Environmental and socioeconomic correlates of extinction risk in endemic species

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Environmental and socioeconomic correlates of extinction risk in endemic species

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Abstract

Aim: Our current understanding of the causes of global extinction risk is mostly informed by the expert knowledge-based "threats classification scheme" of the IUCN Red List of Threatened Species. Studies based on this dataset came to different conclusions about the relative importance of threats to species, depending on which taxonomic groups and levels of extinction risk were considered, and which version of the database was used. A key reason may lie in data limitations as causes of threat are well known for charismatic and well-studied species, but not for the majority of species assessed. Here, we aim to fill current knowledge gaps about the importance of drivers of global extinction risks by focusing on endemic species.

Location: Global.

Methods: We examined country-level variation in the proportion of globally threatened and extinct endemic species (Index of Threat, IoT) with a range of spatially explicit information about anthropogenic pressures, mitigation measures and data limitations.

Results: IoT coincided with several anthropogenic pressures, with substantial differences among kingdoms, life-forms, levels of extinction risk and geographic locations. IoT of plants, particularly tropical woody plants of moderate extinction risk, was higher in countries with higher GDP and more invasive species. Furthermore, IoT of animals, particularly tropical mammals and invertebrates of moderate extinction risk, was higher in countries with higher GDP and smaller roadless areas.

Main conclusions: The extinction crisis for endemic species is associated with a complex network of potential drivers that need to be considered in concert in conservation policy and practice. Although our results require careful interpretation and remain sensitive to data limitations, we encourage similar studies at smaller scales to identify potential drivers of extinction risk at a higher resolution, particularly in regions where species assessments have been conducted consistently or on organisms with a uniform response time to pressures.

KEYWORDS

anthropocene, biodiversity crisis, data limitation, global change, sixth mass extinction

1 | INTRODUCTION

Recently, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services estimated that humans are potentially putting one million species at risk of extinction (IPBES, 2019). Available data indeed suggest that current species extinction rates are at least hundreds of times higher than average background extinction rates so that a sixth mass extinction might be underway (Barnosky et al., 2011; Ceballos et al., 2015; Humphreys et al., 2019; Purvis et al., 2019). However, our understanding of where the most threatened species live, where and how humanity changes the planet, and how this drives extinctions remains biased and patchy (Pimm et al., 2014).

Analysing the potential causes of species declines and extinction risks is vital to mitigate the currently rampant biodiversity loss. Several global overviews and rankings of extinction threats have become available in recent decades (e.g. Bellard et al., 2016; Blackburn et al., 2019; IPBES, 2019; Maxwell et al., 2016; MEA, 2005; Ripple et al., 2019; Sala et al., 2000; Tilman et al., 2017). However, whether the strengths of these threat factors differ between countries that vary in the proportion of globally threatened animal and plant species that they hold is not fully understood (e.g. Howard et al., 2020). This might hamper conservation efforts and compromise achievement of international biodiversity goals (e.g. Aichi Biodiversity Targets: https://www.cbd.int/sp/targets/; Sustainable Development Goals: https://sustainabledevelopment.un.org/).

The IUCN Red List of Threatened Species is the most comprehensive source of information on the global extinction threat to species (https://www.iucnredlist.org). For the majority of assessed species, the likely causes of species decline have been identified using a standard scheme with categories such as "residential and commercial development," "agriculture and aquaculture," "invasive alien species" (IAS) or "climate change and severe weather" (i.e. the "threats classification scheme"; Salafsky et al., 2008). Studies based on this IUCN dataset came to different conclusions about the relative importance of threats to species, depending on which taxonomic groups and levels of extinction risk of species were considered and which version of the database was used (Cardillo & Meijaard, 2011). For instance, Maxwell et al. (2016) ranked overexploitation (including logging/gathering and hunting/fishing) as the largest threat to all threatened or near-threatened species belonging to taxonomic groups for which all known species have been assessed. Furthermore, Tilman et al. (2017) identified habitat loss associated with the expansion of agriculture, logging and development as the main threat to mammals and birds. Ripple et al. (2019), in turn, found that hunting primarily for meat consumption is the top threat to megafauna, followed by IAS. In contrast, Bellard et al. (2016) concluded that IAS are the leading cause of recent (over the past 500 years) extinctions of mammals and herptiles (i.e. amphibians and reptiles). Despite these variable findings, all studies agree that anthropogenic factors such as habitat change and fragmentation, biological invasions and climate change impose major threats to species survival and that the threatened species require protected areas.

A key reason for the various outcomes of previous approaches may lie in limitations in available IUCN Red List data. In particular, the information provided in the IUCN classification of threats is largely based on the individual opinions of experts, as for the vast majority of species, detailed analyses of threats are not available (Brooks et al., 2016; Gurevitch & Padilla, 2004; Hayward et al., 2015). Causes of threat are well known for charismatic and well-studied species, but not for the majority of assessed species (Donaldson et al., 2017). This represents a major knowledge gap in our understanding of the importance of drivers of global extinction risks.

Here, rather than using the IUCN classification of threats, we jointly considered a wide range of spatially explicit factors to determine how anthropogenic factors reported as global threats to species, as well as mitigation measurements such as protected areas, correlate with the proportion of globally threatened endemic species (i.e. species occurring naturally within one country only; IUCN, 2020) per country using structural equation modelling (Figure 1). We focused on endemic species to make sure that species are threatened by pressures exerted in our spatial unit (the country) and not beyond, and because it is likely that most endemic species in a country have been assessed. Moreover, national endemics are high-priority species because their conservation can only be guaranteed inside the country. Due to their restricted distribution and unique evolutionary history, endemic species are more susceptible to anthropogenic threats than non-endemic species and have a disproportionately high share of threatened species (Pitman & Jørgensen, 2002). However, endemic and non-endemic species appear to be impacted by a similar set of threats in a given country (see, e.g., Orsenigo et al., 2018 and Orsenigo et al., 2021, for vascular plant species in Italy). Thus, the outcome of this study may also have implications for a wider range of species. We accounted for biodiversity-inventory completeness and for the fact that biological invasions may be drivers of native species decline and passengers of anthropogenic environmental change (MacDougall & Turkington, 2005). Specifically, we examined which variables correlate with variation in the proportion of endemic species in each country that are globally at risk of extinction. Further, we refined this analysis for different taxonomic groups, life-forms and geographic regions.

2 | METHODS

2.1 | Threatened and extinct species

To better capture the relationship linking anthropogenic pressures, mitigation protection and data limitations with the risk of species extinction, we excluded species with distributions over several countries with a risk of extinction that is not necessarily homogeneous between their different populations. This means that we limited our dataset to endemic species, that is reported as occurring in a single country (Material S1). Information on a total of 65,125 terrestrial and marine endemic species including 27,294 globally threatened and extinct species (55% plant species, 45% animal species) was extracted from the IUCN Red List (IUCN, 2020). The categories of threatened species used in the analyses included all IUCN Red List categories, that is Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW) and globally Extinct (EX). The last two categories were merged into a single extinct category (abbreviated EX). For analyses, we calculated an Index of Threat (IoT) for each country, defined as the proportion of globally threatened and extinct endemic species among the total number of assessed extant and extinct endemic species per country (Figure 2). This was done to account for the large differences in country size (see Figure S1 of Material S2) and thus species richness. In addition, using the IoT was expected to reduce biases in completeness of Red List assessments compared with the described regional species pool among taxonomic groups (Figure S2 of Material S2) to some extent. However, to further account for this bias, we also considered a metric of completeness of biodiversity information later in our analyses. We also expect assessment completeness to be higher for endemic species to which countries pay particular attention than for non-endemic ones.

Further, to account for possible differences in extinction risk among endemic species of different life-forms (Lee & Jetz, 2011), we calculated the IoT for different subsets of species. Plants were differentiated into herbaceous species (6,814 species, i.e. 26% of the plant dataset), shrubs (5,443; 20%), trees (13,754; 52%) and vines (638; 2%) based on the IUCN data. Animals were differentiated into mammals (2,530; 7% of the animal dataset), birds (3,183; 8%), herptiles (10,175; 26%), fishes (7,942; 21%) and invertebrates (14,628; 38%, including arthropods, molluscs, annelids, echinoderms and cnidarians). Furthermore, we calculated the IoT of each country

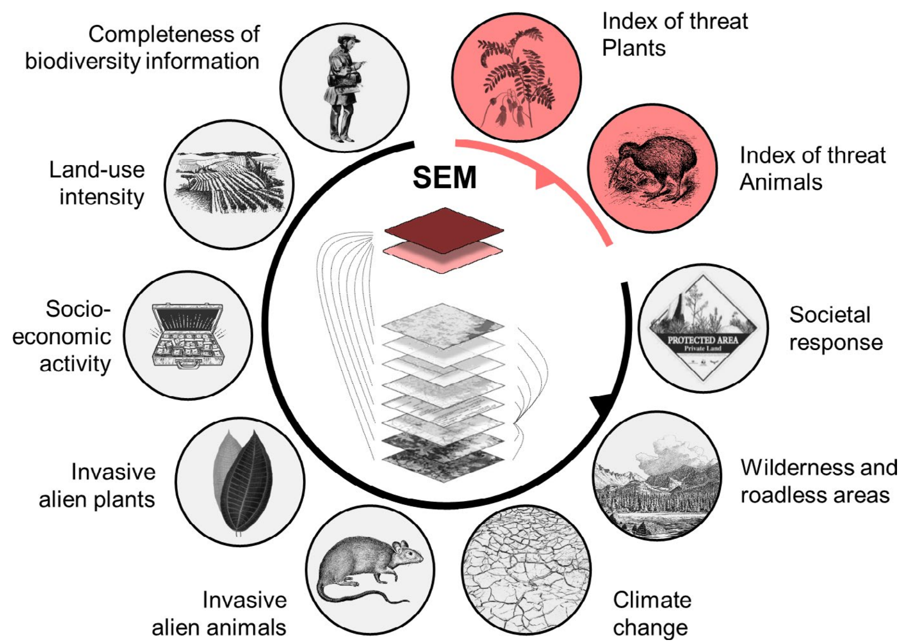

FIGURE 1 Conceptual diagram representing the principle of this study. We used structural equation models (SEMs) to test hypothesized connections linking country-level environmental and socioeconomic variables related to anthropogenic pressures, mitigation measures and data limitations (predictor variables) and the proportion of threatened endemic species in each country (response variables) or interlinking country-level environmental and socioeconomic variables

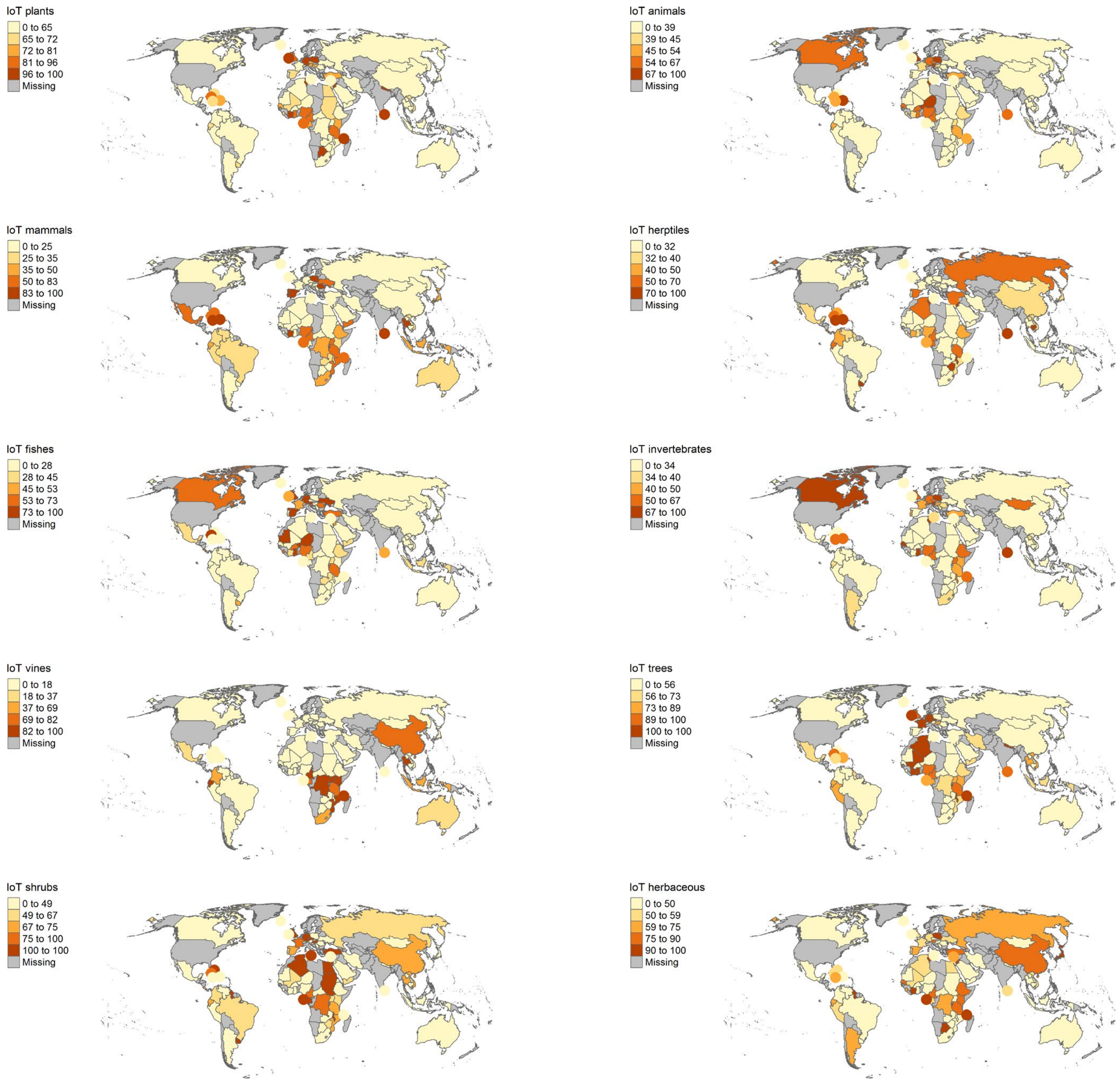

FIGURE 2 Map of the proportion of threatened and extinct endemic species among assessed endemic species (Index of Threat, IoT) per country and for different taxonomic and life-form groups (before standardization). The gaps show countries where at least one variable is not complete across the whole set of selected variables

separately for species of different Red List categories, that is VU (10,471; 38% of threatened and extinct species), EN (9,736; 36%), CR (6,188; 23%) and EX (899; 3%), as distinct human pressures might act at distinct steps of species decline. All data were extracted with the R package "rredlist" (Chamberlain et al., 2020).

2.2 | Explanatory variables

Extinction risk is the result of both the extrinsic environment (anthropogenic pressures and mitigation measures) and intrinsic species traits. It has been shown that environment prevails over species traits at least in determining species' geographic range size, and because of that, we focused our study on extrinsic pressures (Di Marco & Santini, 2015). To comprehensively analyse major threats of and mitigation options against global extinction risk, we used eight variables (selected from a set of 17 candidate variables; see Appendix S1 of Material S2 and Material S3 for details on the preselection method and the associated data, respectively) that we could relate to the IoT of countries. These variables were available for 94 countries, of which 15 are island nations and 79 are countries located on continents (Australia was treated as a continent). Both tropical—that is countries with a centroid within the tropics (52)—and extra-tropical countries (42) were well represented in the dataset. We performed

TABLE 1 Summary of the eight explanatory variables used to cover different facets of anthropogenic pressures to species, societal responses and possible data limitations due to incomplete recording of species. Per area GDP is expressed in international dollars (Intl$)

Variable class	Variable name	Unit	Calculation of variable	Data source
1. Land use intensity	Cropland	%	Proportion of 5 arcmin pixels covered by croplands, pastures and meadows	von Velthuizen et al. (2007)
2. Socioeconomic activity	Per area GDP	Intl$	Median value of GDP per 5 arcmin pixels	Kummu et al. (2018)
3. Invasive alien plants	Invasive alien plants	#	Number of species	Essl et al. (2019)
4. Invasive alien animals	Invasive alien animals	#	Number of species	GRIIS (see main text)
5. Climate change	Delta temperature	°C	Change in median value of 0.5° pixels between 1901–1910 and 1981–1990	Mitchell and Jones (2005)
6. Wilderness and roadless areas	Roadless areas	Km^2	Median size of roadless fragments	Ibisch et al. (2016)
7. Societal response	Protected areas	%	Proportion of designated protected areas	World Database of Protected Areas
8. Completeness of biodiversity information	Completeness of biodiversity information	None	Average of indices of recorded vertebrate and plant species numbers in GBIF weighted by estimated species richness	Meyer et al. (2015), Meyer et al. (2016)

the same analyses with 149 countries, by excluding the variable responsible for exclusion of the largest number of countries from the analysis (invasive alien animals, available for only 132 countries) and found the outcome to be relatively robust (Figure S4 of Material S2).

Specifically, the following variables were included (see Table 1, Table S1 and references therein of Material S2 and Figure S3 for details on how the variables were computed):

1. the proportion of each country covered by cropland, pasture and meadow (including food, fibre and fodder crops and pasture grasses; von Velthuizen et al., 2007) as a measure of habitat destruction by conversion of natural lands into agriculture.
2. the per area gross domestic product (GDP; Kummu et al., 2018) as an indicator of economic development and its ecological footprint on species and their habitat. This index was found to better represent the dimensions of socioeconomic activities that pose threat to plant and animal species than the total GDP divided by the land area of the country (Figure S5 of Material S2).
3. the number of invasive alien vascular plant species recorded in each country (Essl et al., 2019), which contributed to the decline of native species potentially through competition and community or habitat alteration. However, it remains unclear to what extent invasive vascular plants act independently of other human pressures.
4. the number of invasive alien animal species (http://griis.org/ accessed on 27-6-2018) for the same reasons as for invasive vascular plants.
5. the median change in annual mean temperature between 1901–1910 and 1981–1990 (Mitchell & Jones, 2005), which is associated with a variety of changes such as distributional range shifts, loss of habitat, changes in competitive ability and fecundity, desynchronization of dispersal events and uncoupling of species relationships.
6. the median area of a roadless fragment (Ibisch et al., 2016), because roads provide access to previously remote areas (including coastlines), thus opening them up for more roads, land use and sea-use changes, associated resource extraction and human-caused disturbances of biodiversity.
7. the proportion of total land area covered by terrestrial protected areas (https://www.iucn.org/theme/protected-areas/our-work/world-database-protected-areas), which are still considered the most effective way to overcome the threats that are causing the current biodiversity crisis.
8. completeness of biodiversity information (Meyer et al., 2015, 2016) as less inventoried regions could be misinterpreted as harbouring fewer species and thus fewer threatened species.

Endemic marine species were mainly species occurring in coastal zones, the world's most densely populated regions. Like terrestrial species, coastal species are also expected to be affected by cropland (pesticide and nutrient run-off into water catchments) and roadless areas (limiting human access to the coast). Moreover, temperature change is expected to be similar in continental and coastal ecosystems (Harter et al., 2015) and the proportion of total land area covered by terrestrial protected areas was found to be highly correlated with the proportion of total territorial area (i.e. land area + territorial waters) covered by terrestrial and marine protected areas ($r = .62$; p-value $<.001$; $n = 211$).

Data from the latest version of the IUCN Red List and from most of the selected explanatory variables (2–4, 6–8) stemmed from a similar time period (2015–2019), although assessments for many species might be from earlier years (Rondinini et al., 2014). The proportion of cropland, pasture and meadow data were only available for the early 2000s, which, however, seems suitable to account for the often substantial time-lags between changes in habitat conditions and its impact on species dynamics (Tilman et al., 1994). The change in annual mean temperature covered the period between 1901–1910 and 1981–1990, which allowed quantifying global warming in the recent history to which some organisms may still be responding. Moreover, these data may also represent ongoing climate change as regions that have been the most affected by global warming over the last century likely continue to be the most affected (IPCC, 2013). Although the extinction risk was assessed between 2015 and 2019, for most EX species, extinction happened earlier, mainly between 1900 and 2000. However, we expect that our set of current anthropogenic pressures would still be indicative for that longer period, because, for example, the road network and the conversion of natural lands into croplands developed over centuries and particularly during the 20th century.

2.3 | Analyses

Relationships of IoT with explanatory variables were quantified using structural equation models (SEMs). Structural equation modelling is an increasingly used multivariate statistical analysis technique that can disentangle direct and indirect connections among multiple variables in complex networks (Grace, 2006). It combines factor analysis and multiple regression analysis, and is used to analyse the structural relationship between measured variables and unobservable latent constructs. A major advantage of this approach is that it estimates multiple and interrelated dependencies and allows for explicit tests of complex hypotheses. However, as *SEM* is a priori dependent on theory and previous empirical evidence, it requires sound theoretical or empirical evidence of a relationship between the variables and the likely direction of that relationship. As with other correlative approaches, *SEM* does not demonstrate causality per se. Rather, it highlights whether the hypothesized causal model is consistent with the empirical data.

SEM pathways were identified a priori to represent hypothesized dependencies between predictor and response variables (Figure 3a and Table S1 of Material S2). Full SEMs included connections between all explanatory variables and IoT. We added connections between the number of invasive alien species (both plants and animals) and all other explanatory variables, because biological invasions have been posited to be symptoms of human pressures rather than drivers per se (MacDougall & Turkington, 2005). Invasive species are defined here as alien species that spread widely and cause negative impacts on the environment (CBD, 2000). As there are many different complex relationships between GDP and other explanatory variables, we also added the covariance between GDP and the proportion of cropland, pasture and meadows, roadless areas, the proportion of protected areas and inventory completeness. We built seven SEMs: (a) for plants (threatened and extinct) and animals (threatened and extinct), and separately for (b) different plant life-forms (herbaceous, shrubs, trees and vines), (c) animal taxonomic groups (birds, fishes, herptiles, invertebrates and mammals), (d) different plant threat categories, (e) different animal threat categories, (f) extra-tropical countries and (g) tropical countries as many of the eight explanatory variables that we tested differ between extra-tropical and tropical countries (e.g. lower GDPs in tropical countries, lower invasion rates and less climate warming).

All variables were natural log-transformed and standardized (centred on the mean and scaled by the standard deviation) to improve linearity and comparability of predictor–response associations (Figure S6 of Material S2). Reduced SEMs were obtained by sequentially deleting the least significant connection until all remaining connections had p-values below the critical value of .05 as long as the reduced SEMs stay significant (backward elimination). Model parameters were estimated through maximum-likelihood optimization, which maximizes the agreement between observed and predicted variance–covariance matrices. A bootstrapped estimate and its associated standard error were also calculated for each connection based on 1,000 replications. This was done to check the statistical robustness of the selected model due to limited sampling size. Reduced SEMs were evaluated based on three accuracy metrics: a chi-square statistic used to test the hypothesis of model-data consistency (p-value), the root mean square error of approximation (RMSEA), which measures the difference between the observed covariance matrix per degree of freedom and the hypothesized covariance matrix that denotes the model (Browne & Cudeck, 1993), and a comparative fit index (CFI), which indicates the fit improvement relative to a null model. A p-value below .05 indicates a significant deviation between observed and modelled IoT, while a p-value above this threshold indicates concordance. Values of RMSEA closer to 0 and values of CFI closer to 1 represent a good fit. These analyses were performed with the R package "lavaan" (Rosseel, 2012; see R script and the associated data in Appendix S2 of Material S2 and Material S4, respectively).

3 | RESULTS

The observed and modelled IoT (i.e. the proportion of globally threatened and extinct endemic species in a country) did not deviate significantly from concordance (p-value of chi-square test >.05), and the *SEM* provided a good fit to the data (RMSEA < 0.11; CFI > 0.91; Table 2). The bootstrapped estimates of the path coefficients were similar to those obtained through maximum-likelihood estimation (Table S2 of Material S2). The IoT was strongly correlated, either directly or indirectly, with several anthropogenic pressures, mainly per area GDP, roadless area and number of invasive alien plants (see below for details on the signs of the correlations).

The IoTs of plants and animals were not related to our estimate of inventory completeness (Figure 3b). However, both the number of invasive alien plants and the number of invasive alien animals increased with inventory completeness of the country (Figure 3b).

Overall, the IoTs of plants and animals were not significantly correlated with the proportion of croplands and pastures per country, the number of invasive alien animals, the change in annual mean temperature or the proportion of protected areas (but see below for exceptions), and the latter was also not correlated with the numbers of invasive alien plants (Figure 3b).

The IoT of plants was significantly higher in countries with a high per area GDP than in countries with a low per area GDP (Figure 3b).

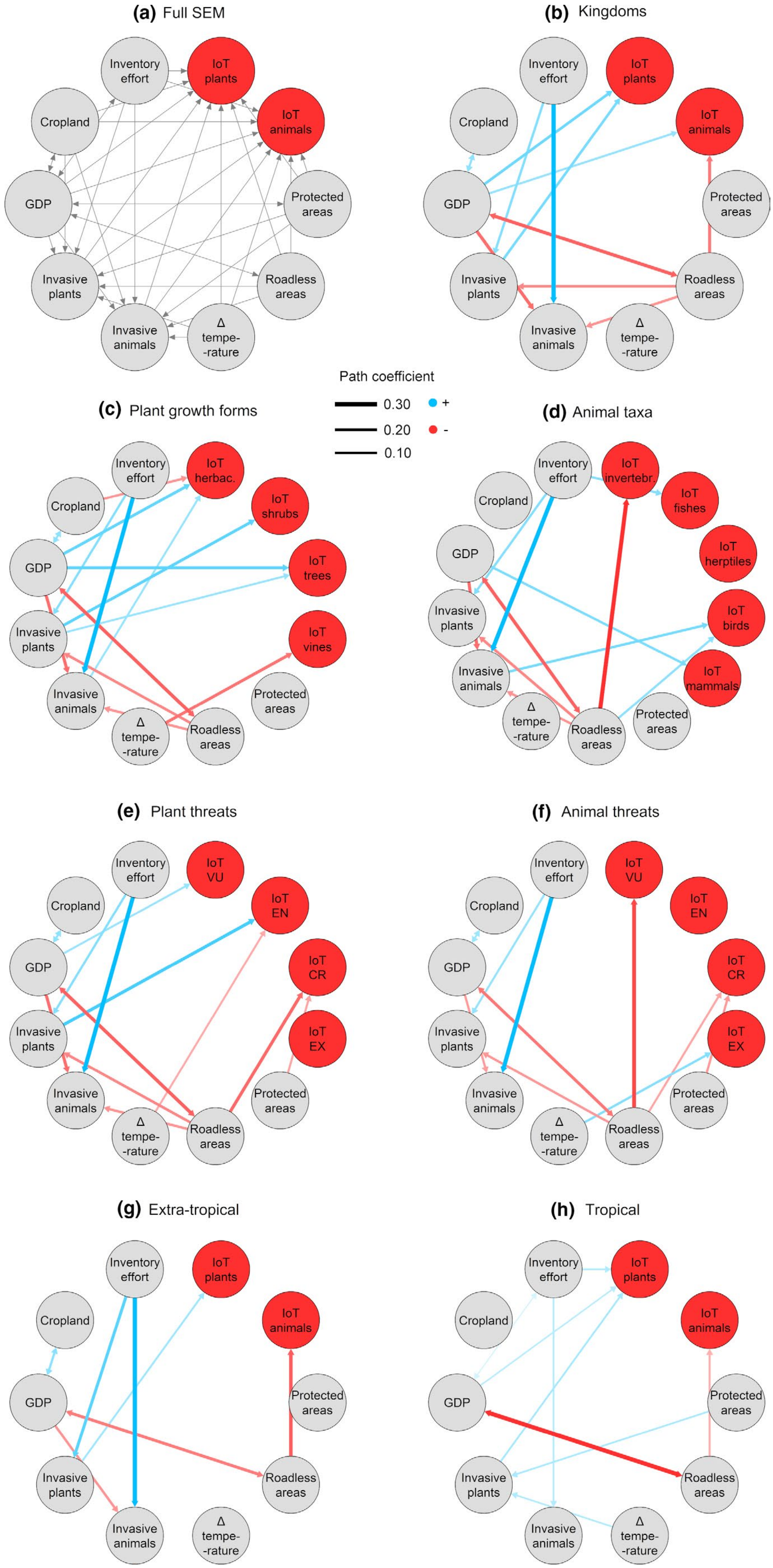

FIGURE 3 Correlates of global species extinction threat for plant and animal kingdoms (a), for different plant life-forms (b) and animal taxa (c), and for plant (d) and animal species (e) according to their threat categories (VU = Vulnerable, EN = Endangered, CR = Critically Endangered, and EX = globally Extinct or Extinct in the Wild), in non-tropical (f) and tropical countries (g). The structural equation model shows the correlation of different human variables, mitigation measures, and possible data limitations (grey circles) with the proportion of threatened and extinct plant and animal species per country (Index of Threat, IoT; red circles). The thickness of the lines is proportional to path (correlation or regression) coefficients, that is the strength of the relationship (non-significant effects are not shown). Blue lines indicate positive effects, and red lines indicate negative effects

TABLE 2 Validation statistics of the structural equation models (SEMs)

SEM	Figure	*p*-value	RMSEA	CFI
Kingdoms	3b	.05	0.11	0.92
Plant life-forms	3c	.06	0.07	0.91
Animal taxa	3d	.40	0.02	0.99
Plant threats	3e	.75	0.00	1.00
Animal threats	3f	.21	0.04	0.92
Extra-tropical	3g	.76	0.00	1.00
Tropical	3h	.46	0.00	1.00

Note: p-value: probability value of the chi-square test of independence between observed and predicted Indexes of Threat (IoTs).
Abbreviations: CFI, comparative fit index; RMSEA, root mean square error of approximation.

This pattern was mainly accounted for by herbaceous and tree species (Figure 3c), particularly those found in tropical regions (Figure 3h). The IoT of animals was also significantly higher in countries with a higher per area GDP, especially for mammals (Figure 3d). On the other hand, countries with a higher per area GDP had fewer invasive alien animals (Figure 3b).

The IoT of animals was lowest in countries with large roadless areas (Figure 3b). This pattern was mainly accounted for by invertebrates (Figure 3d), and by the proportion of Vulnerable species (Figure 3f), and was more pronounced in the tropical than in the extra-tropical regions (Figure 3g,h). The IoT of plants was not directly correlated with the size of roadless areas (Figure 3b). However, countries with larger roadless areas also had fewer invasive alien plants and animals (Figure 3b).

The IoT of plants was significantly higher in regions with more invasive alien plants (Figure 3b), particularly for threatened shrubs and trees (Figure 3c), and plants in the threat category EN (Figure 3e), and this was more pronounced in the tropical than in the extra-tropical regions (Figure 3g,h). IoT of animals did not significantly vary with the number of invasive alien plants (Figure 3b).

The IoT of herbaceous plants was significantly lower in countries with a large proportion of croplands, pastures and meadows (Figure 3c). The IoT of vines was significantly lower in countries with stronger climate warming (Figure 3c), while the IoT of animals in the threat category EX was significantly higher in countries with stronger climate warming (Figure 3f). Countries with stronger climate warming had more invasive alien plants but only so in the tropics (Figure 3h). The IoTs of plants and animals in the threat category CR were higher in countries with small proportions of protected area (Figure 3e,f). The IoT of birds was significantly higher in countries with more invasive alien animals (Figure 3d).

4 | DISCUSSION

The analysis of our Index of Threat (IoT) shows that the proportion of globally threatened and extinct endemic species in a country correlates with several anthropogenic pressures. Overall, the IoTs were higher in countries with a higher per area GDP, smaller roadless areas and more invasive alien plant species. However, we found substantial variation in the congruence of IoTs with anthropogenic pressures for species of different kingdoms, life-forms, threat categories and regions.

The largest proportions of globally threatened endemic species, particularly for mammals and tropical plants, were found to occur in areas with a high per area GDP. As economic wealth is often associated with profound alteration of natural habitats (Rainham & McDowell, 2005), these areas are typically prone to a range of negative impacts on species survival such as land use intensity and urban sprawl. On the contrary, countries with a high per area GDP had fewer invasive alien animals. This might partly reflect that large countries, such as Australia, Brazil, Canada and China, have more invasive species than small countries, but due to their sheer size also low per area GDPs (Figure S2). In addition, it could be that countries with a high GDP have the resources to impose better biosecurity measures and to manage invasive animals. So, while economic development has resulted in increasing numbers of threatened species, it could also provide the financial resources required for biosecurity and conservation.

Countries with a less dense road network, particularly those located in the tropics, such as Brunei, Eritrea and Mozambique, have lower proportions of threatened endemic invertebrates among those assessed (Figure 3 and Figure S2). This probably reflects that an increase in road infrastructure usually leads to more land conversion and habitat fragmentation, which calls for maintaining large roadless areas in those countries (Laurance & Balmford, 2013; Selva et al., 2011). Countries with a less dense road network also have fewer IAS, which provides further evidence that road corridors promote the spread of invasive alien plants (e.g. Follak et al., 2018; Joly et al., 2011; Lázaro-Lobo & Erwin, 2019) and animals (e.g. Brown et al., 2006; Komine et al., 2016; Recio et al., 2015).

We showed that regions with more threatened endemic plants, particularly woody tropical plants, also tend to have more invasive alien plants (Figure 3b,c,h). Interestingly, all the native plant species that are reported to be threatened by invasive alien plants in the IUCN Red List (i.e. in which invasive alien plants are listed as at least one of the factors contributing to a species decline) are endemic to islands (IUCN, 2020). Furthermore, all recent plant extinctions facilitated by alien species occurred on islands (Sax & Gaines, 2008). Islands harbour depauperate and disharmonic native floras, as well as a disproportionately high percentage of woody species (insular woodiness), compared with similarly sized mainland regions (Carlquist, 1974; König et al., 2020). Because of the special characteristics of islands in which endemic species have evolved, island floras are considered to be very susceptible to invasive alien plants (Russell et al., 2017). Countries with more invasive alien animals also have a larger proportion of threatened endemic birds (Figure 3d). According to the IUCN Red List (IUCN, 2020), about fifteen animal species including mammals (cats, rats, wild boars, wolves, goats, rabbits, sheep, chital, cows and guinea pigs), birds (*Bubo virginianus*), reptiles (*Boiga irregularis*), fishes (*Micropterus salmoides*, *Oncorhynchus mykiss*) and insects (bees) have contributed to extinctions of >80 bird species (Bellard et al., 2016).

While the association between IAS and IoTs likely partly represents a causal effect, many invasive alien plants and animals are likely to be passengers of other human pressures (MacDougall & Turkington, 2005). For instance, our results indicate that higher numbers of IAS might be due to external environmental (e.g. climate change) and socioeconomic factors (e.g. land use intensity, increased fragmentation by roads). While our approach does not allow disentangling of actual causal effects on IoT from correlative ones, our findings emphasize that invasive plants may reflect combined threats to endemic species from other sources, and could therefore be used as an indicator of extinction risk, especially for tropical woody species.

The observation that the IoT of vines is low in countries with high temperature change would be consistent with the emerging idea that climate change overall benefits climbing plants (Figure 3c). Climbers may suffer less from water stress and thus grow better than trees during increasingly frequent dry periods (Schnitzer, 2005). We also showed that regions with more elevated temperature overlap with regions with more reported endemic animal extinctions (Figure 3f). Although it has been shown that local extinctions related to climate change are already widespread (Wiens, 2016), evidence that climate change has caused widespread global extinctions remains lacking (Bellard et al., 2016; Le Roux et al., 2019). This nevertheless suggests that global warming will primarily impact regions that have already undergone widespread extinctions of endemic animals. Furthermore, the observation that IoT of CR plant and animal species is high in regions with a small proportion of protected areas suggests that more protected areas are needed in those countries (Figure 3e,f). Another possible explanation could be that limited national resources may have resulted in a focus on assessing only the most obviously threatened endemic species, resulting in a high IoT of CR species. In addition, the same resource limitation may mean that protected areas are not effectively managed and therefore limited in their overall effectiveness, except with respect to CR species.

Surprisingly, IoTs were little associated with land use intensity, although it is known to be a major threat to global biodiversity (e.g. Maxwell et al., 2016; Ripple et al., 2019). We even found that there are fewer threatened endemic herbaceous plants in countries with large cropland areas, pastures and meadows, which could reflect that the latter provide habitat to many herbaceous species (Figure 3c). This variable was quantified with the proportion of each country covered by crops, pastures and meadows, and thus does not necessarily capture other facets of land use intensity (e.g. biocide application, fertilizer input), and recent rates of land use changes. Furthermore, time-lags of changes in the pressures we have used here and their full impact on species abundances and distributions are known to be widespread and may extend over substantial time periods causing extinction debt (Tilman et al., 1994). Thus, impacts of recent increases in pressures, which are known to be frequent (e.g. Steffen et al., 2015), may be masked by delayed species decline, and result in delayed recognition of a species as being globally threatened. This phenomenon may be particularly important in regions that have undergone massive socioeconomic development in recent history (e.g. Brazil, China, India), and many of these regions are located in megabiodiverse regions (Brooks et al., 2016). In addition, the poor association between the IoT of EX species and our set of explanatory variables suggests a geographic mismatch between the past anthropogenic pressures that caused widespread extinctions since 1500 AD, mainly in the 1900–2000 period, and current anthropogenic pressures. Therefore, the full extent of species extinction threat caused may not be fully captured by our analysis.

Overall, our correlative approach provides a useful new perspective of the associations between extinction risk of endemic species and regional environmental and socioeconomic characteristics independently of the IUCN threat classification. However, as the approach is correlative and is limited by the availability and quality of data, both with regard to threatened and extinct species and potential predictor variables, the results require careful interpretation. For instance, species richness of invasive alien plants stood out as a major correlate of global plant extinction risk (e.g. Figure 3b), which might indicate that invasive species are indeed a major threat to many native plant species. However, invasive species richness could also be an integrative and multifaceted indicator of other pressures rather than being a leading cause of plant extinctions. Moreover, some well-documented relationships were assessed as not significant in the SEMs, which probably arises from artefacts of the method or data. For example, although the expansion of agriculture is recognized as a major threat to mammals and birds (Tilman et al., 2017), we did not find a significant relationship between the proportion of cropland and pasture and the IoT of these taxonomic groups (Figure 3d). Part of the data limitation comes from the fact that IoT data are only available at the country level and that the countries vary tremendously in size. Moreover, although our IoT score was found to be useful to account for the differences in species richness, this index might be skewed if previous assessments were not random and priority has been given to species more likely to be threatened, which would overestimate IoT. This is at least the case for plants for which 48% of assessed species are considered threatened, while global estimates place this proportion at 21% (Brummitt et al., 2015). However, this is unlikely to explain our findings because such an IoT overestimation would be expected to happen mostly in countries with limited scientific and economic resources (low GDP), where IoT is rather low. More importantly, it has been reported that many national Red Listing initiatives generating assessments in non-English language have not published their results on the global Red List, and this would affect particularly national endemic species (Bachman et al., 2019). This gap is likely to lead to an underestimation of IoT (e.g. in Africa and South America) whose impact on our results is difficult to estimate precisely. This calls for a better connectivity between national scale assessments, including those in languages other than English, and the global Red List.

Therefore, we encourage further correlative studies at smaller scales (e.g. in regions with more high-quality data) or on specific well-studied taxonomic groups (e.g. vertebrates, Cycads), preferably with a relatively uniform response time to pressures. A particularly promising development is that gridded distribution maps have become available for an increasing number of species in the IUCN Red List (but still not enough to ensure taxonomic completeness). This offers scope for future analyses of potential drivers of environmental and socioeconomic correlates of global extinction risk at a higher resolution and for non-endemic native species.

Expert knowledge has been critical to identify drivers of global species decline (e.g. habitat destruction, overexploitation). Here, we identified how variation in the magnitude of these threats correlates with the proportion of threatened and extinct endemic species in a country. Our approach does not make expert assessment obsolete but instead introduces another view and dimension to threat categorization, which may allow us to more easily assess larger numbers of species. Although some of the correlations do not reflect causal relationships but chance associations, they nevertheless provide guidance for conservation efforts. For example, we found that countries with large proportions of endemic animals are categorized by global Red List assessment as CR tend to have a relatively low proportion of their territory covered by protected areas, which points to a need for more protected areas. Our analyses, however, also detected less perceptible or more systemic threats that appear to be less frequently reported as important drivers up to now, such as IAS (see Downey & Richardson, 2016) and climate change (see Trull et al., 2017). This echoes another recent correlative study reporting that islands with and without plant extinctions are better discriminated when IAS and climate change velocity are considered besides proxies of agricultural activity (% of population in agriculture) or development (growth rate and GDP) than when they are not considered (Gray, 2018). These and our findings call for avoiding simplistic ranking of single threats and rather support a view of considering human pressures and societal responses as a complex network (Lee & Jetz, 2011). Our study also highlights that more effort is required for documenting the local extinction threat of endemic species, for example by developing more national and subnational red lists that would allow for linking local drivers with local threat statuses. Our results show that the extinction crisis in endemic species is associated with a complex network of interacting human pressures and societal measures that need to be considered in conservation policy and practice.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and R codes that support the findings of this study are available in supporting information. A shapefile representing the proportion of threatened and extinct endemic species per country in relation to environmental and socioeconomic drivers (Material S3) has been deposited in Dryad (https://doi.org/10.5061/dryad.79cnp5hw5).

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BIOSKETCH

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