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Body size and latitude predict the presence of multiple stressors in global vertebrate populations

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Body size and latitude predict the presence of multiple stressors in global vertebrate populations

Nicola Noviello

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Summary

With anthropogenic threats driven by human expansion and resource requirements, multiple, interacting stressors are impacting wild populations like never before. Yet the time and cost involved in assessing these stressors in the field can be prohibitive, and as such, an ability to monitor population stressor number *ex situ* would provide a fast and economical alternative to costly surveys. Our study aims to achieve this capability by using population-specific threat data, alongside spatial and body mass records, to identify new ways of forecasting the number of stressors impacting real-world populations. Utilising the Living Planet Database alongside supplementary species trait catalogues, we examine 7470 populations of 2516 vertebrate species, across terrestrial, marine and freshwater ecosystems to show that both body size and latitude can be used as predictors of stressor number in wild vertebrate populations. Results demonstrate a positive relationship between body mass and the number of stressors in terrestrial bird and mammal, freshwater mammal, and marine cartilaginous fish populations. Additionally, we find peaks in stressor number between 20°N and 40°N latitude, and again towards polar regions for most groups. These findings suggest that high body mass taxa are of specific conservation concern, particularly given that larger species typically have the greatest influence within ecosystems. Spatial analysis also indicates that stressor numbers peak in areas of high human population density, with increases in stressors towards the poles suggesting that climate change also contributes to threat predictions. Body size and latitude are therefore shown to be useful predictors of stressor number across three ecological systems and multiple taxa, providing an efficient and convenient way to assess population risk by enabling the triage of more focused investigation.

Dedication

For Daniel

Acknowledgements

I would firstly like to extend my thanks to Chris Clements, whose support throughout the year has been constant, patient and understanding, even where my personal decisions might have been a detriment to his work. As I look back through my draft works, I can see just how far I have come, and this is largely due to his influence, for which I count myself lucky and my work enriched.

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Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

SIGNED: Nicola Noviello DATE: Monday, 28th September 2020

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1

Introduction

The majority of stressors threatening biodiversity are due to the rapid and unrelenting expansion of human activity (Davidson, Hamilton, Boyer, Brown, & Ceballos, 2009; Dirzo et al., 2014; Hoffmann et al., 2010; Ripple et al., 2017), with a suite of threats such as habitat loss, exploitation, invasive species, pollution and climate change increasing as the human population continues to grow (Keith et al., 2015). Given the ever-advancing nature of anthropogenic threats (Galli, Wackernagel, Iha, & Lazarus, 2014), wild populations are increasingly likely to suffer the impacts, with species declines and extinctions becoming ever more probable (Cardillo et al., 2004).

Despite the potentially catastrophic effects that one stressor can have on a population, the effects of multiple stressors acting together are often worse (Lande, 1998). Yet there is little clarity on what makes species predisposed to multiple stressors in wild populations. With such uncertainty as to why populations with different traits and in different locations are affected by more than one of these stressors, immediate research is required to identify predictors which can forecast the presence of multiple stressors, in a world increasingly suffering their consequences. Indeed, with stressor combinations able to exert differing pressures dependent upon factors such as taxa and ecological system, a holistic understanding of stressor presence is crucial prior to the deployment of truly targeted and effective intervention. Such knowledge could lead to a framework for the assessment and prioritisation of species and populations, allowing targeted conservation interventions to maximise returns on limited conservation funding.

1.1 Current Threats to Biodiversity

A threat, or stressor, can generally be defined as a physical factor that has an adverse impact on an ecosystem or its biotic components (Alexander, 2006). In individuals, this may increase mortality risk or impact growth and reproductive output, with the resulting lower fecundity hindering overall population growth or recovery (Alexander, 2006; Folt, Chen, Moore, & Burnaford, 1999).

The United Nations Environment Programme (2006) has defined five principal anthropogenic stressor categories impacting biodiversity: habitat loss/degradation, pollution, overharvesting (i.e. exploitation), climate change, and the movement of invasive species. Each of these stressors in isolation can have a devastating effect on populations, and may successively compromise biodiversity within the ecosystem they are part of (Lande, 1998). For instance, droughts caused by climate change can cause water stress, mortality and even local extinction in terrestrial populations which, in turn, can indirectly impact the predatory or parasitic species which rely upon them by removing their food source (Cahill et al., 2013). Similarly, fishing intensity can have a dramatic effect on trophic structures with non-selective practices putting marine predators at risk of extinction (Zhou & Smith, 2017).

1.2 Multiple Stressors

While single stressors alone can be disastrous for a population - given the prevalence of stressors globally – of particular concern is the potential for stressors to interact, creating challenges for conservation managers and increasing the risk of negative impacts on biodiversity (Cooney, Beauchamp, & Gehrs, 1983; Hanazato & Dodson, 1995).

While populations facing one stressor may demonstrate complete resilience, their coping ability may become compromised once a second or third threat is introduced (Breitburg et al., 1998; Crain, Kroeker, & Halpern, 2008). As such, the consequences of exposure to multiple stressors can be numerous and profound, including geographical range shifts (Beaugrand, Reid, Ibañez, Lindley, & Edwards, 2002; Perry, Low, Ellis, & Reynolds, 2005; Sunday, Bates, & Dulvy, 2012); reductions in growth and metabolic rate (Holliday, Elskus, & Roosenburg, 2009); changes in the composition of ecological interactions (Pincebourde, Sanford, Casas, & Helmuth, 2012); deviating migratory paths (Byrne, Selvakumaraswamy, Ho, Woolsey, & Nguyen, 2011); changes in population structure and dynamics (Rohr et al., 2004) and, in the most concerning scenarios, population collapse and extinction of species (McCauley et al., 2015; Davies, Margules, & Lawrence, 2004; Hedrick, Lacy, Allendorf, & Soule, 1996; Hodgson et al., 2017). In addition, multi-stressor effects are likely to change between taxa, population, ecological system and location. For instance, exploitation for food or medicinal products will disproportionately target larger species close to human settlements, making the same population more vulnerable to other local stressors such as land use change (Bonnot et al., 2013). Meanwhile, climate change is more likely to impact smaller species towards polar regions due to their limited dispersal ability (Vincent, 2019; Genner et al., 2010), while their comparatively high surface areas make them simultaneously more vulnerable to chemical pollutants (Kaufmann and Dohmen 2016; Watling and Braga 2015). Moreover, once individual populations are impacted, there will be likely ramifications at higher and / or lower trophic levels, impacting the structural integrity of the food network (Purvis et al., 2000).

Past research into multiple stressors has largely focussed on their combined effects in small scale and /or in experimental settings (Hodgson et al., 2017), with far less known of the effects of stressor exposure in wild populations. Considering the impacts possible in multi-stressor scenarios, research on their effects on wild populations is therefore lacking, principally due to difficulties of obtaining the long-term, high-quality datasets required to reliably ascertain both population trends and information on the stressor combinations acting upon them (Côte, Darling, & Brown, 2016).

Complicating matters further are the potential effects of species-specific traits on vulnerability to multiple stressors. For example, body size, life cycle duration, feeding behaviour, etc., are all known to alter susceptibility to anthropogenic threats (Böhm et al., 2016; Collen et al., 2009), begging a more comprehensive incorporation of these characteristics and enabling the prediction of multiple stressors on a larger scale. Moreover, with threats intrinsically linked to human populations, an understanding of how stressors are spatially distributed would provide a more complete picture of a population's risk. By incorporating this analysis across populations, it is possible to forecast the probability of stressor presence and detect the most threatened taxa throughout ecological systems by extending our knowledge beyond small-scale laboratory experiments to preserve biodiversity despite increases in stressor number and magnitude (Sala et al., 2000).

1.2.1 Multiple Stressor Interactions

The interactions between multiple stressors have long been recognised as a one of the most prominent ecological concerns (as reviewed by Côte et al., 2016). Yet most research remains focused on single stressor scenarios (O'Brien, Dafforn, Chariton, Johnston, & Mayer-Pinto, 2019) or artificially manipulated multi-stressor experiments using aquatic invertebrates, which may be unrepresentative of larger, wild vertebrate species. This is despite significant evidence demonstrating the

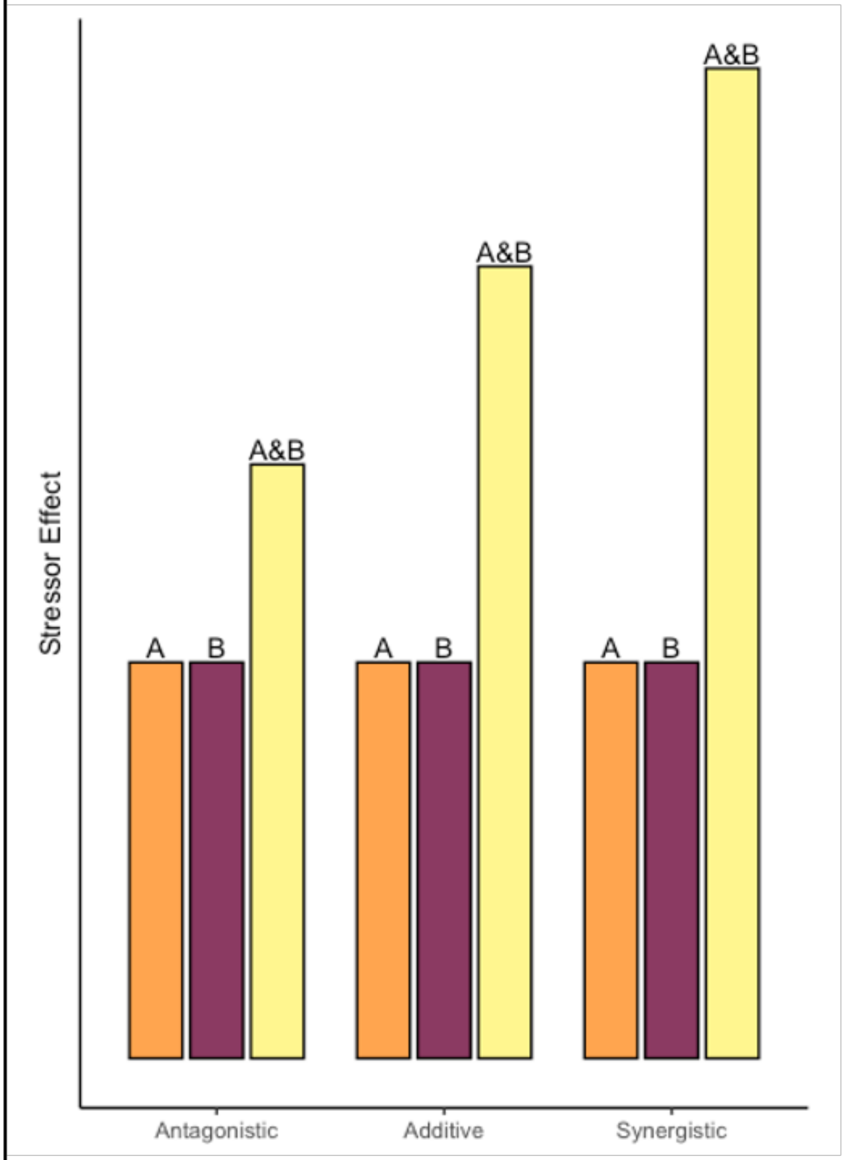

Fig. 1.1 | Stressor interaction effects

Visualisation of multiple stressor interactive effects

potential damage inflicted by combined anthropogenic threats in real-world systems (Côté et al., 2016). Acting together to create composite effects, multiple stressor interactions can be defined by three overall terms, developed to describe the varying impacts they exert on respective populations: additive, synergistic and antagonistic (Fig. 1.1).

1.2.1.1 Additive Interactions

Additive interactions are the simplest, describing combination effects equal to the sum of each stressor's individual part. As such, it can be argued that additive stressors are independent of each other, devoid of interactions and simply ‘stacking’ on top of one another (Fig. 1.1). Stressors behaving additively can therefore be mitigated hierarchically, in order of their adverse impacts on populations (Brown et al., 2013). For instance, where fishing and UV radiation has been identified as an additive interaction (Crain et al., 2008), the removal of either stressor would reduce impacts on the focal population.

1.2.1.2 Antagonistic Interactions

Antagonistic interactions, in contrast to additive, produce a combined effect less than the sum of their individual stressors (Crain et al., 2008; Folt et al., 1999; Schinegger, Palt, Segurado, & Schmutz, 2016) (Fig. 1.1). For instance, an antagonism might comprise a marine environment in which sediments are beneficial for corals at risk of bleaching, but only due to the - otherwise damaging - high turbidity levels reducing physiological light stress on corals (see Anthony, Connolly, & Hoegh-Guldberg, 2007). Antagonisms also encompass scenarios where individuals particularly vulnerable to one stressor experience higher mortality and so are removed from a population, being replaced by those more resistant, thus reducing the combined effect of multiple stressors (e.g. Darling, McClanahan, & Côté, 2013). Management techniques in antagonistic interactions may, therefore, be more challenging due to the possibility that mitigative action has the opposite effect to that intended; hindering, rather than promoting population recovery (Fong, Bittick, & Fong, 2018). Accordingly all, or at least a large majority, of stressors working antagonistically would require elimination before ecosystem / population recovery is possible (Crain et al., 2008), unless antagonisms are driven by a dominant stressor (e.g. Bray et al., 2019; Folt et al., 1999). With various papers suggesting that antagonistic relationships represent the largest proportion of interactions in multiple stressor environments (see Crain et al., 2008; Darling & Côté, 2008; Folt et al., 1999; Teichert et al., 2016), these combinations represent perhaps the greatest challenge of multiple stressor scenarios.

1.2.1.3 Synergistic Interactions

Finally, synergistic interactions are present where combined stressor effects exceed those of additive ones, such as where exposure to pollutants increases a population's vulnerability to parasitism (e.g. Coors and De Meester, 2008) (Fig. 1.1). As with additive interactions, synergistic effects may be more reliably mitigated by the treatment of just one stressor, accelerating recovery with significant reductions in net stressor effects on the community (Fong et al., 2018). Recent reviews on multiple stressors have highlighted a bias towards the research of synergies (e.g., Brown et al., 2013; Côte et al., 2016; Darling, Mcclanahan, & Côté, 2010; Maher, Rice, McMinds, Burkepile, & Vega Thurber, 2019), perhaps due to due to the compelling narrative favoured by authors and publishers, or by the misinterpretation of definitions (Côte et al., 2016). Accordingly, it could be argued that, as less prevalent (Côte et al., 2016) and easier to manage (Brown et al., 2013; Crain et al., 2008), research attention should be directed more towards alternative interactions to provide equivalent complementary knowledge.

1.3 Stressors and Systems

The drivers of change between ecosystems are heterogeneous (Halpern et al., 2015), and may differ between aquatic and terrestrial systems (Bowler et al., 2018) (Fig. 1.2). For example, sensitivity to climate change is greater in aquatic realms, yet species are presented with fewer boundaries to dispersal than in terrestrial habitats (Poloczanska et al., 2013; May, 1994), resulting in trait and system-dependent population composition (Pinsky et al., 2019; Crain, Kroeker and Halpern, 2008). Hence, in order to fully understand the nuanced effects of stressor combinations on populations, each must be reviewed independently and between ecological systems.

1.3.1 Terrestrial

It is estimated that up to 83% of the planet's land surface has been directly affected by human expansion (Sanderson et al., 2002), with at least 75% exposed to some form of measurable human pressure (Venter et al., 2016). Stressors, perhaps predictably, show greatest impacts on habitats surrounding large cities due to the presence of stressors local to areas of high population density, such as pollution and exploitation (Bowler et al., 2018; Venter et al., 2016). Urbanisation also creates longer-lasting effects than other forms of habitat loss, due to the relative permanence of metropolitan areas (McKinney, 2002). Correspondingly, urbanisation and agricultural practices commonly result in damaged and fragmented terrestrial habitats, limiting the abundance of food or foraging locations, increasing competition and restricting land-based dispersal ability (Salice, Rowe, Pechmann, & Hopkins, 2011). As such, deterioration of terrestrial habitats can inhibit the diversity and abundance of species present, with more than half of threatened terrestrial vertebrates considered endemics of biodiversity hotspots (Brooks et al. 2002). Meanwhile, boreal forest, desert, arctic tundra and the Amazon basin remain least affected by multiple anthropogenic stressors (Venter et al., 2016), perhaps due to a reduction in local stressors.

1.3.2 Freshwater

Only around half of the planet's freshwaters remain unaffected by humans, with large expanses of European river and freshwater bodies affected by anthropogenic change (Birk, 2019; EEA European waters assessment, 2018). These largely consist of chemical and nutrient pollution derived from agricultural practices (EEA European waters assessment, 2018; EPA Environmental Protection Agency, 2002). With climate change further complicating existing stressor effects, additive effects are likely created in freshwater habitats when eutrophication is already present (Alahuhta et al., 2019). Conversely, Jackson, Loewen, Vinebrooke, & Chimimba, 2016 found that antagonistic interactions were most common in freshwaters, followed by synergistic, and then additive. This was supported by Crain et al., 2008, who found that 40% of freshwater interactions were antagonistic; creating

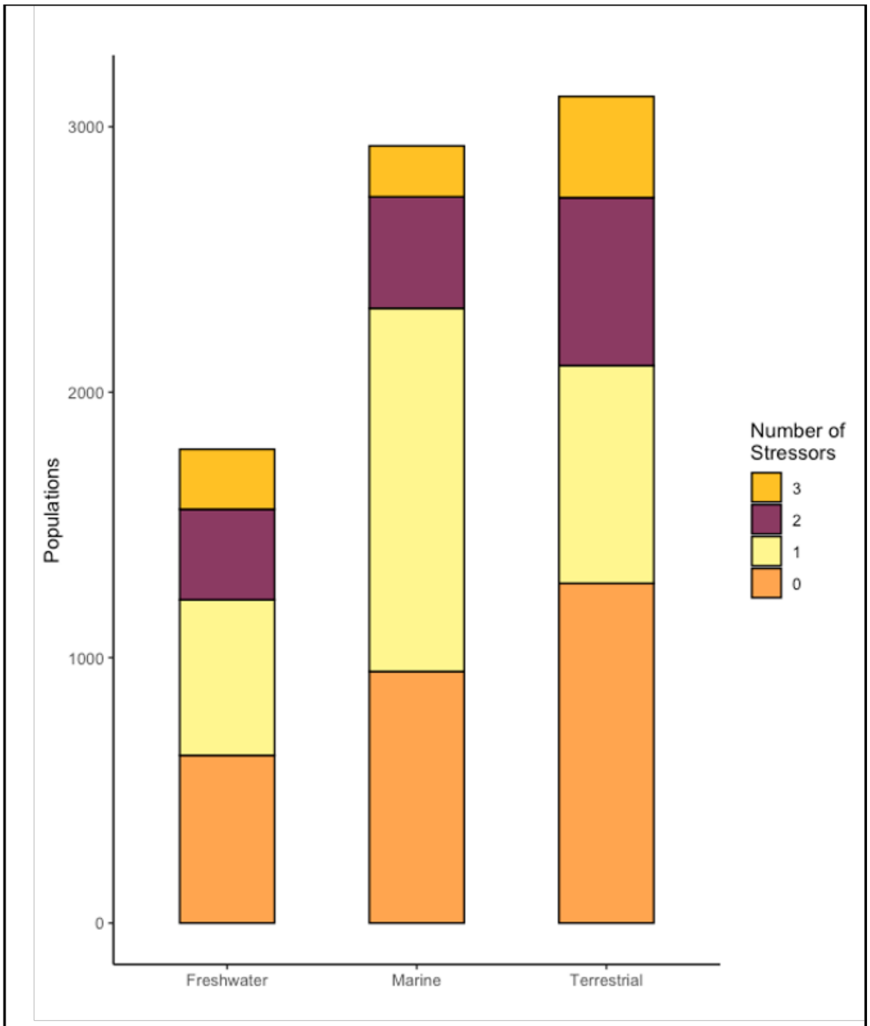

Fig. 1.2 | Stressors by ecological system within the Living Planet Database.

Distribution of Living Planet Database population stressor number (0 – 3) by freshwater, marine and terrestrial ecological systems significant challenges in management strategies, with all or most stressors requiring elimination for any substantial recovery to be seen (Crain et al., 2008).

Freshwater stressors are heavily associated with human population density and dilution factors, such as rainfall, but are also subject to cross-boundary atmospheric pollution (Vörösmarty et al., 2010) and water use conflicts (Ormerod, Dobson, Hildrew, & Townsend, 2010). Threat levels tend to accumulate directionally downstream, with compound upstream threats exacerbated by highly developed river corridors and the prevalence of coastal megacities (Vörösmarty et al., 2010). Developing and corruption-prone countries with reduced capacity for water treatment are even less able to offset already high stressor levels, and so taxa remain more vulnerable to pressures in freshwater bodies, jeopardising both human water supplies, and biodiversity (Venter et al., 2016; Vörösmarty et al., 2010).

1.3.3 Marine

Almost all marine environments are affected by stressors, with notable 'hotspots' of cumulative activity found in the North Sea and South and East China Seas, with global increases in climate change driving the cumulative impact (Halpern et al., 2015). However, coral reefs (Ban, Graham, & Connolly, 2014), coastal and estuarine areas often suffer more direct, local anthropogenic threats, with stressor combinations becoming progressively more complex and diverse (Adams, 2005; Halpern et al., 2015). In controlled marine settings, the most common interaction type appears to vary by ecological level (e.g., at the community level antagonistic, at the population level synergistic), demonstrating context-dependency which differs between covariate and population resilience, and highlighting how interactions are both trait and scenario specific (Crain et al., 2008; Lange & Marshall, 2017). With 90% of marine species found within coastal and coral reef habitats (World Wide Fund for Nature, WWF, 2019), nutritionally and economically important fish stocks risks population collapse unless multiple threats (notably including exploitation) can be adequately addressed (Jackson et al., 2001), with failure to do so jeopardising both fishing communities and species survival (Pinsky, Jensen, Ricard, & Palumbi, 2011).

1.4 Species Traits and Stressor Risk

A widely used null hypothesis for extinction is that of the "Field of Bullets" (Raup, Gould, Schopf, & Simberloff, 1976; Van Valen, 1976), which theorises that the loss of species occurs entirely randomly. A multitude of research has since rejected this model to reveal significant predispositions to extinction risk shaped by intrinsic (biological) and extrinsic (abiotic / geographical) traits (Collen et al., 2011; Brook et al., 2008; Hughes & Connell, 1999; Steudel et al., 2012) (Table 1.1). Species traits consequently affect a population's vulnerability to the stressors driving extinction risk (see Ripple et al., 2017).

Past research has been successful in identifying traits which predispose species to increased risk of individual stressors (e.g. Böhm et al., 2016; Collen et al., 2011; Ripple et al., 2017); a promising sign that it may be possible to determine what makes species more likely to be affected by multiple stressors. This would not only streamline assessment of a population's risk to multiple stressors - particularly if species are cryptic or reside within challenging surveying conditions - but would allow the prioritisation of safeguarding measures if deemed necessary according to forecasts.

Table 1.1 | Species trait-stressor risk relationships

Intrinsic traits	**Rationale**	**Relevant References**
Body mass	Larger animals are more conspicuous and so at higher risk of experiencing persecution and exploitation. Generally slower reproductive rates may create higher stressor sensitivity and slower population recovery.	Cardillo & Bromham, 2001; Cardillo et al., 2008; Cardillo, Mace, Gittleman, & Purvis, 2006; Cardillo et al., 2005; Fisher, Blomberg, & Owens, 2003; Harcourt & Schwartz, 2001; Johnson, 2002; Purvis, Agapow, Gittleman, & Mace, 2000; Ripple et al., 2017; Sallan & Galimberti, 2015; Verde Arregoitia, 2016; Ripple et al., 2015; Sodhi et al., 2008; Seibold et al., 2015; Terzopoulou, Rigal, Whittaker, Borges, & Triantis, 2015; Verde Arregoitia, 2016

Inter-birth interval	Longer intervals and lower fecundity infer a reduced capacity in compensating for increases in mortality. Similar rationale to age at first birth (fecundity).	de Silva & Leimgruber, 2019; Harcourt & Schwartz, 2001; Jager, Rose, & Vila-Gispert, 2008; Jones, Purvis, & Gittleman, 2003
Litter / clutch size	Low reproductive output reduces population growth and recovery success (fecundity).	Cardillo, 2003; Cardillo et al., 2006; Purvis et al., 2000; Smith & Quin, 1996
Age at maturation / first birth	Higher age at sexual maturity reduces reproductive output until reached. Similar rationale to inter-birth interval (fecundity).	Cardillo et al., 2008, 2006; González-Suárez & Revilla, 2013; Hutchings, Myers, García, Lucifora, & Kuparinen, 2012; Price & Gittleman, 2007; Purvis et al., 2000
Home range size	Large home range suggests high resource requirements and vulnerability to habitat alterations (loss, degradation, fragmentation, edge effects, etc.).	Brashares, 2003; Cardillo et al., 2008; Harcourt, 1998; Woodroffe & Ginsberg, 1998; Purvis et al., 2000
Geographic range size	Small range infers narrow ecological niche. Modifications to habitat may not, therefore, be tolerated.	Cardillo & Bromham, 2001; Cardillo et al., 2006, 2005, 2004, 2008; Ceballos, Ehrlich, Soberón, Salazar, & Fay, 2005; Gaston & Fuller, 2009; Harcourt & Schwartz, 2001; Jones et al., 2003; Price & Gittleman, 2007; Purvis et al., 2000; Runge, Tulloch, Hammill, Possingham, & Fuller, 2015; Sodhi et al., 2008
Phylogeny	Taxa from older or species-poor lineages are most at risk: probability of extinction may increase stochastically through time, and older taxa are more likely to have	Bennett & Owens, 1997; Forest, Crandal, Chase, & Faith, 2015; Gaston & Blackburn, 1997; González-del-Pliego et al., 2019; Isaac, Turvey, Collen, Waterman,

	developed specialisations lessening plasticity within ecological niche, behaviour or morphology.	& Baillie, 2007; Jennings, Reynolds, & Polunin, 1999; Johnson, Delean, & Balmford, 2002; Meijaard, Sheil, Marshall, & Nasi, 2008; Purvis, 2008; Purvis et al., 2000; Redding, Dewolff, & Mooers, 2010; Russell, Brooks, Mckinney, & Gregory Anderson, 1998; Isaac et al., 2007
Trophic level	Species at higher trophic levels generally have larger home ranges, exposing them to more stressors, whilst also being more vulnerable to the cumulative effects of disturbance to species lower down the food chain.	Crooks and Soulé 1999; Diamond 1984; Purvis, Gittleman, et al. 2000
Migratory	High mobility increases susceptibility to multi-stressor effects; migratory destinations less food-rich and predictable in space and time, human land-use and activity patterns constrain species ability to modify migratory routes and may increase the stress induced by climate change; increased possibility of mistimed breeding / feeding, habitat loss.	Both, Bouwhuis, Lessells, & Visser, 2006; Faaborg et al., 2010; Nõges et al., 2016; Rappole & McDonald, 1999; Robinson et al., 2009; Vickery et al., 2014; Wilcove & Wikelski, 2008

With many, interlinked traits affecting a species' vulnerability to anthropogenic stressors, body mass represents a convenient proxy for a number of related traits which may be less widely available or more difficult to assess.

1.4.1 Trophic Level

Humans affect ecosystems at every trophic level (Dorresteijn et al., 2015), but many of the threatened, large-bodied vertebrates are secondary or tertiary consumers (Cohen, Jonsson, and Carpenter 2003; Deudero et al. 2004; Estrada et al. 2006; Riede et al. 2011; Romanuk, Hayward, and Hutchings 2011) with large home ranges often required to fulfil their nutritional requirements (Gittleman & Harvey, 1982). This not only heightens their susceptibility to exploitation as contact with humans becomes more likely, but increases their vulnerability to habitat change and fragmentation (Duffy, 2003). Furthermore, the inherent human fear of large apex predators can cause a different type of exploitation, as human-wildlife conflict causes the persecution of carnivores considered dangerous to people or livestock (Gusset, Swarner, Mponwane, Keletile, & McNutt, 2009).

Disruption to populations at high trophic levels can be particularly concerning (Estes et al., 2011; Reeves, Jensen, Dolph, Holyoak, & Trust, 2010; Ripple et al., 2014; Woodward et al., 2005), with any change in predator numbers likely causing repercussions for the stability of ecosystems due to the top down control they elicit (Terborgh et al., 2001). Predatory species moreover highlight the importance of prey dependencies, with seemingly large, resilient populations often still vulnerable to the cumulative effects of stressors if the species on which it depends become compromised (Purvis et al., 2000).

1.4.2 Phylogenetics

With evolutionary influences often dictating species traits congruent with taxonomic position (Chen et al., 2019), and with strong phylogenetic signal in traits such as body size (Yessoufou & Davies, 2016), further parallels may be drawn between vulnerability to stressors and phylogenetic relatedness (Ripple et al., 2014).

Patterns of risk can be reflected in the biological differences among lineages, as evolutionary relatedness generates similar levels of threat because of shared heritable traits (Jetz & Freckleton, 2015). As such, comparative phylogenetic analysis has indicated that small-bodied fauna face extinction risks largely governed by their location and the intensity of threats, whereas large-bodied animals face challenges relating to both intrinsic and extrinsic traits (Yessoufou & Davies, 2016). For example, amphibians may be at high risks as their permeable skin provides little resistance to water loss under similar stresses (Hillyard, 1999), a problem exacerbated in smaller taxa, which have comparatively high surface area to volume ratios (Kaufmann and Dohmen 2016; Watling and Braga 2015). Poikilotherms generally are further thought to be particularly sensitive to temperature and moisture changes, and suffer further exacerbations due to their often-limited dispersal ability (Gibbon et al., 2000).

Extinction risk - and so vulnerability to stressors - therefore can often be attributed to 'bad genes' rather than 'bad luck' (Yessoufou & Davies, 2016). This phylogenetic selectivity of extinction (e.g. Bennett & Owens, 1997; Chichorro et al., 2018; Gaston & Blackburn, 1997; Andy Purvis et al., 2000; Russell et al., 1998) therefore suggests that heritable traits should be accounted for throughout the forecasting of population declines (Cardillo et al., 2005; Purvis et al., 2009).

1.4.3 Home Range Size

A species' home range refers to the size of territory required by an individual to provide it with sufficient space to fulfil resource and reproductive requirements (Pearl, Boitani, & Fuller, 2000). Here again, there are correlations with body size as increased energy requirements generally require larger territories, placing a clear lower limit on the range size needed to support minimum viable populations (Brown & Maurer, 1987). As such, vertebrates with large home ranges typically face greater exposure to stressors due to their higher mobility, with larger species generally requiring larger home ranges to provide the sufficient dietary requirements and opportunities for reproduction (Cardillo et al., 2008). Broad ranges also subject niches to a greater probability or fragmentation or degradation, whilst predatory species with large home ranges are more prone to human conflict as their search for prey takes them further afield (Woodroffe & Ginsberg, 2000).

1.4.4 Fecundity

Traits relating to fecundity (i.e., an organism's reproductive output, including inter-birth interval, age at maturation / first birth, litter size), play an obvious role in a population's ability to endure stressors, with low reproductive output slowing population recovery, and making extinction more likely (Gårdmark, Enberg, Ripa, Laakso, & Kaitala, 2003). Once more, this draws strong parallels with body size: larger, species with slow life histories generally have small litter sizes, as with the white rhinoceros (*Ceratotherium simum*) which generally has one calf per gestation (Myhrvold et al., 2015); longer inter-birth intervals, as with the Sumatran Orangutan (*Pongo* Spp.) which produces young every 7.6 years (van Noordwijk et al., 2018); and those older at first birth, for example the Aldabra Giant Tortoise (*Aldabrachelys* *gigantea*) which takes between 16 and 20 years to reach sexual maturity (Griffiths et al., 2012).

Although fecundity can be affected by a number of anthropogenic pressures - for instance, pollution has been shown to suppress reproductive behaviour in fish (Martinović, Hogarth, Jones, & Sorensen, 2007) - body size also renders species with slow life histories more vulnerable to exploitative practices (Ripple et al., 2016). For example, larger, reproductively active individuals may be at greater risk of being targeted by hunting, thus suppressing reproductive output and minimising the growth or recovery of populations (Ripple et al., 2016). Most notably, this can be seen in African megafauna, such as the northern white rhino (*Ceratotherium simum cottoni*), which in recent years has faced hunting and poaching practices which have pushed the species to the brink of extinction (Hermes et al., 2005). With a particularly low reproductive output averaging of one calf every 2.6 years on average (Rachlow & Berger, 1998) this illustrates this how large taxa with low fecundity may more vulnerable to the long-term impacts of anthropogenic stressors.

1.4.5 Geographic Range Size

Differing to home range, geographic range refers to the entire spatial area in which a species is found (Gaston, 1991). Geographic range is frequently described as having a positive relationship with body size (Gaston & Blackburn, 1996); that is, larger species tend to occupy larger geographic ranges. Though, this is not always the case, particularly in smaller species, whose range sizes vary considerably when compared to larger bodied taxa (Gaston & Blackburn, 1996).

A wide geographical range has been illustrated to consistently to safeguard against extinction risk in fossil records (Finnegan et al., 2015; Harnik, 2011; Kiessling & Aberhan, 2007; Kiessling & Kocsis, 2016; Purvis, Gittleman, et al., 2000; Sodhi et al., 2008; Tietje & Rödel, 2018), as those with small range sizes are more readily impacted by unforeseen or rapid environmental change, such as those brought about by wildfire, predation, disease or invasive species (Bower et al., 2019; Kats & Ferrer, 2003; Leach & Givnish, 1996; Scheele et al., 2019; Wilting, Sollmann, Meijaard, Helgen, & Fickel, 2012). Climate change is particularly prevalent and influential in shaping geographic distributions (Caughley, Short, Grigg, & Nix, 1987; Estrada et al., 2015; Gaston, 2013), driving rapid latitudinal and elevational shifts, with the largest range changes particularly great where levels of warming are most acute (Hellman et al., 2012). Indeed, some species will inevitably suffer greater declines where changes to their geographic range are limited by the dispersal ability (Gaston, 2013; Penner & Rödel, 2019; Sodhi et al., 2008), a scenario which may disproportionately affect smaller species in terrestrial habitats (Stevens et al., 2014). It is important to note that geographic range refers specifically to an entire species and unless species comprise only one population, it has limited application in population-level studies such as this, despite affecting overall species' vulnerability to anthropogenic stressors.

1.4.6 Migration

Migratory species are often more vulnerable to multiple stressors as seasonal routes invite ever-less predictable conditions throughout migratory cycles, with human land-use and activity patterns inhibiting species' ability to adapt migratory routes (Nõges et al., 2016). The loss or degradation of breeding habitats can also impact the demography of populations (Vickery et al., 2014). Meanwhile, long migration routes and resulting dependence on different locations and at different times subject travelling species to 'multiple jeopardy' scenarios (Vickery et al., 2014; Newton, 2004). Unlike previous traits which can be related to body mass, migratory behaviour seems to take little influence from interspecific size; taxa from butterflies (Stefanescu et al., 2013) to whales (Pomilla & Rosenbaum, 2005) all complete migrations of thousands of miles, increasing their vulnerability to stressors regardless of their size. Thus, although body size remains a useful proxy for numerous characteristics, the lack of a relationship with migratory behaviour illustrates that it cannot be used as a catch-all for every species trait.

1.4.7 Body Size

It can be argued that body size (Fig. 1.3) is the dominant of the intrinsic traits (Gillooly & Allen 2007; Reuman et al. 2014), being associated with almost every aspect of life (Brown, Gillooly, Allen, Savage, & West, 2004; Kleiber, 1932; Peters, 1983; Smith, 1985) and demonstrating strong correlations with other intrinsic factors such as litter size, low metabolic rate, phylogeny and home range size in many species (e.g., Chichorro, Juslén, & Cardoso, 2019; Gillooly & Allen, 2007). Moreover, body size can be used as an indicator of vulnerability to stressors, with larger species at higher risk of threats such as exploitation due to their conspicuousness and greater return as a resource (Chichorro et al., 2019). A recent review of extinction drivers (Ripple et al., 2017) further reinforced this, confirming that the heaviest vertebrates were most threatened by anthropogenic exploitation; with the probability of being harvested (fished, trapped, or hunted) significantly and positively related to body mass in threatened species for all vertebrate classes. However, the same study also highlighted vulnerabilities at the opposite end of the body mass spectrum, with smaller taxa demonstrating greater susceptibility to stressors such as habitat destruction, due to limited home ranges and dispersal ability (Ripple et al., 2017).

Despite some suggestion that larger species with lower metabolic rates tend to have a higher tolerance to multiple physiological stressors (Parsons, 1991), increased body

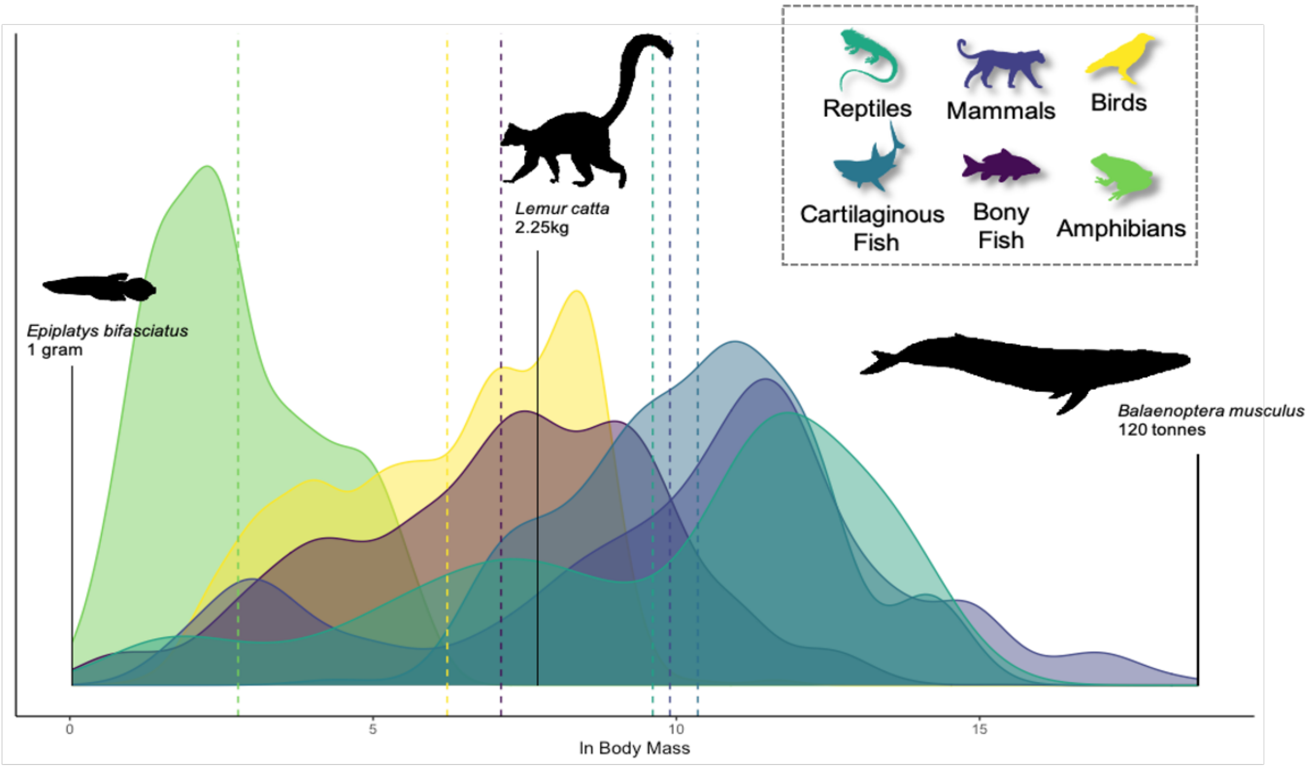

Fig. 1.3 | Body mass distribution of species within the Living Planet Database.

Natural log body mass distributions for each species comprising threat data within the Living Planet Database, with dotted lines representing mean body size for each class. For context, mass points are provided for the zweibandhechtling (1g, *Epiplatys bifasciatus*), the ring-tailed lemur (2.25kg, *Lemur catta*) and the blue whale (120 tonnes, *Balaenoptera musculus*).

size is known to increase extinction risk, due to heightened vulnerability to stressors affecting population recovery (Bennett & Owens, 1997; Cardillo & Bromham, 2008; Cardillo et al., 2005; Gaston & Blackburn, 1997; Purvis, Gittleman, et al., 2000; Smith & Quin, 1996). This means that larger taxa are liable to face more stressors, due to the compound vulnerability of their intrinsic traits, and knock-on impacts of low reproductive output (Salice, 2012).

1.4.8 Conclusion

Despite uncertainties and contradictions regarding stressor-trait relationships (see Côte et al., 2016), extinction risk is evidently not a simple Field of Bullets, but shows patterns of vulnerability to stressors dependent on traits, taxa and ecological system (Baillie et al., 2004; Russell et al., 1998; Mace & Blamford, 2000). As a widely available, dominant and ubiquitous trait, this paper will use body size as a hypothetical predictor of stressor number, aiming to shed further light on the vulnerabilities of species traits and laying the foundations for future research to build upon.

1.5 Spatial Distribution of Stressors

The spatial distribution of stressors is not uniform, but can be largely predicted by presence of human settlements (Bowler et al., 2020; Halpern et al., 2015) (Fig. 1.4). Populations of taxa close to areas of high human density are, accordingly, more likely to endure localised threats such as habitat loss, hunting, pollution and human-wildlife conflict, (Nelson, 2008; Santini, González-Suárez, Rondinini, & Di Marco, 2017). As human presence is generally dictated by land availability, thermal limits and resource accessibility (e.g. water) we can expect human population to be densest in the higher land mass areas of the northern hemisphere, and near to water bodies within subtropical and temperate zones (Jendritzky & Tinz, 2009; Salvacion & Magcale-Macandog, 2015). Consequently, only a minority of the human population lives beneath the equator (12.5%), whilst around half of humanity reside within the comparatively limited area between 20°N and 40°N (Kummu & Varis, 2011). These areas, then, are where we might expect to see wild populations subject to the most numerous local stressors, when compared to those in remote locations of low human population density.

Global stressors may similarly be forecast using spatial metrics, as areas at latitudinal extremes endure faster climatic change than the rest of the planet (Roots, 1989). As this expansion of warmer regions pushes ever closer towards the poles (Staten, Lu, Grise, Davis, & Birner, 2018), conditions change faster than populations can evolve, and taxa are forced beyond their climatic niche (Quintero & Wiens, 2013). As these near-ubiquitous stressors mingle with local stressors, such as exploitation and pollution from direct human influence, multi-stressor scenarios become ever-more prevalent, creating greater challenges for high population density countries already struggling to accommodate explosive population growth (Van Bavel, 2013).

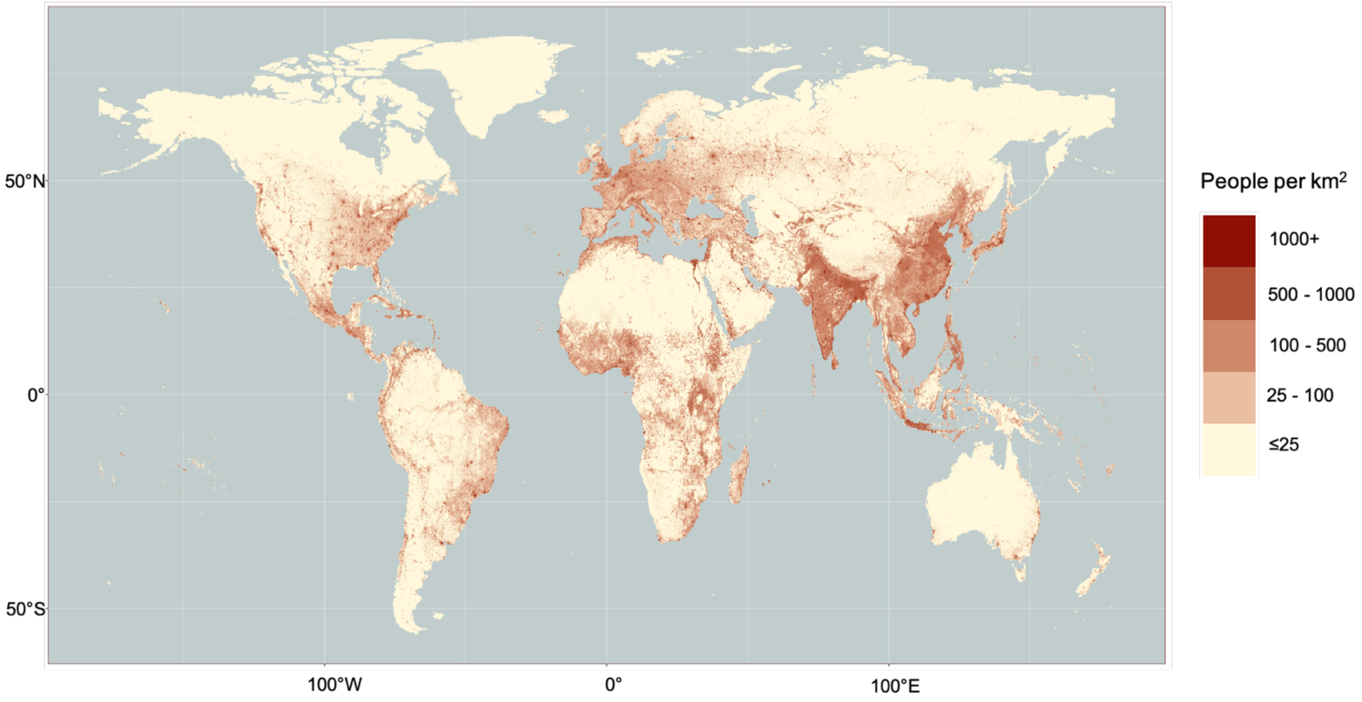

Fig. 1.4 | Global map of human population density

Global distribution of human population density as of 2015 (data: Florczyk et al., 2019), showing the estimated number of people per square kilometre.

1.6 Quantifying Stressors

Whilst the exact impact of multiple stressors tends to be species, or more likely population specific (Crain et al., 2008), it is clear that increasing numbers of stressors are likely to have a significant negative impact on a population or community. Consequently, identifying those populations most at risk of being impacted by multiple stressors would pave the way for deeper, more specific investigative work into the threats present.

With threats and pressures on the environment continuing largely unchallenged, the need to quantify stressor number necessitates parallel analysis with global population data (Dirzo et al., 2014; Tittensor et al., 2014). Despite this, global studies assessing stressor number on a macro scale have yet to be executed, largely due to the lack of collated threat data relating to specific, wild populations across multiple taxa. Until now, this has restricted studies on vertebrate research and their collective meta-analysis (Armitage & Fong, 2004; Burkepile & Hay, 2006).

To remedy this knowledge gap, data for this research has been sourced from the newest version of the Living Planet Database (LPD), consisting of >25,000 vertebrate population records collated from predominantly scientific literature, online

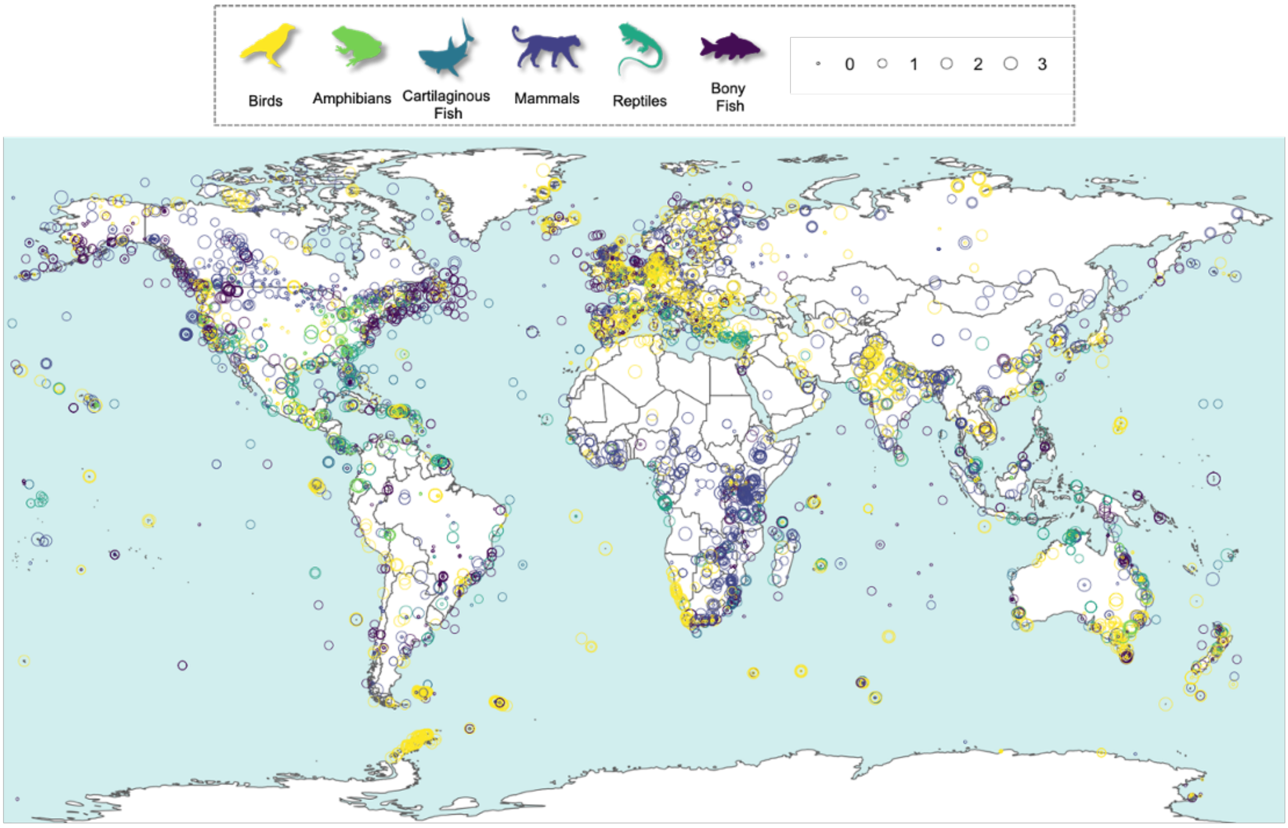

Fig. 1.5 | Spatial distribution of Living Planet Database population threat data by class.

Global distribution of Living Planet Database population stressor number (0 – 3), separated by taxonomic class, with circle size denoting stressor number.

databases and grey literature published since 1970 (Loh et al., 2005). To ensure the quality of the data and data collation, a standardised procedure of data gathering is applied, which mandates that records are only included if they meet certain criteria:

- Population size data must be available for at least two years
- The method of data collection must be stated
- Unit of measurement must be included
- Geographic location must be stated
- Data must be collected using the same method and on the same population throughout the time series
- Data source must be referenced and traceable

Care is also taken to avoid duplications and to retrieve data from the highest quality sources where time series of the same population are encountered.

Attesting to the dataset's quality, the LPD provides the foundations for the Living Planet Index, a global measure of changes in biodiversity and a convenient proxy for conveying the complexities of biodiversity (Collen et al., 2009). Its editions have also been used as a powerful tool to assess the status of biodiversity as a global measure of change (e.g., by the Convention on Biological Diversity, CBD) and to assess progress towards the Aichi Biodiversity Targets (CBD, 2017), whilst communicating information to conservation managers and the wider public (Butchart et al., 2010; Collen et al., 2009).

As with all long-term monitoring datasets, the LPD's reliance on publicly available data brings with it taxonomic and geographical biases (see Fig. 1.5). For example, there is the 'usual' gap in tropical regions, whilst temperate mammal and bird species are significantly overrepresented (see Fig. 1.5, Collen et al., 2009; McRae, Deinet, & Freeman, 2017). Regardless, the scale and breadth of the dataset makes it the largest and most comprehensive of its kind, with a global coverage encompassing tens of thousands of population time series from all major vertebrate classes, covering freshwater, marine and terrestrial systems. The LPD therefore provides the uncommon benefit of permitting intraspecific analyses, where multiple population records for one species permits the direct comparisons of spatiotemporal variations and threat exposure. With most other threat evaluations considering species only in their entireties (e.g. International Union for the Conservation of Nature, IUCN, 2001) the LPD's collation of population level stressor data is the key allowing this nuanced analysis on a global scale.

Stressor data within the LPD are listed as primary, secondary or tertiary, based on the order in which they are mentioned in the source publication. Differing to United Nations Environment Programme's five stressors, the LPD lists seven, including: invasive species/genes, habitat loss, habitat degradation/change, exploitation, climate change, pollution and disease (Fig. 1.6). The LPD therefore has the potential to evaluate mitigative procedures and develop our comprehension of core ecological processes and the predeterminants of stressor

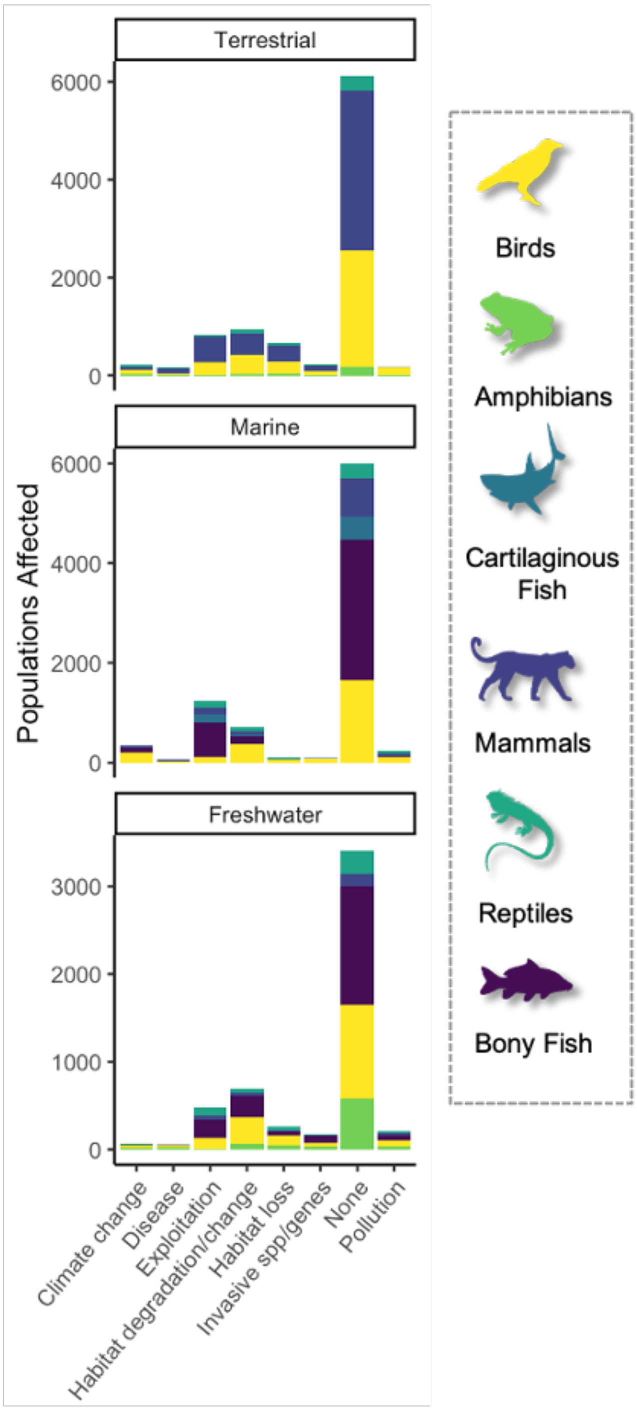

Fig. 1.6 | Living Planet Database population stressor exposure.

Stressor exposure by ecological system and taxonomic class within the Living Planet Database exposure (Leadley et al., 2010; Walpole et al., 2009). This enables us to fill a critical gap in our knowledge where little prior work has been undertaken (Leadley et al., 2010; Pereira et al., 2010). A recent publication derived from the LPD has shown strong declines in larger freshwater animals as a suspected result of their exposure to threats (Deinet et al., 2020); hence trait-based measure of population stressor prevalence would provide conclusive evidence of the basis of these trends.

1.7 Supplementary Data Sources

Given the apparent benefits afforded by the analytical inclusion of species trait information, augmenting the LPD with life history data via the use of complementary databases may add significantly to our understanding of a population's vulnerability to multiple stressors. The resulting compilation comprises a far-reaching assembly of population records alongside species-specific body mass data, offering a dynamic resource to interrogate and initiate new hypotheses never before explored in ecological research. Sources for the complementary databases used for this can be found in Supplementary Information Table S1.

1.8 Thesis Aims and Content

This thesis explores the relationship between anthropogenic stressor number, latitude and species traits; namely, body size. Following this overview, Chapter 2 makes use of composite databases of wild population data, stressor number counts, latitude and species body size to ascertain how vulnerability to stressors changes in accordance with species mass and latitude for over 7000 populations across the six major vertebrate classes. With prior research largely biased towards experimental invertebrate studies, or a narrow range of wild taxa, this thesis goes beyond by providing a comprehensive overview of more than 2500 wild vertebrate species, containing multiple intraspecific records and working with stressor data specific to those populations across terrestrial, marine and freshwater ecosystems. The resulting study provides unparalleled understanding of vulnerability to stressors by examining body mass as a dominant intrinsic trait and latitude as a spatial parameter, to predict the number of stressors that wild vertebrate populations are exposed to.

Chapter 3 expands upon the results by discussing the potential underlying processes behind the presented trends, and how they could be used to further investigate high risk populations. Also discussed are study limitations, alternative methodological approaches, and suggestions for future research trajectories in the field. The thesis concludes by addressing the changes needed to safeguard biodiversity against multiple stressors as the planet faces an uncertain future, both in terms of human population trends, and its impact on ecological systems.

1.9 Conclusion

By employing a long-term, real-world database of wild populations (the LPD, Collen et al., 2009), a tangible opportunity has arisen to fill a critical gap in our knowledge, allowing the population-level causes of vertebrate declines to be brought in to focus from a multiple stressor perspective; complimented by spatial and species trait data we provide the tools necessary to identify those populations and species most at risk of catastrophic declines before it's too late.

It will thus provide decision makers with the tools to allocate conservation resources towards the species most in need, offering a streamlined framework to avoid the misallocation of hard-fought conservation funding and provide a vital insight into the ever-changing dynamics of anthropogenic stressors in a world already altered by their presence.

2

Data Chapter

Body size and latitude predict the presence of multiple stressors in global vertebrate populations

Body size and latitude predict the presence of multiple stressors in global vertebrate populations

2.1 Abstract

Multiple stressors are recognised as a key threat to global biodiversity, but our understanding of what factors make species susceptible to multiple stressors remains limited. Here we analyse a global database of >7000 marine, freshwater, and terrestrial vertebrate populations, supplemented with information on species-specific traits, to identify factors which influence the number of stressors a species is subjected to. We find that body size and latitude can both influence the number of stressors a species is likely to be threatened by, but the strength of this relationship changes across systems and between taxonomic classes. Models show that large-bodied species are more likely to be threatened by multiple stressors in four taxonomic groups. Moreover, populations are generally affected by a higher number of stressors between latitudes 20°N and 40°N, and towards the poles. The spatial distribution of global stressors suggests a link between human population centres and stressor frequency, which disproportionately affects larger-bodied species. Latitude and body mass hence provide key predictive tools to identify which vertebrate populations are likely to highly threatened, enabling conservation management to be triaged for species at greatest risk.

2.2 Introduction

Global vertebrate populations are in decline (Li et al., 2016), a fact attributed to the overarching trend of anthropogenic stressors (or 'threats') increasing in line with human populations (Sala et al., 2000). Such threats can act at both a local and global scale, with locally detrimental stressors such as the overharvesting of species for food (Zhou & Smith, 2017) occurring simultaneously against a backdrop of global stressors such as climatic change altering energy flows (Bartley et al., 2019), the strength of trophic interactions (Smoliński & Glazaczow, 2019), and the physiological stress of populations (Iknayan & Beissinger, 2018). Thus, as human populations increase, biodiversity is being exposed not only to increasing levels of stress, but to multiple stressors impacting simultaneously; with resulting effects creating novel challenges for the effective conservation of species (Côté et al., 2016). Our ability to inform conservation in the face of multiple stressors has been limited by an incomplete understanding of their interactive effects (Darling et al., 2013). However, whilst there remains a deficiency in our understanding of exactly how multiple stressors will impact biodiversity, there is mounting concern that stressor interactions will be responsible for increasing disruption to community assemblages (Vinebrooke et al., 2004; Zavaleta et al., 2009). Consequently, a central challenge exists to identify how and why populations are exposed to multiple stressors (Hodgson et al., 2017).

Identifying ecological and biotic factors which influence the number of stressors a population is threatened by has clear conservation implications, potentially allowing species to be prioritised – at least for initial appraisal – without the need to collect detailed data at the site or population level. Achieving this requires identifying predictors where data are widely available, and which *a priori* may influence a species' predisposition to multiple stressors. Here, body mass holds some promise; labelled a 'supertrait' (Bribiesca, Herrera-Alsina, Ruiz-Sanchez, Sánchez-González, & Schondube, 2019; Madin et al., 2016) due to its role in numerous ecological processes, wide availability, and universality, it provides a convenient tool enabling direct comparison between taxa. Further linked with an increased vulnerability to strong population declines (Deinet et al., 2020) and extinction, body mass has also been suggested as a potential predeterminant of stressor exposure (Collen et al., 2011). The reasons for larger bodied organisms being at higher risk of facing one or more stressors are multifaceted, ranging from an increased conspicuousness exposing species to exploitation via human consumption or recreational hunting practices (Ripple et al., 2015, 2019; Sodhi et al., 2008; Verde Arregoitia, 2016); wider home ranges with high resource requirements and subsequent vulnerabilities to habitat degradation (Böhm et al., 2016; Brashares, 2003; Cardillo et al., 2008), and higher trophic level increasing vulnerability to cumulative disturbances lower in the food chain (Purvis et al., 2000). Stressor exposure may also be affected by ecological system, as marine, terrestrial and freshwater systems each demonstrate their own vulnerabilities to anthropogenic threats. For example, freshwater species may be more commonly subject to nutrient enrichment (Birk et al., 2020), whilst exploitation and climate change represent more pressing threats for large species (Halpern et al., 2019). Meanwhile, land-use change was shown to be the most common terrestrial threat (Tilman et al., 2017) with declines in biodiversity often attributed to the alteration of habitats (Newbold et al., 2015).

Neither local nor global stressors are uniformly distributed in space (Bowler et al. 2020; Halpern et al. 2015). Because many local stressors are intimately linked to human populations (e.g. habitat loss, hunting, etc.) the presence and frequency of these stressors is likely to change in line with human population density (Nelson, 2008; Santini et al., 2017). The global distribution of human population density varies dramatically between latitudinal belts, with less than 12.5% living below the equator, but around half residing within the comparatively narrow belt between 20°N and 40°N (Kummu & Varis, 2011); equating to around 3.85 billion people dwelling within 20 degrees of latitude (United Nations: Department of Economic and Social Affairs, 2019). However, the global effects of climate change are also known to be non-uniform, with much impact expected in the rapid warming of high-latitude, arctic regions (Roots, 1989), alongside the recent poleward expansion of the tropics and dryer conditions in mid-latitude regions (Staten et al., 2018). Consequently, latitude is likely to be a significant determinant of where stressors occur, and thus identifying how stressor number changes on a latitudinal basis would provide further detail on broad threat variability, helping local efforts to mitigate interactions between global and localised stressors.

Disentangling how life history traits, and the spatial heterogeneity of stressors, impact vertebrate populations provides the opportunity to enhance stressor mitigation by combining latitude and body size, allowing finer differentiation and enabling area-based action across taxa by providing a framework applicable to vertebrates worldwide. Here we take a novel approach in the study of multiple stressors by seeking to identify factors which predict the number of stressors a population is affected by across freshwater, marine, and terrestrial systems at a global scale. To do this we make use of recently available population-level threat data from the LPD, supplemented with data on body size from multiple sources, to generate a composite, spatially explicit database for more than 7400 vertebrate populations, comprising 2500 species, across seven continents and all key ecological systems. We use data from the six major taxonomic classes: amphibians, birds, bony fish, cartilaginous fish, mammals, and reptiles, to test whether body mass and latitude alter the number of stressors a population is affected by. We show how latitude and body size can predict the number of stressors a population is exposed to, with forecasts varying by vertebrate class and ecological system. This research provides new insight on the determinants of multiple stressors in vertebrates, using widely available data on body size and latitude to provide prioritisation tools for species conservation.

2.3 Methods

2.3.1 Data

2.3.1.1 The Living Planet database

The LPD (http://livingplanetindex.org/data_portal) contains information on over 25,000 vertebrate populations around the world, comprising all vertebrate classes across marine, freshwater and terrestrial systems and providing population-specific information such as spatial location, abundance and threat exposure. Data are collected from scientific literature, online databases and grey literature published since 1970, and included if at least two years of abundance records are present, assuming comparable data collection methodologies are used throughout; detailed inclusion criteria for the LPD can be found in (Collen et al., 2009).

Of the 25,054 population time series making up the LPD, 7826 contained data relating to population threat exposure; comprising up to three of the following stressors: climate change, disease, exploitation, habitat degradation or destruction, habitat loss, invasive species or genes, and pollution. These stressors were counted for each population, with values from a minimum zero, to a maximum of three.

Latitude, ecological system, and taxonomic class variables from the LPD were also included in analysis.

2.3.1.2 Body Mass Data

Body mass data were collated from a number of pre-existing databases and scientific literature (see Supplementary Information Table S1 for a full list of sources utilised). Where minimum and maximum values where given, maximum was taken to ensure measures were most likely those of mature individuals, and thus in line with commonly reported measures from the other databases. The majority of data sources did not contain sex-specific body size measurements; however, where sex was indicated an average of the male / female record was taken to account for dimorphism. Finally, where multiple records of the same species were present between datasets, the mean was taken, with all records then standardised to reflect a common unit (g, grams).

2.3.1.3 Body Mass Estimations

For some taxa body size data were unavailable, and so were estimated using allometric regression equations with clade and measurement-specific values, where possible (Feldman & Meiri, 2013; Feldman, Sabath, Pyron, Mayrose, & Meiri, 2016; Santini, Benítez-López, Ficetola, & Huijbregts, 2018; Stark, Pincheira-Donoso, & Meiri, 2020). These were configured $W = a\,L^b$, where W = body mass, L = length and priors a and b are the intercept and slope of a regression line over log-transformed weight-at-length data, respectively (Froese & Pauly, 2019; Ripple et al., 2017). This method was applied to 47 amphibian species using snout to vent length (SVL) records and clade-specific priors (Santini et al., 2018; Stark, Pincheira-Donoso, & Meiri, 2020), and a further 320 fish species' mass were estimated, based on maximum total length (TL) and regression priors, as listed on FishBase (Froese & Pauly, 2019). Where a measure other than TL was listed (e.g. standard length (SL), fork length (FL)), regression coefficients were used to convert these to total length before then estimating body mass.

2.3.1.4 Final Dataset

Upon the merging of body mass and LPD threat data, the final database totalled 7470 population records, representing 2516 vertebrate species; ~ 3.5% of described vertebrate species (International Union for the Conservation of Nature, IUCN Red List of Threatened Species, 2020a). To normalize residuals and reduce heteroscedasticity, body mass (g) data was log transformed prior to the analyses (Cardillo et al., 2005; Stark, Pincheira-Donoso, et al., 2020; White et al., 2007). The full dataset was partitioned by taxonomic class and ecological system, providing 14 subsets used for model building, with each representing one group e.g. marine birds, terrestrial mammals, etc. Freshwater cartilaginous fish were discounted from this procedure due to a paucity of data.

2.3.2 Statistical Analysis

We used a generalised linear mixed modelling (GLMM) framework with a truncated Conway-Maxwell Poisson family using the ‘glmmTMB’ package (Brooks et al. 2017). This accounted for the discrete, count data of stressor number present for each population. Our model building strategy employed the use of existing knowledge (e.g. Bowler et al. 2020; Ripple et al. 2017) to construct a logical and plausible set of *a priori* predictors to describe relationships between stressor number and traits which predispose populations to vulnerability of stressors. This approach minimised explanatory variables in the global model, avoiding reliance on data-dredging for predictor selection via the testing of specific hypotheses (Burnham & Anderson, 2002). Prior to analysis, latitude and the natural log of body mass were evaluated using Variance Inflation Factor (VIF) and were considered beneath the threshold to constitute collinearity in all cases (threshold = 2). The combination of generalized linear models with splined data has been shown to provide a straightforward parametric approach to modelling non-linear terms, whilst performing better than their additive counterparts (Chung et al., 2009; Dominici, McDermott, Zeger, & Samet, 2002; He, Mazumdar, & Arena, 2006). Consequently, natural (restricted) cubic splines with four degrees of freedom, corresponding to five knots (Shepherd & Rebeiro, 2017; Stone, 1986) were applied to the latitude variable within all models to account for the non-linear relationship with stressor number (see Fig. 2.1). Evolutionary relatedness was accounted for using nested random-effect structures (Genus / Species), maintaining random intercepts and helping to inform where genera have fewer species (Gelman & Hill, 2006).

Table 2.1 | Model interaction term selection process.

Group	Models	df	AICc	ΔAICc (≤ 4)
Terrestrial				
Amphibians	**NS ~ BS + (1 | G/S)**	5	262.846	0.000
	No parameters suggested	4	263.534	0.688
Birds	**NS ~ BS + L + BS:L + (1 | G/S)**	13	2855.263	0.000
Mammals	**NS ~ BS + L + (1 | G/S)**	9	3582.615	0.000
Reptiles	**NS ~ BS + L + (1 | G/S)**	9	435.258	0.000
	NS ~ L + (1 | G/S)	8	436.555	1.297
Freshwater				
Amphibians	**NS ~ BS + L + BS:L + (1 | G/S)**	13	557.312	0.000
Birds	NS ~ L + (1 | G/S)	8	1450.655	0.000
	NS ~ BS + L + (1 | G/S)	9	1452.013	1.358
Bony Fish	**NS ~ BS + L + BS:L + (1 | G/S)**	13	1171.734	0.000
Mammals	**NS ~ BS + L + (1 | G/S)**	9	195.803	0.000
Reptiles	NS ~ L + (1 | G/S)	8	390.013	0.000
	NS ~ BS + L + (1 | G/S)	9	391.705	1.692
Marine				
Birds	**NS ~ BS + L + BS:L + (1 | G/S)**	13	1952.918	0.000
Bony Fish	**NS ~ BS + L + BS:L + (1 | G/S)**	13	2081.295	0.000
Cartilaginous Fish	**NS ~ BS + L + (1 | G/S)**	9	283.275	0.000
	NS ~ BS L + BS:L + (1 | G/S)	13	287.087	3.812
Mammals	No parameters suggested	4	770.302	0.000
	NS ~ BS + (1 | G/S)	5	772.332	2.030
	NS ~ L + (1 | G/S)	8	772.699	2.397
Reptiles	NS ~ L + (1 | G/S)	8	495.149	0.000
	NS ~ BS + L + (1 | G/S)	9	497.332	2.182

Model selection process to determine appropriate interactive terms. Models were ranked according to their corrected Akaike Information Criterion (AICc) values, with models ≤ΔAICc 4 shown for each ecological system. NS = number of stressors; BS = body size (ln of mass in grams); C = taxonomic class; L = latitude; G = genus; S = species; colons (:) represent interactive terms. Models selected for use in analysis are highlighted in bold.

Full models generally failed to converge, and so to identify the best combination of two-way interaction terms for each group, 'dredge' from the 'MuMIn' package was implemented (Bartón, 2014) using the model structure: *number of threats ~ body mass + Latitude* and including two-way interactions between body mass and latitude. With corrected Akaike Information Criterion for small sample sizes (AICc) used to identify the best model for each system (Burnham & Anderson, 2002), we highlight candidate models with ΔAICc ≤4, and selected the best model for each system scenario, based on AICc and including at least one predictor were reasonable (see Table 2.1).

AICc was used to aid model selection by making inferences from multiple models whilst considering fit and complexity (Johnson and Omland 2004). Estimates of pseudo-R^2 were used to assess model fit in the final models; with marginal R^2 estimating the variance explained by fixed effect variables, and conditional R^2 representing the variance explained by both fixed and random effects (Nakagawa & Schielzeth, 2013). Due to difficulties in calculating accurate R^2 values for our models, we provide two measures of conditional R^2 (using r2.corr.mer() and r2_nagakawa() functions) for transparent model appraisal. All statistics were performed in R V3.6.1.

2.4 Results

Stressor number showed a clear latitudinal gradient, with midrange latitude populations typically subject to fewer stressors than those between 10°S and 30°N, or at the poles (Fig. 2.1). Countries with highest mean number of stressors are typically those with high human population density and large population sizes, notably China and the Indian subcontinent. Indeed, of those populations affected by three stressors Asia accounts for the most (23.53%) whilst also having the highest mean number of stressors across populations (1.53). Conversely, Europe represents the highest proportion of populations subject to zero stressors (31.54%) and further demonstrates the lowest mean number of stressors (0.74).

The number of stressors a population was affected by appeared to be a function of body size, with smaller species typically affected by fewer threats (Fig. 2.2). The noticeable exception to this was in amphibians, where the heaviest species were generally affected by fewer stressors (59 populations; Fig. 2.2b). Single stressors were

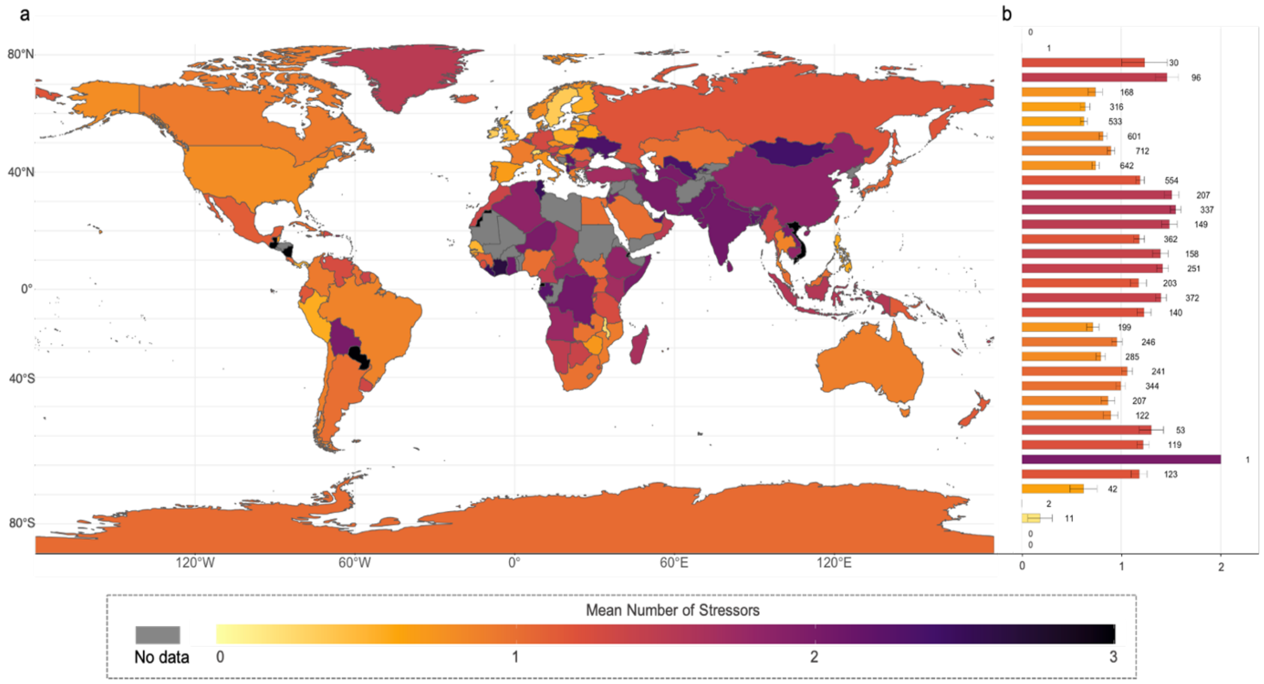

Fig. 2.1 | Global distribution of mean number of stressors by country and latitude.

Global overview of the mean number of stressors **a** within each country and **b** by latitude with numbers alongside bars representing sample sizes for each 5° latitude bin.

observed in 35.0% of vertebrate populations, but most frequently seen in mid-sized birds, mammals, reptiles and fish species. Again, amphibians differed from this pattern, showing a more normal body mass distribution across populations and a reduced exposure to single stressors when viewed alongside other vertebrate classes (Fig. 2.2b). Populations exposed to two stressors accounted for 18.0% of records with the heaviest bird, mammal and bony fish populations (249, 109 and 78, respectively) more likely to be impacted than those with a lower body mass, with bird species demonstrating the clearest distinction (Fig. 2.2a). Exposure to two stressors differed in amphibians and cartilaginous fish, while 33% of reptile populations were exposed to two stressors; more than any other group. Populations were least likely to be exposed to three stressors (10.3% overall), with fish populations experiencing the fewest populations subjected to three stressors (bony fish 77 populations; cartilaginous fish just one; Fig. 2.2e and f). Remaining classes showed similar exposure levels but differed throughout body mass ranges, with no clear pattern demonstrated.

Consistent with patterns demonstrated by body mass quartiles (Fig. 2.2), our models suggested a largely positive relationship between species body mass and the likelihood of populations being exposed to higher stressor numbers (Table 2.2 and Fig. 2.3), although only a minority of these achieved statistical significance at $p \leq 0.05$.

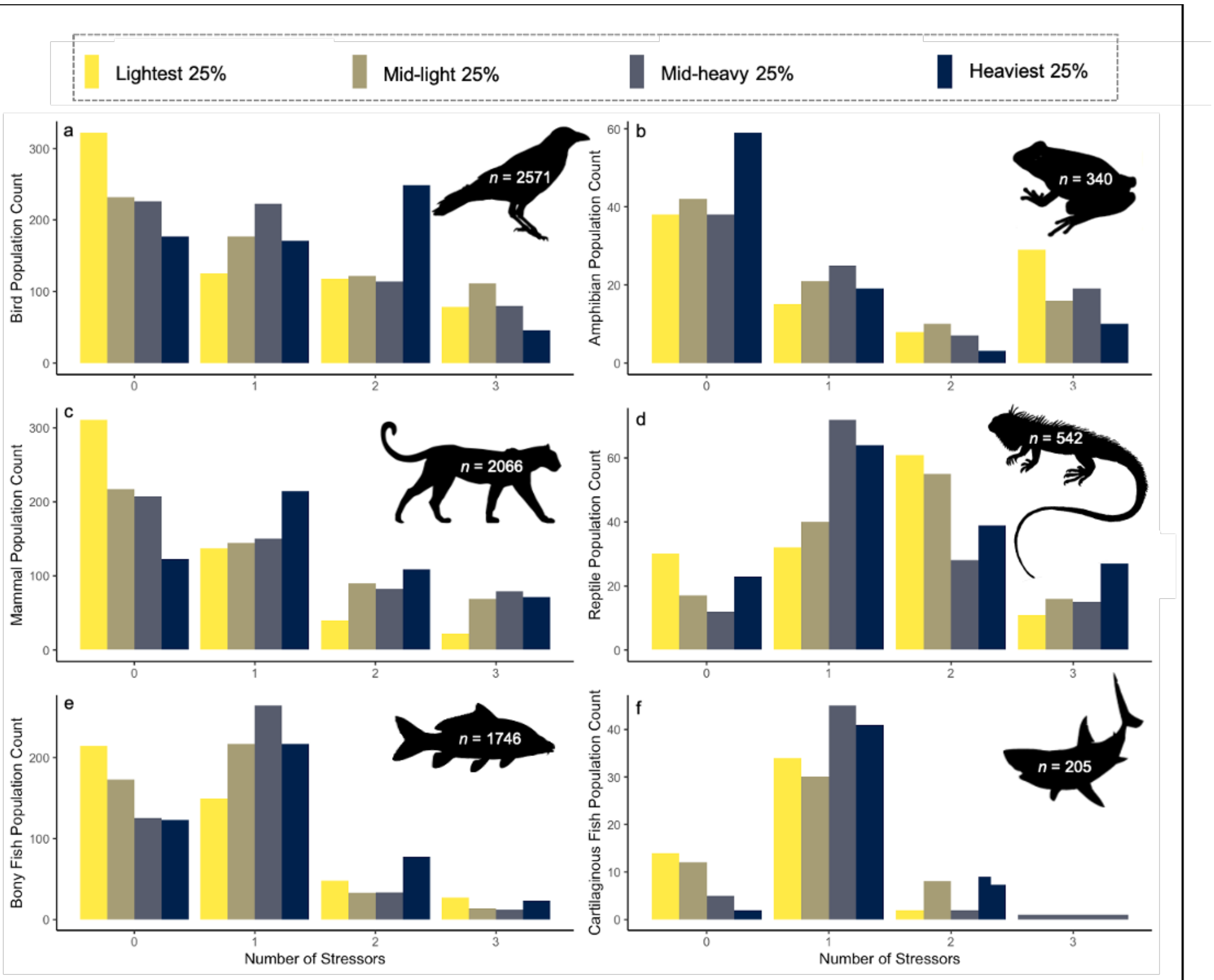

Fig. 2.2 | Number of stressors by body mass quartile.

Populations exposed to each number of stressors (0 - 3) shown as counts for the lightest 25%, mid-light 25%, mid-heavy 25% and heaviest 25% species, within each taxonomic class. Panels represent **a** birds **b** amphibians **c** mammals **d** reptiles **e** bony fish and **f** cartilaginous fish.

Table 2.2 | Summary of generalised linear mixed model (GLMM) coefficients for body mass parameter for each class and ecological system.

Group	Intercept	Estimate (a)	SE	95% CI	p-value	Marginal R^2 r2_nagakawa()	Conditional R^2 r2_nagakawa()	Conditional R^2 r2.corr.mer()
Terrestrial								
Amphibians	-0.031	-0.137	0.083	-0.298 / 0.025	0.097*	0.072	0.762	0.848
Birds	-1.550	0.173	0.049	0.076 / 0.270	0.000***	0.216	0.824	0.722
Mammals	-1.340	0.049	0.009	0.031 / 0.067	0.000***	0.270	0.783	0.568
Reptiles	0.020	0.026	0.014	-0.001 / 0.054	0.059*	0.418	N/A	0.716
Freshwater								
Amphibians	-2.203	0.781	0.462	-0.125 / 1.687	0.091*	0.428	0.774	0.696
Birds	-0.556	-0.016	0.018	-0.051 / 0.020	0.398	0.145	N/A	0.443
Bony Fish	-0.383	-0.052	0.042	-0.135 / 0.030	0.213	0.154	0.940	0.776
Mammals	-2.308	0.111	0.045	0.022 / 0.200	0.015**	0.710	0.913	0.788
Reptiles	0.200	0.013	0.017	-0.021 / 0.046	0.460	0.546	N/A	0.539
Marine								
Birds	-3.722	0.279	0.228	-0.168 / 0.726	0.221	0.237	0.769	0.198
Bony Fish	0.367	-0.102	0.060	-0.219 / 0.016	0.090*	0.225	0.884	0.659
Cartilaginous Fish	-0.311	0.035	0.010	0.014 / 0.055	0.001***	0.683	N/A	0.300
Mammals	-0.367	0.005	0.029	-0.052 / 0.061	0.871	0.001	0.630	0.479
Reptiles	-0.458	0.000	0.026	-0.050 / 0.050	0.999	0.205	N/A	0.198

$^{*}p \leq 0.1$, $^{**}p \leq 0.05$, $^{***}p \leq 0.01$

Body mass fixed effects parameter estimates from generalised linear mixed models of stressor number across ecological system and taxonomic class. For each group model, parameter estimates are shown with upper and lower 95% confidence intervals and *p*-values. With the complexities involved in estimating pseudo-R^2 values for GLMMs, here we show two values for conditional effects (using r2.corr.mer() and r2_nagakawa() functions) to provide a frank overview of evaluations. Marginal effects are also provided. Body size is the natural log of body mass in grams. No model was fit for freshwater cartilaginous fish due to insufficient data. Body mass was not stipulated for model inclusion in marine and freshwater reptiles, so these groups are not represented here. As estimates for splined variables are largely meaningless, predicted values for Latitude splines and their interaction terms are not included here, but can be found in Supplementary Information, Tables S2 - S4. Random effect estimates are omitted from the table.

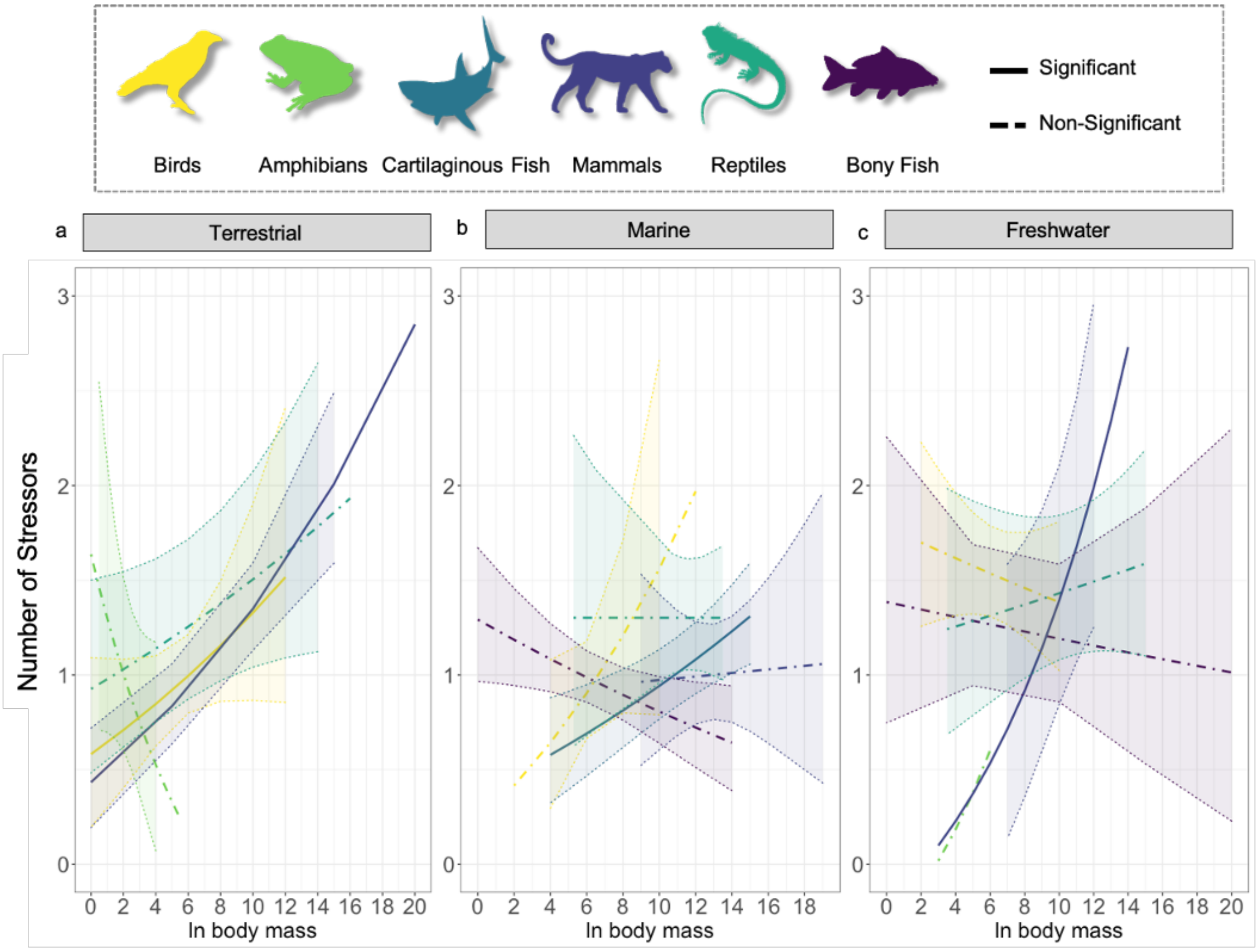

Fig. 2.3 | Model predictions of stressor number as a function of body mass.

Generalized linear mixed model predictions of stressor number as a function of natural log of body mass in grams for **a** terrestrial ecosystems **b** marine ecosystem, and **c** freshwater ecosystems. Class predictions with *p* = ≤0.05 are represented by a solid line whilst non-significant estimates are shown by dashed lines. Solid lines represent parameter estimates, with ribbons showing 95% confidence intervals.

Terrestrial systems showed the clearest relationships (Fig. 2.3a), with predicted stressor number significantly increasing with body size for terrestrial mammals and birds (ß = 0.049 ± 0.009, *p*-value = <0.001 and ß = 0.173 ± 0.049, *p*-value = <0.001, respectively). Marine cartilaginous fish produced the only significant estimates in marine ecosystems (ß = -0.035 ± 0.010, *p*-value = 0.001, Fig. 2.3b). Freshwater mammals showed similar trends, with predictions forecasting more stressors as body mass increases (ß = 0.111 ± 0.045, *p*-value = 0.015, Fig 2.3c.). Several estimates bordered on significance, with terrestrial amphibians, terrestrial reptiles, freshwater amphibians and marine bony fish all achieving p-values of less than 0.1.

Model predictions of stressor number as a function of latitude showed varied results, but with some common patterns (Fig. 2.4). For the majority of groups (e.g. marine mammals, terrestrial reptiles, freshwater amphibians) the most stressors were predicted to be experienced towards extreme latitudes for populations within each class. This

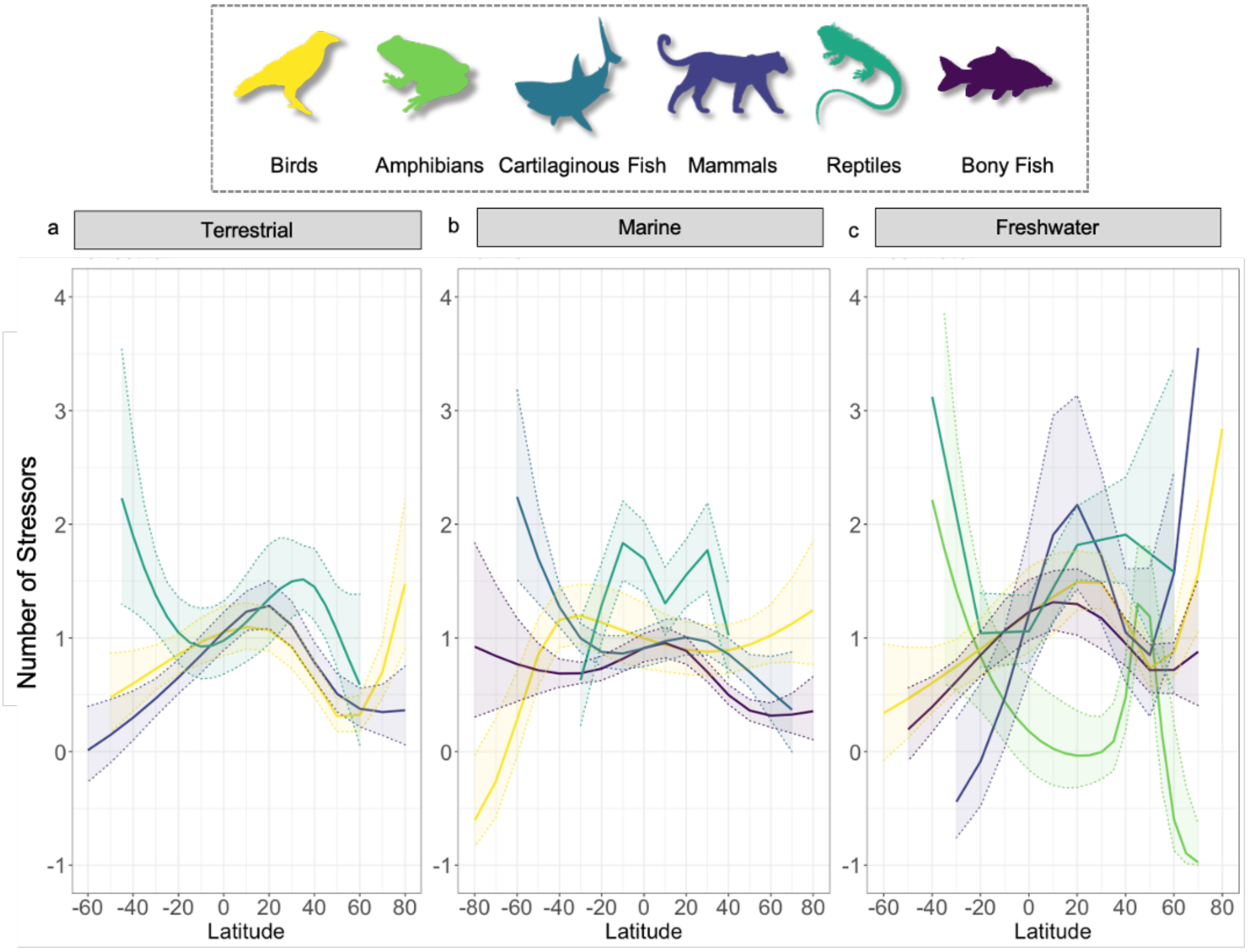

Fig. 2.4 | Model predictions of stressor number as a function of latitude.

Generalized linear mixed model predictions of stressor number as a function of natural log of body mass in grams for **a** terrestrial ecosystems **b** marine ecosystem, and **c** freshwater ecosystems. Solid lines represent parameter estimates, with ribbons showing 95% confidence intervals. Splined parameter predictions cannot be numerically interpreted, and so all estimates are displayed graphically here for interpretative purposes.

pattern is often reversed at the opposite pole, with the fewest stressors predicted for that class. For instance, marine bony fish experience the most stressors towards the southern pole, but fewest in northernmost latitudes (Fig. 2.4b), a trend which is reversed in freshwater mammals, where more stressors are predicted at northern latitudes, and fewer towards southern extremities. There were also several groups, across systems, with local maxima between approximately 20°N and 40°N, such as terrestrial mammals and reptiles, marine cartilaginous fish and freshwater birds, mammals, amphibians and reptiles.

Stressor number also varied considerably by latitude in interaction with body mass (Fig. 2.5). Again, peaks and lows were predicted towards polar regions for marine birds (Fig. 2.5b), and freshwater amphibians (Fig. 2.5c). However, body weight seems to play a part in stressor exposure for most classes,

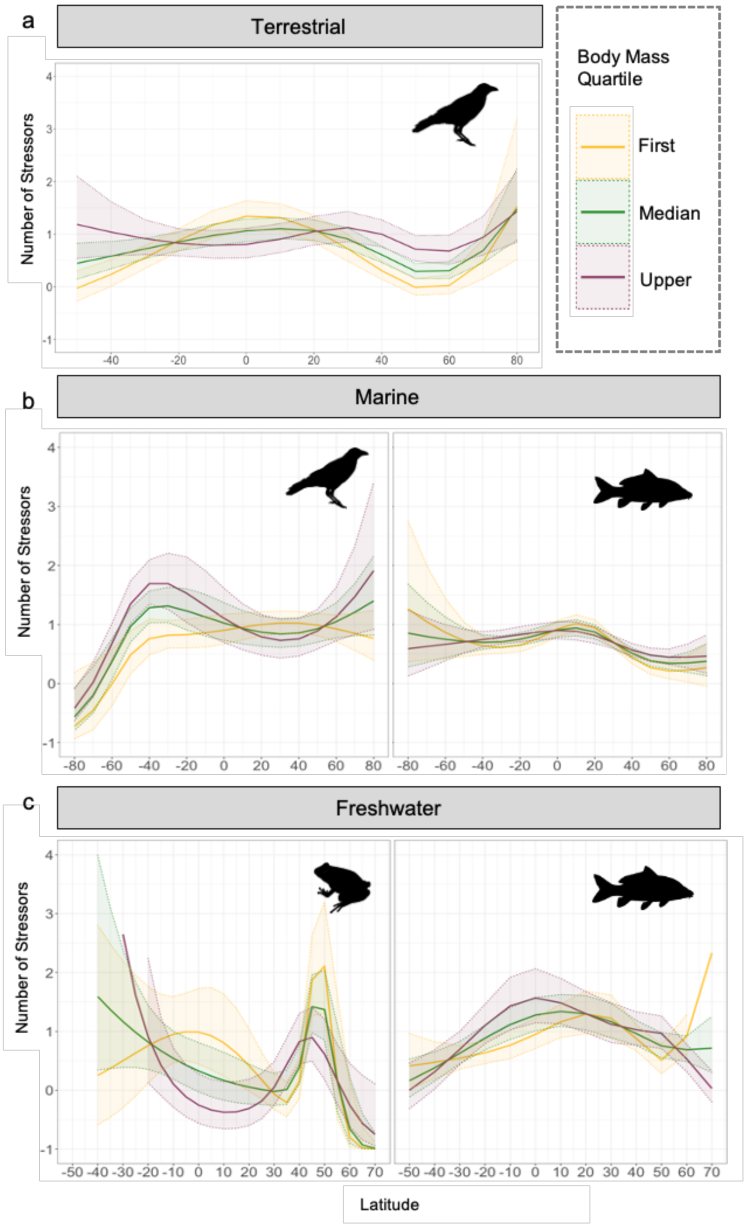

Fig. 2.5 | Model predictions of stressor number as a function of latitude by interaction with body mass.

Generalized linear mixed model predictions of stressor number as a function of latitude with splines and four degrees of freedom for **a** terrestrial birds **b** marine birds and bony fish, and **c** freshwater amphibians and bony fish. Solid lines represent parameter estimates, with ribbons showing 95% confidence intervals. Splined parameter predictions cannot be numerically interpreted, and so all estimates are displayed graphically here for interpretative purposes.

with the heaviest quartile tending to experience the most stressors regardless of latitude, except in amphibians, where it is the lightest quartile that are predicted to suffer higher stressor numbers, except at lower latitudes where the heaviest seem most at risk of stressor exposure (Fig. 2.5c). Freshwater bony fish suffer greatest stressors between 10°S and 30°N, with local peaks apparently dependent on body mass, as larger species suffer greater stressors at lower latitudes and lighter taxa reach a local peak at around 20°N (Fig. 2.5c). Heavier marine birds also suffer a peak in stressor number at 40°S, while the first quartile peaks at around 30°N (Fig. 2.5b). Marine bony fish show a gentle summit at around 10°N, but body mass seems to have a lesser effect than in other classes (Fig. 2.5b).

While plots are provided, note that coefficient estimates for the latitude variable are absent from Table 2.2. As interpretation of splined variable coefficients and their interactive terms is essentially meaningless (Shepherd & Rebeiro, 2017) our predictions are instead displayed visually in Fig. 2.4 and Fig. 2.5 to elucidate our findings. Full coefficient estimates and intercept values have been provided within Supplementary Information Tables S2, S3 and S4.

2.5 Discussion

An inability to identify correlates of exposure to multiple stressors could hinder broad efforts to maintain biodiversity and the mitigative actions implemented to protect species (Hodgson et al., 2017). Using a new and comprehensive collation of vertebrate body mass data, alongside population records taken from the LPD, we show that both body size and latitude can provide valuable estimates of stressor number in global vertebrate populations. Our results reveal class and system specific patterns in stressor number as a function of body size, and latitude. Spatial patterns show mean stressor number is highest between 20°N and 40°N, and again towards the poles, with model predictions further supporting these latitudinal findings while producing more nuanced predictions of stressor number when combined with body mass differentiated by ecological system and class. Uncovering the relationship between body size and number of threats has useful applications for vertebrate conservation. Though we know comparatively little about the world’s rarest species because of their scarcity (Ripple et al., 2017), an easily measured and universal predictor such as body mass, provides an accessible tool for approximating threat status where little other data exists. Likewise, latitude provides a secondary measure and greater specificity to population threat estimates. As such, we provide an adaptive framework for further exploration of stressor predictors, using ubiquitous traits both biological and geographical.

Our models revealed positive relationships between body size and the number of stressors affecting terrestrial mammals and birds, marine cartilaginous fish and freshwater mammals within the LPD. This trend was generally anticipated, given the well-documented challenges faced by large-bodied species. These include heightened levels of exploitation, damage to habitats and larger home range increasing the chances of stressor exposure in heavier species (Böhm et al., 2016; Collen et al., 2011; Ripple et al., 2017). This is further supported by complementary research from the Living Planet Index, which most recently demonstrated a link between larger body size and strong population declines in freshwater ecosystems (He et al., 2019). Whilst no significant negative relationships were identified where lower body size might predict higher stressor number, examination of raw data shown in Fig. 2 shows a possible trend in this direction for amphibian species. Prior research has already produced instances of amphibians standing alone in threat trends when compared to other vertebrate classes, with the lightest amphibian species subject to higher instances of threats signifying habitat degradation or loss, than heavier species (Ripple et al., 2017). Smaller species may also generally have a limited dispersal ability, restricted geographic range (Cardillo et al., 2008) and occupy narrow niches incapable of enduring change (González-Suárez & Revilla, 2013). Arboreal amphibians are also the lightest of their class (Santini et al., 2018) and are likely more prone to impacts from deforestation and land clearing. It remains uncertain why amphibians are the apparent exception amongst vertebrates with regards to exposure to multiple stressors, but more data would enable the specialist analysis required to further explain whether amphibian declines are due to the currently suspected fungal disease (Carvalho, Becker, & Toledo, 2017), or disease in combination with additional stressors.

Previous work has highlighted that predators are particularly at risk of anthropogenic change (Ripple et al., 2017), with the effect that predators are being disproportionately lost worldwide (Estes et al. 2011; Hoffmann et al. 2011). Given that body size is often positively related with trophic level, particularly in aquatic environments (Cohen, Jonsson, and Carpenter 2003; Deudero et al. 2004; Estrada et al. 2006; Riede et al. 2011; Romanuk, Hayward, and Hutchings 2011), our analysis suggest that predators are likely to be disproportionately threatened by multiple stressors, which may in part account for these observed losses. These impacts on predators are known to have cascading effects on the stability of food webs by changing the strength of direct and indirect top-down effects (Terborgh et al., 2001). By altering the stability of predator populations, changes in biodiversity (Sergio, Newton, & Marchesi, 2005), biomass (Lefcheck et al., 2015; Soliveres et al., 2016), disease and carbon sequestration are all possible, with extensive cascading effects already seen across ecosystems worldwide (Estes et al., 2011). Moreover, with trophic downgrading shown to interact with pre-existing anthropogenic threats such as pollution and habitat change (Estes et al., 2011), and pressures becoming ever more prevalent globally (Halpern et al., 2015), further integration of trophic level into predictive estimates of stressor number would provide greater insight in to these relationships. Nevertheless it should be noted that species at the bottom of the consumer triangle can also be powerful influencers within their communities, with large herbivorous species commanding architectural power over ecosystem structures via the physical removal of vegetation and increased influence on the biomass cycle (Mosepele, Moyle, Merron, Purkey, & Mosepele, 2009).

Human population density has long been considered a proxy for anthropogenic disturbance factors (Nelson, 2008; Santini et al., 2017), with local-population driven stressors such as pollution and exploitation leading to an increase in the frequency of stressors in the northern hemisphere where most economic activity takes place (Kaufmann and Stern 1997; Moore 2016). Median body mass is also generally higher for terrestrial mammals in the northern hemisphere (Santini et al., 2017), and with the additional impact of human pressures, heavier species are at a greater probability of being afflicted by multiple stressors. Findings from our latitudinal models (Fig. 2.4) and Fig. 2.1 support this throughout, indicating locally increased risks across the northern hemisphere where human population is densest. Indeed, some of the world's densest cities – including Mumbai, Taipei, Shanghai, Karachi and Dhaka – fall between 19°N and 34°N, with around 50% of the human population living between 20°N and 40°N (Kummu & Varis, 2011). Notable exceptions in this pattern are marine birds and, arguably, marine reptiles which show a bimodal latitudinal pattern. For marine birds, it is plausible that many species are pelagic and so avoid coastal areas associated with the highest levels of population density and greatest cumulative impact of human activity (Halpern et al., 2008). With fishing pressures greatest in the northern hemisphere (Kroodsma et al., 2018), and fewer people below the equator (Kummu & Varis, 2011) climate-related threats may be more influential than suspected in some groups. This is demonstrated in populations showing southerly maxima in predicted stressor number (such as marine mammals, and terrestrial reptiles), as minimal human population density infers scant local stressors in the southern hemisphere. Indeed, several classes were predicted an increase in stressor number further towards at least one polar region (see terrestrial reptiles and birds, marine mammals, and freshwater reptiles, birds, amphibians and mammals; Fig. 2.4a-c). As estimates differ by class and by body mass quartile, this may indicate differing abilities of taxa in coping with climate-related changes to niches, with polar amplification a pertinent concern for many species whose ranges reach into Arctic and Antarctic regions (Vincent, 2019). Species reliant on sea ice, the Pacific walrus (*Odobenus rosmarus*) for instance, might be subject to both climate change pressures and degradation of habitat as sea ice levels experience record minima (Post et al., 2013).

Congruent with peaks in mean stressor number (Fig. 2.1) and latitudinal stressor predictions (Fig. 2.4) are several low- and middle-income economies, with a suite of socio-economic issues leading to heightened stressor numbers and a compromised ability to mitigate threats (Vörösmarty et al., 2010). For instance, quickly developing countries typically see rapid surges in infrastructure, pollution, poor regulation of exploitative activities such as hunting, and further unsustainable use of natural resources, which can all increase the stress exerted on biological systems (Glaeser & Henderson, 2017; Venter et al., 2016; Vörösmarty et al., 2010). The lack of regulatory guidance on hunting for food and medicinal products is of particular concern, and with nearly all threatened mammals occurring in developing countries (Ripple et al., 2016), large threatened species are again more likely to be impacted than lighter less endangered groups. Moreover, wealthy countries commonly export their waste processing abroad, effectively outsourcing their environmental impact to lower income countries which are less able to deal with the effects (Brooks, Wang, & Jambeck, 2018). Yet it is also plausible that threatened species are over-represented in low- and middle-income countries, where a paucity of conservation funding compels prioritisation towards species considered most at-risk. Despite more developed countries demonstrating generally lower mean stressor number in this study, existing research suggests that even high stressor numbers tend to be tolerated until their impacts become detrimental, at which point it is generally not the cause of stressors treated, but the symptoms (Vörösmarty et al., 2010). Alas, this pattern may be more consequential for developing countries which will likely have to manage the repercussions, thus further increasing already high stressor numbers for low- and middle-income nations.

Human activity is widely considered liable for the incipient sixth mass extinction (Barnosky et al., 2011; Ceballos, Ehrlich, & Dirzo, 2017). The long history of combining highly modified landscapes alongside exploitation, climate change and the introduction of invasive species has already driven many modern species to extinction (Otto, 2018), and multiple stressor combinations are forecast to push yet more populations beyond the point of recovery (Symes, Edwards, Miettinen, Rheindt, & Carrasco, 2018), with large bodied species particularly prone to loss (Otto, 2018). As population growth is forecast to undermine the protection of natural environments (Crist, Mora, & Engelman, 2017), humanity presents itself with daunting challenges for multiple stressor mitigation, and resource provision for a quickly expanding populace. Corresponding growth in food demand will likely, therefore, place even greater pressure on the species targeted for harvesting; highlighting not only the plight of favoured, large-bodied vertebrates, but jeopardising the viability of long relied-upon resources should these species be exploited beyond recovery (Ripple et al., 2017). Yet, it is suspected that measures developed to curtail such impacts would not be sufficient, with the reduction of food waste, changes to diet, restrictions to the harvesting of wild species, and the intensification (rather than expansion) of food production worthy, but deficient, approaches (Crist et al., 2017). The minimisation, and eventual reversal, of population growth has been suggested as one of the few measures capable of generating the changes required to sufficiently manage stressors, whilst maintaining biodiversity and human resource requirements concurrently (Crist et al., 2017). Recent research has provided some hope for this strategy, with a fall in human fertility projected to dramatically reduce population growth worldwide (Vollset et al., 2020). Notwithstanding the social implications of this, such news may bring some hope for conservationists conscious of the cumulative impact that multiple anthropogenic stressors have had on the natural world since the beginning of the Anthropocene.

This research describes stressor number as a function of body mass for thousands of vertebrate populations, yet it should be noted that analyses were only possible for those with threat data available for respective populations within the LPD; as such we were able to generate predictions for around 3.5% of described vertebrate species. Although we see no obvious reason for overall trends to differ, the quantity of non-significant predictions illustrate how unexpected results are possible, even where groups display strikingly similar patterns. Thus, despite differentiation by class and system providing some generalisability within specific groups, caution should be exercised when applying our findings to the management of species beyond our analyses; particularly in classes represented by smaller sample sizes within the LPD. While the LPD draws from high quality published literature, this also means its data inherits any biases derived from its sources. This has resulted in the over-representation of well-studied regions and taxa, with research also inclined towards populations within protected areas and terrestrial ecosystems (McRae et al., 2017). To this end, we advocate explicit reference to threats within ecological research to enable the expansion of current databases and to keep multiple stressor processes at the forefront of developing research; particularly in underrepresented areas and classes such as cartilaginous fish and amphibians.

2.6 Conclusion

Our findings that body size and latitude can be used as predictors of stressor number in vertebrates offer the ability to streamline conservation prioritisation, whilst emphasising opportunities for the dramatic change required to minimise stressors for the future of our planet. With threat level differing by class and ecological system, we present a framework universally applicable, yet capable of distinguishing between multiple species and population-specific factors. Our results support previous research suggesting that the large charismatic creatures fronting conservation initiatives globally are likely to be the species most at risk. Yet by highlighting the plight of large-bodied species, we hope that protection of these ecosystem architects is enhanced and expedited.

3

Discussion

3.1 Aims and Approach

As the human population grows around the world, so too does the frequency and intensity of stressors acting on biodiversity (Sala et al., 2000). With stressor exposure often triggering vertebrate population declines (Li et al., 2016), an ability to quantify threats without direct access to the focal population would enable a fast and economical assessment of risk. Targeted and in-depth investigations could then be directed towards communities considered to be at high risk of multiple stressors, without prior need for costly field work in often challenging conditions.

Prior work has largely focused on the impact of these multiple stressors and their interactions, with far less known about why populations might be vulnerable to threats in the first instance. So, as previous studies have focused on *how* populations are affected by threats, this study endeavours to complement existing knowledge by uncovering *why* populations may have a predisposed vulnerability to multiple stressors.

Here, we go beyond taxonomic and ecosystem level effects by assessing how a critical fitness related phenotypic trait - body size - impacts the number of stressors populations are exposed to. By using this universal and widely available trait we have enabled the assessment of rare, cryptic and inaccessible species, with minimal use of funding allocations and resource requirements.

We also used latitude as a spatial predictor to forecast stressor number, uncovering the relationships between stressor number and areas of human population density (Nelson, 2008; Santini et al., 2017). Using latitude as a predictor also provided a proxy measure of pole-oriented climate change impacts. This enabled further differentiation between taxonomic class and ecological system, by providing a ubiquitous method of predicting vertebrate stressor exposure.

To apply this concept, we used the LPD as our primary data source, taking variables class, system, latitude, and a count of threat number from the comprehensive assembly of population-specific data for vertebrates around the world. Further supplementary data sources were used to generate a database of body mass, while allometric regressions were used to estimate mass-from-length where body mass measurements were not available. This final dataset comprised records for 7470 populations, representing 2516 species of amphibian, reptile, mammal, bird, bony fish and cartilaginous fish from every continent, and throughout marine, freshwater and terrestrial systems. We then used a generalised linear mixed modelling (GLMM) approach to assess the impact of body mass and latitude and their interaction on the number of stressors a population was affected by, with the nested random effects species within genus.

3.2 Summary of Findings

Our findings suggest that body size and latitude can be used as predictors of stressor number, but that results vary by ecological system and taxonomic class. Preliminary visual analysis of stressor number by body mass quartile indicated that the lightest species most often avoided stressors, except in amphibians, where the heavier species seemed exposed to the fewest stressors (Fig. 2.2). Findings from our models generally supported these patterns, with all significant estimates predicting a positive relationship between body mass and the number of stressors a population is exposed to. This was particularly evident in terrestrial vertebrates, with bird and mammal estimates both showing statistical significance. Marine cartilaginous fish and freshwater mammals also produced significant results, showing the same positive correlation between stressor number and body mass. Given preliminary analysis and prior research on vulnerability to stressors by body size (Collen et al., 2011), this trend was entirely anticipated, yet it was not necessarily consistent throughout classes and systems. No other body mass estimates showed statistical significance at $p = \leq 0.05$, although a number of groups reached values below $p = 0.1$. For instance, terrestrial reptiles showed a positive relationship between body mass and stressor number (ß = 0.026 ± 0.014), and a p-value of 0.059, suggesting a significant trend may emerge should larger sample sizes be attained.

Viewing mean population stressor number by country and latitude provided indications of stressor origins (Fig. 2.1), as local peaks in mean stressor are seen towards polar regions and then at latitudes between 20°N and 40°N. Again, our estimates largely supported these patterns, with a number of groups showing peaks in predicted stressor number in at least one polar region, with some demonstrating additional local maxima at latitudes between 20°N and 40°N. As with body mass predictors, these patterns were broadly anticipated given prior research on human population density and the subsequent prevalence of anthropogenic threats (Bowler et al., 2018; Venter et al., 2016). Similarly anticipated were peaks in stressor number towards the poles, suggesting influence from global stressors, like climate change (Vincent, 2019), which impact vertebrate populations despite a comparative lack of human presence at these latitudes (Kummu & Varis, 2011).

Our findings provide a method to quickly and efficiently assess risk in vertebrates, whilst providing a framework for the exploration of alternative species traits as predictors of multiple stressor exposure. We therefore fill a gap in research by asking 'why', rather than 'how', and in doing so highlight the plight of large-bodied vertebrates, and the nuances involved in predicting stressor exposure, in an era dominated by human-driven change.

3.3 Limitations and Solutions

Every effort was made throughout this research to minimise limitations on the final analyses and subsequent interpretation. However, given that research was largely reliant on pre-existing data availability, there are some qualities that should be taken into consideration.

3.3.1 The Living Planet Database

Despite the global approach taken in curating the LPD, the collation itself is prone to the research biases experienced throughout the study of vertebrate species. These are well-documented, with a full dissemination of spatial and taxonomic biases explored by McRae, Deinet and Freeman (2017). These include a bias towards temperate regions and an underrepresentation of tropical regions; overrepresentation of bird and mammal species and underrepresentation of amphibian and reptile species in terrestrial and freshwater realms.

Accordingly, a more comprehensive spread of data would have led to a greater generalisability across populations lacking threat information, where representation currently stands at ~3.5% of described species. It would further have given more reliable estimates across the lesser-studied latitudes towards the northern and southern poles and provided a clearer background of the effects of climate change in the form of polar amplification. It should also be noted that the LPD provides records of vertebrate *populations*; not species in their entirety. Various vertebrate species will therefore have multiple data points included within the LPD, and will likely demonstrate different conditions, highlighting their individual situations and providing the prospect of assessing the external impacts (and threats) of different populations in different spatial contexts.

The inconsistencies shown in representation between classes - for example birds contribute over 12 times the data of cartilaginous fish species (2571 to 205) - may be due to limited funding and resources available to reach areas with challenging climates or terrain, or access to aquatic environments. Moreover, with greater interest in bird species from a very general perspective - hobbyist bird watchers are far more prolific than those with the ability to SCUBA dive - there may also be a trend for such enthusiasm driving avian research beyond background levels for classes generally. Greater exposure of less 'charismatic' species in amphibian and cartilaginous fish classes may go some distance in raising their profile from a research perspective, but until funding bodies and the wider public acknowledge the value of these species to biodiversity, their representation may continue to remain minimal.

The comparatively small amount of data from tropical regions is also an acknowledged bias issue in the LPD and wider research, and likely driven by the difficulties involved in accessing these locations and the challenging conditions they create. Moreover, as vegetation is typically denser in tropical regions (Karr, 1981), it may be more difficult to locate and identify fauna, creating a bias against cryptic or camouflaged species and in favour of conspicuous species which are more vulnerable to exploitation. Occupancy models have been shown to alleviate imperfect detection in this capacity, yet the time consumption and difficulty in their fitting may make them an undesirable choice for many (Welsh, Lindenmayer, & Donnelly, 2013).

With large datasets like the LPD, undetected errors such as process errors (e.g. stochastic variations in population) and observation inconsistencies (e.g. poor detectability of cryptic species, mismatched observer techniques) will likely be present (Clark & Bjørnstad, 2004; Buckland, Newman, Thomas, & Koesters, 2004; Dennis, Ponciano, Lele, Taper, & Staples, 2006; Gotelli & Colwell, 2001). Such errors may have been overlooked during collation and are therefore difficult to determine during future uses. However, as data are largely sourced from peer reviewed literature, there can be tentative confidence that the methodologies used were the most appropriate for the technology and methods available at those points in time. Moreover, with >7000 LPD threat data time series, error caused by any irregularities in methodology should not impact results considerably, with minimal impact to the overall integrity of the dataset and its resultant trends (Lin, 2018).

will likely be only a small proportion of a very large dataset and therefore not affect overall results much

The earliest starting year for datapoints within the LPI is 1970. Despite some data points now spanning almost 50 years, starting points should not be used to suppose a comprehensive baseline for a population's vulnerability to stressors; species have endured anthropogenic pressures since the beginning of the Holocene Epoch (Dulvy, Pinnegar, & Reynolds, 2009) and particularly since the industrial revolution (Hunter, 2007). Thus, to infer such measures from the commencement of any time series in such recent history would subject any analysis to a shifting baseline paradigm.

Finally, the number of stressors recorded within the LPD is capped to a maximum of three stressors per population; this is despite many literature sources explicitly mentioning stressors numbering greater than this quantity. Thus, with many populations enduring more stressors than are recorded within the database, there a) may be more scope for - currently excluded - stressor inclusion and subsequent research of population exposure, but b) may mean that current predictions of stressor number are underestimated in some cases. This issue would be time-consuming to remedy but recommended where possible if future research plans to build upon this study to more accurately predict stressor exposure in wild populations.

3.3.2 Body Mass Estimates

The use of authentic trait data is always preferable where possible. However, given the general paucity of body mass data for amphibians, and a large number of fish species, it was considered necessary to use allometric regression equations, with species and clade-specific priors, to estimate body mass in a number of instances (367 amphibian and fish species). By doing so, representation of amphibian species was increased by over 16%, and by over 19% for fish species.

One obvious solution to this deficit of real-world body mass data may be the collection of information from captive populations. However, many lesser-known marine bony fish species may never have captive populations to represent their species. In these instances, allometric calculations may be the best option that one could hope for.

Alternatively, amphibians are a much smaller class (an estimated 8,121 amphibians compared to 34,300 fish, AmphibiaWeb.org, 2020; FishBase.us, 2020) and so it is more realistic to expect that body mass records would be fully available in their entirety at some future point. Researchers have already undertaken this endeavour to collate amphibian trait data and so this target, it seems, is on the horizon.

3.4 Auxiliary Research Suggestions

With findings from this research posing their own questions, suggestions of further research into study-specific areas are proposed here to fully understand the nuances of our results.

The majority of predictions (significant and non-significant) followed a varied pattern throughout the analytical process, with stressor number predictions varying with body mass. Yet one group suggested a similar pattern throughout analysis, despite estimates not always being significant: terrestrial amphibians were predicted to have fewer stressors as body mass increased. Amphibians have already proved something of an anomaly in stressor exposure in past research (e.g. Ripple et al. 2017), and evidence already exists of a negative relationship between amphibian threat risk and body mass (Sodhi et al., 2008). Smaller species are often targeted for the pet trade (Ruland & Jeschke, 2017) and their increased surface area exposes them to greater climate-induced desiccation and dermal toxicity via chemical contaminants (Kaufmann and Dohmen 2016; Watling and Braga 2015). Furthermore, with disease remaining a prevalent threat to many populations (Carvalho et al., 2017) we suggest specialist investigation into why terrestrial amphibians stand alone in this trend. As an open access resource, the LPD and its population-specific stressor data represent an accessible route to uncovering this enigma held by amphibian populations and their stressor patterns, and we recommend utilisation of the database accordingly.

The uncertain relationship between body mass and the number of stressors in aquatic classes also warrants further consideration. Bony fish, for example, showed weak, non-significant negative relationships between stressor number and body mass, with no consistency or significant values (Fig. 2.3). It may simply be that exposure at a finer taxonomic resolution differs too much for an overall trend to become clear. For example, it is reasonable that some fish orders suffer disproportionately greater exposure to exploitation due to their size or desirability as a food source; and with only ten species making up 86% of the consumed seafood in the United States by volume (National Fisheries Institute, 2020), exploited taxa seem heavily biased towards only a few extant species, in North America, at least. Thus, not all species will be exposed to (targeted) fishing practices, relieving a significant number of species - perhaps within specific clades - from multi-stressor scenarios. We therefore suggest the study of aquatic species at lower taxonomic classifications, perhaps by order or family, in order to ascertain whether body mass can be used as a predictor of stressor number at these levels where it has failed by class.

Compared with other groups, latitudinal predictions for marine birds showed little increase in stressor number in high human population density regions (Fig. 2.4b). This would infer a susceptibility to global pressures, such as climate change, due to the low human population density below the equator, where predictions in stressor number peak for this group. Accordingly, this would suggest fewer populations occupying coastal areas damaged by local anthropogenic change and pollution. Drawing more detailed threat data from the LPD would help reveal these distinctions and provide context for the weak trends demonstrated in such groups.

Of over 25,000 populations within the LPD, only 7827 included data about threats, of which 2860 were recorded as having no threats, and the rest having at least one recorded threat. Thus, with less than a third of the total LPD populations (31.2%) drawing threat data from its source literature, we believe that one simple change to future publications could greatly improve multiple stressor research going forward. If all future vertebrate studies included explicit statements of population threat vulnerability, the collation of stressor data within the LPD would increase dramatically. Future studies would therefore enjoy larger datasets with improved representation from current minority classes, and likely increased reliability in their results. Further, it would permit the long-term monitoring of change with regards to stressor exposure as the human population continues to climb.

Finally, opportunities will soon become available to study LPD population threat categories in far greater detail. The LPD is currently in the process of being recoded to incorporate finer-resolution threat cataloguing via use of the International Union for the Conservation of Nature's (IUCN) classification scheme (IUCN, 2020b). For instance, where the LPD currently lists 'exploitation' as a stressor, the IUCN categories provide further differentiation to groupings such as, 'persecution / control', 'intentional use as a target species', 'Unintentional, small scale effects as non-target species', etc. Once complete, this update will provide even greater opportunities for the analysis of stressor exposure across LPD vertebrate populations; allowing a more in-depth comprehension of how populations are affected my multiple stressors and revealing how best to target remedial action.

3.5 Alternative approaches

Our study used generalized linear mixed effects models, one for each group, subset by taxonomic class and ecological system freshwater, marine and terrestrials, with the general structure:

Number of Stressors ~ Body Size + Latitude + (Species / Genus)

Various interactive terms were also specified to account for interactive influences between fixed effect variables. However, GLMMs are not the only valid method which could have been utilised in this study.

3.5.1 Generalised Additive Models

Generalised additive models have enjoyed extensive use in ecological research (Guisan, Edwards, & Hastie, 2002), and represent a simple alternative to GLMMs. Whilst permitting greater flexibility and power in some instances by allowing the data (rather than the model) to dictate the shape of the response, the 'additive' component of their structure means that the estimation of interactive terms is not possible (Roca-Pardiñas et al., 2005). Considering that dredge-selected candidate models, including some selected for final analysis, consistently specified interactive terms, our analysis certainly benefitted from the enhanced capability of GLMMs with interactive conditions. Moreover, with the capacity to include spines within specific variables, GLMMS provide the flexibility to predict non-linear relationships whilst maintaining a simple structure with interactive terms.

It could also be noted that the 'generalised' aspect of the models utilised a comparatively uncommon probability distribution family - truncated Conway-Maxwell Poisson. Whilst several, more common, distribution families were capable of analysing similar discrete count data (e.g., Poisson, negative binomial, binomial, generalised Poisson, Brooks et al. 2017), use of the truncated Conway-Maxwell Poisson family greatly improved model fit, including residual diagnostics and estimated R^2 values, with a dataset that proved considerably difficult to fit.

Finally, the use of random effects, although essentially optional, accounts for heterogeneity hidden within latent variables not used as fixed effects within model composition (Chen & Dunson, 2003). In this case, the non-independence displayed within phylogenetic levels warrants the use of hierarchical random effects within our model structure. Hence our random effects were structured with species nested within genus (Species / Genus), resulting in significantly enhanced AIC values, and providing final models with the data needed to better inform genera with fewer species nested within them.

3.5.2 Bayesian Inference

An increasingly common alternative to generalised models is Bayesian inference, which uses expert knowledge, or 'prior' information to fit data to models (Gelman et al., 2013). These priors comprise probability distributions representing what is already known about a focal parameter (Gelman et al., 2013). This prior distribution is then used to generate a posterior probability distribution able to produce a measure of the 'degree of belief', which can be placed on hypotheses, models, or parameter estimates (Ellison, 2004).

With *p*-values generating some discord amongst researchers (Lu & Belitskaya-Levy, 2015), Bayesian frameworks offer an alternative by eliminating the all-or-nothing results based on arguably arbitrary significance values (Buchinsky & Chadha, 2017; Murtaugh, 2014). Rather, Bayesian analysis relies on a gradient based on the degree of belief, which may be able to provide more nuanced and sophisticated interpretations whilst quantifying uncertainty (Bernardo & Smith, 2008).

Though the use of specialist knowledge itself might be considered a great advantage of Bayesian techniques, it could be argued that development of priors in this way is also a disadvantage (Goldstein, 2006). Although priors are able to make use of expertise relevant to specific parameters, by definition they will also include a degree of subjectivity which may bias outcomes (Ellison, 2004). Moreover, the construction of appropriate Bayesian priors necessitates comprehensive understanding of what is meant by their distributions, lest they become inconsistent or overly precise (Walters & Ludwig, 1994). Bayesian techniques are also notorious for being computationally intensive, particularly if datasets are large, or where multiple variables are being examined (Reichert & Omlin, 1997), an aspect which may limit their use where research time is at a premium.

As 14 models were fit in this study, the development of prior distributions for each would have required significant investment in both the research and formulation of well justified priors. Although the 'degree of belief' concept may have provided more nuanced understanding of stressor number forecasts, the computational and temporal requirements would have proved prohibitive given the number of models implemented, and in-depth knowledge required for the fitting of each.

3.6 Future Steps

This study examined the *number* of threats that populations are exposed to, identifying factors which may affect the probability of a species being exposed to multiple stressors. With research generally determining that larger species are more prone to exploitative practices in latitudes comprising high human population density (Cardillo et al., 2004), it would be interesting to explore whether this is reflected within the LPD, or whether smaller species are more likely affected by certain stressors or combinations of stressors. The reduction in dispersal ability and relatively large surface area would suggest vulnerabilities to climate change pressures in smaller taxa, but it has never been explored where stressor data is directly applicable to corresponding populations. As such, might body size and / or latitude predict the *type* of stressor encountered by populations within the LPD? Whilst our work provides a simple approach to predicting the number of anthropogenic threats, the study of stressor category may prove fruitful in future research; particularly if utilising the LPD, which is explicit in population stressor exposure type.

Body mass was used as a predictor in this study due to its common availability and use as a proxy for numerous related traits; moreover, its universality allows the comparison of groups across taxa and ecological system. Yet there further exists the possibility to explore alternative species traits as predictors of stressor number, for which this study now provides a flexible foundation to achieve. Hme range sizes, trophic position and measures of fecundity are just some of the universal characteristics which could be utilised in the same way as body mass has been in this study. Though, if such studies are undertaken, data availability may well be a constraint for large scale research, with some taxa and locations suffering data deficiencies, with resulting under- and over-representations potentially restricting output.

Although latitude provides a helpful predictor of stressor number, humanity has such strong influences on stressors and their spatiotemporal distributions (Maxwell et al., 2013) that the use of alternative anthropogenic parameters is suggested for investigation. As well as furthering our understanding of the underlying drivers of stressor number in space and time, this would provide greater appreciation of the cross-disciplinary collaboration required to solve the current biodiversity crisis. These parameters may include widely available measures such as gross domestic product (GDP), distance from human settlements, population density, dietary trends, age demographics or corruption levels, amongst others.

The LPD includes vertebrate population records largely between 1970 and the current day (McRae et al., 2017). While this can be a limitation in some capacities - its baseline does not represent that prior to the onset of industrialisation and the great impacts on biodiversity it brought - it will continue to provide measures of a world changing faster than at any other point in history. To this end, an interesting area for future study might be the exploration of changes in stressor number and / or type between 1970 and the current day, with the ongoing monitoring of stressor change a further option. Given that the global human population has increased by 5.1 billion since 1950 alone (United Nations, 2019), it may be assumed that stressors have increased alongside human expansion; yet an exploration of stressors by class, system, trophic level, location, etc. would provide greater context for these changes and enhance our ability to forecast the potential impacts on biodiversity in the future.

3.7 Conclusion

If human population growth maintains its recent historical trajectory, we will see ever-greater impacts on biodiversity and detrimental change to habitats. As such, we are presented with a growing need to identify species at greatest risk from anthropogenic threats before their populations decline beyond recovery. Our demonstration of body mass and latitude as predictors of stressor number provides the ability to forecast stressor number without the need for costly field work by facilitating the appraisal of population risk *ex situ*. We provide a flexible framework, capable of differentiation at both taxonomic and ecosystem levels whilst utilising commonly available spatial, and species trait data to predict stressor number. In doing so, conservation funding can be liberated from costly and challenging survey efforts, and investments redirected towards safeguarding those species identified as high-risk by allowing closer inspection of multiple stressor risk.

Some may find the definitive solution to multiple stressor impacts challenging to concede; for, unless humanity can prioritise the planet's future by minimising population growth and making significant changes to its eating habits, we will continue to see species falling into extinction. In the midst of a global pandemic caused by the consumption of unregulated bush meat, it would be reasonable to assume such changes are on the horizon. Yet our failure to meet any one of the 2020 Aichi Biodiversity Targets (Convention on Biological Diversity, CBD, 2020) emphasises the distance we have yet to cover. Until comprehensive and wide-ranging changes to policy are implemented to counter species loss on a global scale, larger species will continue to bear the brunt of our actions. Some may argue that such strategies will not become viable until financial incentives are in place, or until economic risks arise due to the loss of biodiversity. But with global human population growth now forecast to drop dramatically by the end of the century, there remains some hope that all is not yet lost.

List of Abbreviations

EEA	European Waters Assessment
EPA	Environmental Protection Agency
WWF	World Wide Fund for Nature
LPD	The Living Planet Database
CBD	Convention on Biological Diversity
IUCN	International Union for the Conservation of Nature
SVL	Snout to Vent Length
TL	Total Length
SL	Standard Length
FL	Fork Length
GLMM	Generalised Linear Mixed Model
VIF	Variance Inflation Factor
AICc	Corrected Akaike Information Criterion
GDP	Gross Domestic Product

Equations

$\boldsymbol{W = a\ L^b}$ Allometric regression equation used to estimate body mass where only body length data is available. Priors are clade or species-specific.

Where W = body mass; L = length; a = intercept prior of a regression line over log-transformed weight-at-length data; b = slope prior of a regression line over log-transformed weight-at-length data.

Supplementary Information

Table S1 | Body Mass / Length Sources

This sheet includes all sources of body mass data used within the study, plus measurements used in allometric mass / length equation calculations

Data	**Measurement**	**Reference**
Amniote	Body Mass	Nathan P. Myhrvold, Elita Baldridge, Benjamin Chan, Dhileep Sivam, Daniel L. Freeman, S. K. Morgan Ernest. 2015. An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles. Ecology 96: 3109
AmphiBIO	Body Mass	Oliveira, B., São-Pedro, V., Santos-Barrera, G. et al. AmphiBIO, a global database for amphibian ecological traits. Sci Data 4, 170123 (2017)
Atelopus longirostris	Body mass	Elicio Eladio Tapia, Luis Aurelio Coloma, Gustavo Pazmiño-Otamendi & Nicolás Peñafiel (2017) Rediscovery of the nearly extinct longnose harlequin frog Atelopus longirostris (Bufonidae) in Junín, Imbabura, Ecuador, Neotropical Biodiversity, 3: 1, 157-167, DOI: 10.1080/23766808.2017.1327000
Chalcorana (Rana) chalconota	SVL	Robert F. Inger, Bryan L. Stuart, Djoko T. Iskandar, Systematics of a widespread Southeast Asian frog, Rana chalconota (Amphibia: Anura: Ranidae), Zoological Journal of the Linnean Society, Volume 155, Issue 1, January 2009, Pages 123–147, https://doi.org/10.1111/j.1096-3642.2008.00440.x
Elton Traits	Body Mass	Smith et al 2003, Dunning 2007 – see Elton traits metadata
Encyclopedia of Life	Body Mass	Parr, C. S., N. Wilson, P. Leary, K. S. Schulz, K. Lans, L. Walley, J. A. Hammock, A. Goddard, J. Rice, M. Studer, J. T. G. Holmes, and R. J. Corrigan, Jr. 2014. The Encyclopedia of Life v2: Providing Global Access to Knowledge About Life on Earth. Biodiversity Data Journal 2: e1079, doi:10.3897/BDJ.2.e1079
Fishbase	Length (TL / FL / SL)	Froese R. & Pauly D. (eds). (2020). FishBase (version Feb 2018). In: Species 2000 & ITIS Catalogue of Life, 2020-09-01 Beta (Roskov Y.; Ower G.; Orrell T.; Nicolson D.; Bailly N.; Kirk P.M.; Bourgoin T.; DeWalt R.E.; Decock W.; Nieukerken E. van; Penev L.; eds.). Digital resource at www.catalogueoflife.org/col. Species 2000: Naturalis, Leiden, the Netherlands. ISSN 2405-8858.
Handbook of the Birds of the World Alive	Body Mass	S. M. Billerman, B. K. Keeney, P. G. Rodewald, and T. S. Schulenberg (Editors) (2020). Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA. https://birdsoftheworld.org/bow/home

Leiopelma archeyi	Body mass	Stark, G, Meiri, S. Cold and dark captivity: Drivers of amphibian longevity. Global Ecol Biogeogr. 2018; 27: 1384– 1397. https: //doi.org/10.1111/geb.12804
Litoria australis **aka** ***Ranoidea australis, Litoria dahlia*** **aka** ***Ranoidea dahlii, Ranoidea genimaculata*** **aka** ***Litoria genimaculata***	SVL	Vanderduys, E. (2019). Field Guide to the Frogs of Queensland. In Field Guide to the Frogs of Queensland. doi: 10.1071/9780643108790
Litoria nannotis **aka** ***Ranoidea nannotis***	Body mass	Liem, D.S. (1974). A review of the Litoria nannotis species group and a description of a new species of Litoria from north-east Queensland, Australia. Memoirs of the Queensland Museum 17(1), 151-168. Cogger, H.G. (1994). Reptiles and Amphibians of Australia. Reed Books, Sydney. McDonald, K.R. & Alford, R.A. (1999). A Review of Declining Frogs in Northern Queensland. Pp 14-22 in A. Campbell (ed), Declines and Disappearances of Australian Frogs. Environment Australia, Canberra. 234 pp.
Myotis escalerai	Body mass	Quetglas, J. (2016). Murciélago ratonero ibérico – Myotis escalerai. En: Enciclopedia Virtual de los Vertebrados Españoles. Salvador, A., Barja, I. (Eds.). Museo Nacional de Ciencias Naturales, Madrid.
PanTHERIA	Body Mass	Kate E. Jones, Jon Bielby, Marcel Cardillo, Susanne A. Fritz, Justin O'Dell, C. David L. Orme, Kamran Safi, Wes Sechrest, Elizabeth H. Boakes, Chris Carbone, Christina Connolly, Michael J. Cutts, Janine K. Foster, Richard Grenyer, Michael Habib, Christopher A. Plaster, Samantha A. Price, Elizabeth A. Rigby, Janna Rist, Amber Teacher, Olaf R. P. Bininda-Emonds, John L. Gittleman, Georgina M. Mace, and Andy Purvis. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90: 2648.
Rana tavasensis	SVL	Düşen, S. (2012). First data on the helminth fauna of a locally distributed mountain frog, "Tavas frog" Rana tavasensis Baran & Atatür, 1986 (Anura: Ranidae), from the inner-west Anatolian region of Turkey. Turkish Journal of Zoology, 36, 496-502.
Trachycephalus venulosus	Body mass	Domingos J. Rodrigues, Masao Uetanabaro & Frederico S. Lopes (2005) Reproductive patterns of Trachycephalus venulosus (Laurenti, 1768) and Scinax

		fuscovarius (Lutz, 1925) from the Cerrado, Central Brazil, Journal of Natural History, 39: 35, 3217-3226, DOI: 10.1080/00222930500312244
Various amphibian	Body Mass	Santini L., Benítez-López A., Ficetola G.F., Huijbregts M.A.J. 2017. Length – Mass allometries in Amphibians. Integrative Zoology, 13: 36-45. doi:10.1111/1749-4877.12268
Various amphibian	Body mass	Stark, G, Pincheira-Donoso, D, Meiri, S. No evidence for the 'rate-of-living' theory across the tetrapod tree of life. Global Ecol Biogeogr. 2020; 00: 1– 28. https://doi.org/10.1111/geb.13069
Various amphibian	SVL	AmphibiaWeb. 2020. <https://amphibiaweb.org> University of California, Berkeley, CA, USA.
Various amphibians	Body Mass	Trochet A, Moulherat S, Calvez O, Stevens V, Clobert J, Schmeller D (2014) A database of life-history traits of European amphibians. Biodiversity Data Journal 2: e4123.
Various avian	Body Mass	Terje Lislevand, Jordi Figuerola, and Tamás Székely. 2007. Avian body sizes in relation to fecundity, mating system, display behavior, and resource sharing. Ecology 88: 1605
Various avian	Body Mass	Renner, S.C.; Hoesel, W. Ecological and Functional Traits in 99 Bird Species over a Large-Scale Gradient in Germany. Data 2017, 2, 12.
Various mammals	Body Mass	Smith, F.A., Lyons, S.K., Ernest, S.K.M., Jones, K.E., Kaufman, D.M., Dayan, T., Marquet, P.A., Brown, J.H. and Haskell, J.P. (2003), Body mass of late quaternary mammals. Ecology, 84: 3403-3403.
Various primates	Body Mass	Galán-Acedo, C., Arroyo-Rodríguez, V., Andresen, E. et al. Ecological traits of the world's primates. Sci Data 6, 55 (2019) doi: 10.1038/s41597-019-0059-9
Various vertebrates	Body Mass	Anthony I. Dell, Samraat Pawar, Van M. Savage. 2013. The thermal dependence of biological traits. Ecology 94: 1205.

Table S2 | Terrestrial model coefficients

Estimates for all terrestrial classes, including those for splined latitude variable. Estimates in **bold** denote those included and fully discussed within the main text. Other estimates are included here, but not within the main text, due to their being uninterpretable.

Terrestrial	*Estimate (ß)*	*SE*	*Lower CI*	*Upper CI*	*p-value*
Birds					
(Intercept)	**-1.550**	**0.274**	**-2.087**	**-1.013**	**0.045**
Body Mass	**0.173**	**0.049**	**0.076**	**0.270**	**0.000**
Latitude (1)	0.822	0.316	0.202	1.441	0.009
Latitude (2)	-1.203	0.325	-1.839	-0.566	0.000
Latitude (3)	2.759	0.685	1.417	4.101	0.000
Latitude (4)	0.376	0.542	-0.686	1.438	0.488
Body Mass: Latitude (1)	-0.091	0.055	-0.199	0.018	0.102
Body Mass: Latitude (2)	0.119	0.052	0.017	0.220	0.022
Body Mass: Latitude (3)	-0.413	0.123	-0.654	-0.171	0.001
Body Mass: Latitude (4)	-0.010	0.082	-0.170	0.150	0.905
Mammals					
(Intercept)	**-1.340**	**0.150**	**-1.633**	**-1.046**	**0.023**
Body Mass	**0.049**	**0.009**	**0.031**	**0.067**	**0.000**
Latitude (1)	0.838	0.117	0.609	1.067	0.000
Latitude (2)	-0.010	0.119	-0.243	0.224	0.936
Latitude (3)	0.638	0.295	0.060	1.217	0.031
Latitude (4)	-0.106	0.132	-0.364	0.152	0.420
Amphibians					
(Intercept)	**-0.031**	**0.220**	**-0.462**	**0.401**	**0.000**
Body Mass	**-0.137**	**0.083**	**-0.298**	**0.025**	**0.097**
Reptiles					
(Intercept)	**0.020**	**0.164**	**-0.302**	**0.342**	**0.000**
Body Mass	**0.026**	**0.014**	**-0.001**	**0.054**	**0.059**
Latitude (1)	-0.240	0.226	-0.684	0.203	0.289
Latitude (2)	0.049	0.129	-0.203	0.301	0.704
Latitude (3)	-1.170	0.462	-2.075	-0.265	0.011
Latitude (4)	-0.330	0.220	-0.761	0.100	0.133

Table S3 | Marine model coefficients

Estimates for all marine classes, including those for splined latitude variable. Estimates in **bold** denote those included and fully discussed within the main text. Other estimates are included here, but not within the main text, due to their being uninterpretable.

Marine	*Estimate (ß)*	*SE*	*Lower CI*	*Upper CI*	*p-value*
Birds					
(Intercept)	**-3.722**	**1.968**	**-7.579**	**0.135**	**0.167**
Body Mass	**0.279**	**0.228**	**-0.168**	**0.726**	**0.221**
Latitude (1)	2.293	1.981	-1.589	6.175	0.247
Latitude (2)	4.197	1.584	1.092	7.301	0.008
Latitude (3)	4.931	3.770	-2.458	12.319	0.191
Latitude (4)	0.768	0.991	-1.175	2.710	0.438
Body Mass: Latitude (1)	-0.108	0.236	-0.571	0.355	0.648
Body Mass: Latitude (2)	-0.466	0.191	-0.841	-0.092	0.015
Body Mass: Latitude (3)	-0.299	0.439	-1.160	0.562	0.496
Body Mass: Latitude (4)	-0.023	0.133	-0.284	0.238	0.865
Mammals					
(Intercept)	**-0.367**	**0.377**	**-1.105**	**0.371**	**0.093**
Body Mass	**0.005**	**0.029**	**-0.052**	**0.061**	**0.871**
Reptiles					
(Intercept)	**-0.458**	**0.318**	**-1.081**	**0.164**	**0.088**
Body Mass	**0.000**	**0.026**	**-0.050**	**0.050**	**0.999**
Latitude (1)	0.061	0.151	-0.235	0.357	0.686
Latitude (2)	0.561	0.167	0.233	0.889	0.001
Latitude (3)	0.911	0.279	0.363	1.458	0.001
Latitude (4)	-0.320	0.116	-0.548	-0.092	0.006
Bony Fish					
(Intercept)	**0.367**	**0.542**	**-0.695**	**1.430**	**0.012**
Body Mass	**-0.102**	**0.060**	**-0.219**	**0.016**	**0.090**
Latitude (1)	-0.048	0.507	-1.041	0.945	0.924
Latitude (2)	-1.163	0.428	-2.002	-0.324	0.007
Latitude (3)	-2.886	1.173	-5.185	-0.586	0.014
Latitude (4)	-0.461	0.348	-1.143	0.222	0.186
Body Mass: Latitude (1)	0.031	0.057	-0.081	0.142	0.588
Body Mass: Latitude (2)	0.114	0.049	0.018	0.210	0.020
Body Mass: Latitude (3)	0.326	0.131	0.070	0.583	0.013
Body Mass: Latitude (4)	0.034	0.043	-0.051	0.118	0.432
Cartilaginous Fish					
(Intercept)	**-0.311**	**0.127**	**-0.560**	**-0.062**	**0.000**
Body Mass	**0.035**	**0.010**	**0.014**	**0.055**	**0.001**

Latitude (1)	-0.281	0.118	-0.511	-0.050	0.017
Latitude (2)	-0.233	0.084	-0.398	-0.067	0.006
Latitude (3)	-1.073	0.238	-1.540	-0.606	0.000
Latitude (4)	-0.349	0.125	-0.594	-0.103	0.005

Table S4 | Freshwater model coefficients

Estimates for all freshwater classes, including those for splined latitude variable. Estimates in **bold** denote those included and fully discussed within the main text. Other estimates are included here, but not within the main text, due to their being uninterpretable.

Freshwater	*Estimate (ß)*	*SE*	*Lower CI*	*Upper CI*	*p-value*
Birds					
(Intercept)	**-0.556**	**0.184**	**-0.917**	**-0.195**	**0.016**
Body Mass	**-0.016**	**0.018**	**-0.051**	**0.020**	**0.398**
Latitude (1)	0.636	0.144	0.354	0.918	0.000
Latitude (2)	-0.220	0.120	-0.455	0.015	0.066
Latitude (3)	0.901	0.441	0.037	1.765	0.041
Latitude (4)	0.589	0.186	0.225	0.954	0.002
Mammals					
(Intercept)	**-2.308**	**0.629**	**-3.541**	**-1.076**	**0.038**
Body Mass	**0.111**	**0.045**	**0.022**	**0.200**	**0.015**
Latitude (1)	1.022	0.305	0.424	1.621	0.001
Latitude (2)	0.104	0.405	-0.690	0.899	0.797
Latitude (3)	2.665	0.784	1.129	4.201	0.001
Latitude (4)	0.440	0.255	-0.060	0.939	0.084
Bony Fish					
(Intercept)	**-0.383**	**0.308**	**-0.986**	**0.220**	**0.045**
Body Mass	**-0.052**	**0.042**	**-0.135**	**0.030**	**0.213**
Latitude (1)	0.859	0.367	0.139	1.579	0.019
Latitude (2)	-0.673	0.304	-1.270	-0.077	0.027
Latitude (3)	-0.070	0.804	-1.647	1.507	0.931
Latitude (4)	2.158	0.474	1.229	3.086	0.000
Body Mass: Latitude (1)	-0.032	0.047	-0.124	0.059	0.489
Body Mass: Latitude (2)	0.092	0.036	0.021	0.162	0.011
Body Mass: Latitude (3)	0.133	0.109	-0.081	0.347	0.225
Body Mass: Latitude (4)	-0.294	0.053	-0.398	-0.190	0.000
Amphibians					
(Intercept)	**-2.203**	**1.333**	**-4.815**	**0.408**	**0.366**
Body Mass	**0.781**	**0.462**	**-0.125**	**1.687**	**0.091**
Latitude (1)	-0.427	1.250	-2.877	2.023	0.733
Latitude (2)	4.456	0.949	2.596	6.317	0.000
Latitude (3)	2.126	3.634	-4.995	9.247	0.558
Latitude (4)	-11.502	3.383	-18.132	-4.873	0.001
Body Mass: Latitude (1)	-0.199	0.436	-1.053	0.654	0.647

Body Mass: Latitude (2)	-1.089	0.277	-1.631	-0.546	0.000
Body Mass: Latitude (3)	-1.896	1.217	-4.280	0.489	0.119
Body Mass: Latitude (4)	2.591	0.730	1.159	4.022	0.000
Reptiles					
(Intercept)	**0.200**	**0.256**	**-0.303**	**0.702**	**0.000**
Body mass	**0.013**	**0.017**	**-0.021**	**0.046**	**0.460**
Latitude (1)	-0.434	0.241	-0.905	0.038	0.072
Latitude (2)	0.065	0.203	-0.334	0.463	0.751
Latitude (3)	-1.082	0.492	-2.047	-0.117	0.028
Latitude (4)	0.248	0.170	-0.085	0.581	0.145

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