelli, N. (2010). Phylogenetic, spatial and environmental components of extinction risk in carnivores. *Global Ecology and Biogeography*, *19*(3), 352–362. https://doi.org/10.1111/j.1466-8238.2010.00523.x

Tulloch, V. J. D., Tulloch, A. I. T., Visconti, P., Halpern, B. S., Watson, J. E. M., Evans, M. C., … Possingham, H. P. (2015). Why do we map threats? Linking threat mapping with actions to make better conservation decisions. *Frontiers in Ecology and the Environment*, *13*(2), 91–99. https://doi.org/10.1890/140022

United Nations. (1999). Standard country or area codes for statistical use. Series M, No. 49, Retrieved from https://unstats.un.org/unsd/methodology/m49/

Veach, V., Moilanen, A., & Di Minin, E. (2017). Threats from urban expansion, agricultural transformation and forest loss on global conservation priority areas. *PLoS ONE*, *12*(11), e0188397. https://doi.org/10.1371/journal.pone.0188397

Venter, O., Sanderson, E. W., Magrach, A., Allan, J. R., Beher, J., Jones, K. R., … Watson, J. E. (2016). Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications*, *7*, 12558. https://doi.org/10.1038/ncomms12558

Wirta, H. K., Vesterinen, E. J., Hambäck, P. A., Weingartner, E., Rasmussen, C., Reneerkens, J., … Roslin, T. (2015). Exposing the structure of an Arctic food web. *Ecology and Evolution*, *5*(17), 3842–3856. https://doi.org/10.1002/ece3.1647

Yackulic, C. B., Sanderson, E. W., & Uriarte, M. (2011). Anthropogenic and environmental drivers of modern range loss in large mammals. *Proceedings of the National Academy of Sciences*, *108*(10), 4024–4029. https://doi.org/10.1073/pnas.1015097108

Zuur, A. F. (2009). *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.

## SUPPORTING INFORMATION

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

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