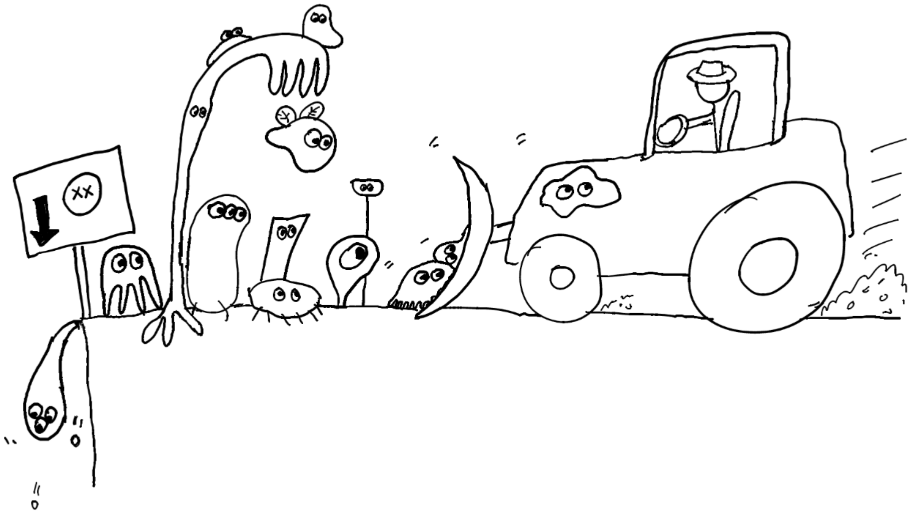
*Finnish Museum of Natural History (LUOMUS)*
*Doctoral Programme in Wildlife Biology (LUOVA)*
*Faculty of Biological and Environmental Sciences*
*University of Helsinki*

# TRAIT-BASED PREDICTION OF EXTINCTION RISK



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DOCTORAL DISSERTATION

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# ABSTRACT

Species are declining and going extinct at unprecedented rates due to human activity. Understanding the drivers of extinction may help conservationists to proactively protect the species most in need. Species' vulnerability to extinction has been hypothesised to be related to both their intrinsic biological traits and external human factors, often in synergy. In the past twenty years, many studies have compared the traits of threatened species to those of non-threatened species, within taxonomic groups. However, the literature in the topic has often focussed on few taxa or geographical realms, which has limited our capacity to find and understand general predictors and mechanisms of extinction.

The primary aim of this dissertation is to identify which traits are related with extinction risk across the generality of life forms and geographical realms. To do so, I have applied a set of three distinct approaches: in Chapter I, I have identified gaps in research and synthesised past literature using a meta-analytical approach. Given the identified gaps and biases, in Chapter II I compiled a dataset including species from all realms and 15 taxonomic groups, to find predictors of extinction risk across taxa. Because traits and human threats are likely to interact, in Chapter III, I have implemented, tested, and analysed a virtual conceptual model to understand how different traits interact with the different threats to increase the extinction risk of species.

The literature review of Chapter included 173 publications with most studies focussing on either mammal or bird taxa. The spatial extent of studies has also been narrow, with a very strong focus on the Palaearctic realm, particularly for invertebrate and plant groups. Body size was the most studied trait, followed by geographical range and fecundity. Among the top 10% studied traits, geographical range size had the greatest percentage of significant relationships with extinction risk. Meta-analyses were possible for geographical range size, habitat breadth and body size, with the first two being negatively related to extinction risk, and the third showing no consistent effect.

In Chapter II, I compiled and analysed trait-extinction risk relationships for 10 traits, with a dataset consisting of 874 species evenly sampled from 15 taxonomic groups ranging from vertebrates, invertebrates, and plants. I identified narrow habitat breadth as a universal predictor of extinction risk across vertebrates, invertebrates, and plants. Long generation length, low fecundity, and large offspring size - characteristic of species with slow life cycles - and small climatic breadth were also identified as general predictors, but available data was limited and therefore results are not conclusive for these traits. Poor dispersal ability is a general predictor among invertebrates and plants, but not among vertebrates. The remaining traits (body size, microhabitat verticality, trophic level, and diet breadth) showed contrasting responses depending on the taxa.

In the third Chapter, my aim was to understand how different anthropogenic drivers may impact species with different traits. I built a conceptual agent-based model with virtual organisms competing in a virtual environment for resources, upon which I simulated human threats. My model simulations showed that traits and threats interact in predictable ways. Namely, threats that directly increase the mortality of individuals - direct killing- have a higher impact on organisms with slow life cycles and poor dispersal ability. Threats decreasing the amount of habitat - habitat loss and fragmentation- negatively affect large sized, poorly fecund organisms. The effect on dispersal ability depends on the spatial configuration of the threat. Finally, threats decreasing habitat quality or the amount of resources available to organisms - habitat degradation and invaders - severely affect large, fast-lived, and highly fecund organisms.

For a clearer picture on which traits predispose species to extinction, more data should be collected on underrepresented groups and regions, such as invertebrates, plants, and fungi in the tropics. Despite this shortcoming, in this thesis I demonstrate that some traits predispose species to and can be used as predictors of extinction. Species with narrow geographical and habitat breadths, two of the classical dimensions of rarity, are more at risk. Slow life cycles and narrow climatic breadths should also drive greater extinction risk. Other traits do not seem to have a general response but are taxon-dependent. Finally, intrinsic traits must in the future be studied considering anthropogenic threat types, as these two dimensions interact to drive species extinctions.

# TIIVISTELMÄ

Lajit vähenevät ja kuolevat sukupuuttoon ennennäkemättömällä nopeudella ihmisen toiminnan vuoksi. Sukupuuttoon johtavien syiden ymmärtäminen voi auttaa luonnonsuojelijoita suojelemaan uhanalaisimpia lajeja ennaltaehkäisevästi. Kuinka ja miksi eri lajit kuolevat herkemmin sukupuuttoon kuin toiset on oletettu liittyvän sekä lajien sisäisiin biologisiin ominaisuuksiin että ulkoisiin, ihmisistä riippuviin tekijöihin. Viimeisten 20 vuoden aikana monissa tutkimuksissa on verrattu uhanalaisten lajien ominaisuuksia ei-uhanalaisten lajien ominaisuuksiin eri taksonien sisällä. Aiheeseen liittyvä kirjallisuus on keskittynyt kuitenkin usein vain muutamaan taksoniin tai maantieteelliseen alueeseen, mikä on rajoittanut kykyämme löytää ja ymmärtää yleisiä, sukupuuttoon liittyviä ennusmerkkejä ja mekanismeja.

Tutkielmani ensisijainen tavoite on tunnistaa, mitkä ominaisuudet liittyvät sukupuuttoriskiin kaikki elämänmuodot ja maantieteelliset alueet huomioiden. Tätä varten olen soveltanut kolmea erilaista lähestymistapaa: luvussa I olen tunnistanut aukkoja tutkimuksessa ja yhdistänyt aiemman kirjallisuuden tuloksia käyttämällä meta-analyyttista lähestymistapaa. Tunnistetut aukot ja vinoumat huomioiden olen luvussa II koonnut tietoaineiston, joka sisältää lajeja kaikilta alueilta ja 15 taksonomisesta ryhmästä selkärankaisten, selkärangattomien ja kasviryhmien joukosta, löytääkseni sukupuuttoriskin ennusmerkkejä eri taksoneissa. Koska lajiominaisuudet ja ihmisten aiheuttamat uhat ovat todennäköisesti vuorovaikutuksessa, olen luvussa III soveltanut, testannut ja analysoinut virtuaalista käsitemallia ymmärtääkseni, kuinka eri ominaisuudet ovat vuorovaikutuksessa eri uhkien kanssa kasvattaen lajien sukupuuttoriskiä.

Aiempaan kirjallisuuteen tutustuminen vahvisti, että suurin osa tutkimuksista on keskittynyt nisäkkäisiin tai lintuihin, ja erityisesti selkärangattomien tai kasvien kohdalla ne ovat maantieteellisesti rajoittuneet palearktiseen alueeseen. Ylivoimaisesti eniten tutkittu ominaisuus oli ruumiinkoko, mitä seurasivat maantieteellinen alue ja hedelmällisyys. 10 prosentissa eniten tutkituista ominaisuuksista maantieteellisen levinneisyysalueen koko oli prosentuaalisesti merkittävin sukupuuttoriskiin vaikuttava seikka. Meta-analyysit olivat mahdollisia maantieteellisen levinneisyysalueen koon, elinympäristön laajuuden ja ruumiinkoon osalta. Kaksi ensimmäistä vaikuttivat negatiivisesti sukupuuttoriskiin, kolmannella ei puolestaan näyttänyt olevan johdonmukaista vaikutusta.

Luvussa II kokosin ja analysoin ominaisuuksien ja sukupuuttoriskin suhdetta 10 ominaisuuden osalta. Tietoaineisto koostui 874 lajista, jotka on valittu tasaisesti 15 taksonomisesta, selkärankaisten, selkärangattomien ja kasvien ryhmästä. Havaitsin suppean elinympäristön olevan yleinen sukupuuttoriskin ennusmerkki niin selkärankaisten, selkärangattomien kuin

kasvienkin kohdalla. Pitkä sukupolviväli, alhainen hedelmällisyys ja jälkeläisten suuri koko – mikä on ominaista lajeille, joiden elinkaari on hidas – sekä pieni ilmastollinen levinneisyys, vaikuttivat myös olevan yleisiä ennusmerkkejä. Tietoja oli käytettävissä kuitenkin rajoitetusti, joten tulokset eivät ole ratkaisevia näiden ominaisuuksien osalta. Selkärangattomien ja kasvien joukossa huono leviämiskyky oli yleinen ennusmerkki. Näin ei kuitenkaan ollut selkärankaisten keskuudessa. Jäljellä olevat ominaisuudet (ruumiinkoko, mikroelinympäristön vertikaalisuus, trofiataso ja ruokavalion laajuus) viittasivat päinvastaisiin tuloksiin taksonista riippuen.

Kolmannessa luvussa tavoitteeni oli ymmärtää, kuinka erilaiset ihmisen aiheuttamat tekijät mahdollisesti vaikuttavat ominaisuuksiltaan erilaisiin lajeihin. Rakensin käsitteellisen, ainepohjaisen mallin, jossa virtuaaliset organismit kilpailevat resursseista virtuaalisessa ympäristössä ihmisten aiheuttamien uhkien ollessa läsnä. Mallisimulaationi osoittivat, että ominaisuudet ja uhat vaikuttavat toisiinsa ennustettavalla tavalla. Yksilöiden kuolleisuutta suoraan lisäävät uhat – suora tappaminen – vaikuttavat nimittäin enemmän sellaisiin organismeihin, joiden elinkaari on hidas ja leviämiskyky huono. Elinympäristöä pienentävät uhat – elinympäristön häviäminen ja pirstoutuminen – vaikuttavat negatiivisesti suurikokoisiin ja heikosti lisääntyviin organismeihin. Vaikutus leviämiskykyyn riippuu uhan spatiaalisesta rakenteesta. Elinympäristön laatua tai organismien käytettävissä olevien resurssien määrää heikentävät uhat – elinympäristön rappeutuminen ja vieraslajit – vaikuttavat erittäin paljon suurikokoisiin ja tehokkaasti lisääntyviin organismeihin, joiden elinkaari on nopea.

Jotta saataisiin selkeämpi kuva siitä, mitkä ominaisuudet altistavat lajit sukupuuttoon kuolemiselle, pitäisi kerätä enemmän tietoa aliedustetuista ryhmistä ja alueista, kuten tropiikissa elävistä selkärangattomista, kasveista ja sienistä. Tästä vajavaisuudesta huolimatta osoitan tässä tutkielmassa, että tietyt ominaisuudet altistavat lajeja sukupuutolle ja että näitä ominaisuuksia voidaan käyttää ennustavina tekijöinä. Lajit, joiden maantieteellinen levinneisyys ja elinympäristö ovat suppeita, eli kaksi klassista, harvinaisuutta kuvaavaa piirrettä, ovat suuremmassa vaarassa. Myös elinkaareltaan hitaiden ja suppeilla ilmastoalueilla asuvien lajien sukupuuttoriski on suurempi. Muilla ominaisuuksilla ei näytä olevan yleistä vaikutusta, vaan ne riippuvat taksoneista. Luontaisia ominaisuuksia on tulevaisuudessa tutkittava antropogeeniset uhkatyypit huomioiden, koska nämä kaksi tekijää vaikuttavat yhdessä lajien sukupuuttoon.

# LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications:

I Chichorro, F., Juslén, A., Cardoso, P., 2019. A review of the relation between species traits and extinction risk. Biological Conservation 237: 220–229. https://doi.org/10.1016/j.biocon.2019.07.001

II Chichorro, F., Urbano, F., Teixeira, D., Väre, H., Pinto, T., Brummitt, N., He, X., Hochkirch, A., Hyvönen, J., Kaila, L., Juslén, A., Cardoso, P., 2022. Trait-based prediction of extinction risk across terrestrial taxa. Biological Conservation 274: 109738. https://doi.org/10.1016/j.biocon.2022.109738

III Chichorro, F., Correia, L., Cardoso, P., 2022. Biological traits interact with human threats to drive extinctions: A modelling study. Ecological Informatics 69: 101604. https://doi.org/10.1016/j.ecoinf.2022.101604

The publications are referred to in the text by their roman numerals.

# AUTHOR CONTRIBUTIONS

| | I | II | III |
|---|---|---|---|
| Original idea | FC PC | PC | PC |
| Study design | FC PC AJ | FC PC AJ | FC PC LC |
| Data collection and preparation | FC | AH AJ DT FC FU HV JH LK NB PC TP XH | FC |
| Data analysis | FC AJ PC | FC PC | FC LC PC |
| Manuscript preparation | FC PC | FC PC | FC PC |
| Supplementary material preparation | FC | FC | FC |

AH = Axel Hochkirch, AJ = Aino Juslén, DT = Dinarte Teixeira, FC = Filipe Chichorro, FU = Fernando Urbano, HV = Henry Väre, JH = Jaakko Hyvönen, LC = Luís Correia, LK = Lauri Kaila, NB = Neil Brummitt, PC = Pedro Cardoso, TP = Tiago Pinto, XH = Xiaolan He.

# ABBREVIATIONS

| | |
|---|---|
| etc. | *et cetera* – and so on |
| i.e. | *id est* – that is |
| e.g. | *exempli gratia* – for example |
| *et al.* | *et alia* – and others |
| ABM | Individual- or Agent-based model |
| GLMM | Generalized linear mixed models |
| IPBES | Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services |
| IUCN | International Union for the Conservation of Nature |

# 1 INTRODUCTION

The current rates of extinction are unprecedented in human history (Cowie et al., 2022; De Vos et al., 2015). The latest IPBES report estimates that up to 1 million animal and plant species (of about 8.7 million total species in this planet) are threatened (IPBES, 2019). Human actions are unarguably behind this rapid biodiversity erosion, the main drivers of which are changes in land and sea use, direct exploitation of organisms, climate change, pollution, and invasive alien species (IPBES, 2019). As biodiversity is eroded, the remaining species may enter an inevitable vortex of extinctions (Strona & Bradshaw, 2018). Understanding the processes underlying extinctions may help guide conservation efforts, as it could allow more efficient use of available resources towards the ecosystems and species more at need (Cardillo et al., 2004; Purvis et al., 2000; Purvis et al., 2005).

The IUCN Red List is one of the most important resources in understanding current drivers of extinction risk at a global scale (IUCN, 2022). As of 2022, the Red List provides assessments of extinction risk for over 147 000 species of animals, fungi, and plants. In each assessment, a species' is classified into one of five categories of increasing extinction risk: Least Concern (LC), Near Threatened (NT), Vulnerable (VU), Endangered (EN), or Critically endangered (CR). In few cases extinction might already have happened, in which case the categories Extinct in the Wild (EW) and Extinct (EX) should be used. An eighth category (Data Deficient) exists when extinction risk determination is not possible due to lack of data. The criteria for classifying species in each threat level are mainly based on the species' population numbers, the size of the geographical range, and the temporal trends, including past, present, and future, in both population numbers or geographical range. Low population size or narrow geographical range sizes predispose species to greater probability of demographic or local catastrophic events, which may extirpate the whole species in a single event. Likewise, species' whose population sizes or geographical ranges have contracted over time are likely to become extinct if the population birth rates or colonisation events do not compensate for mortality rates or local extinction events. The IUCN Red List also compiles complementary data that can be used for understanding the extinction dynamics, from habitat data to current and future anthropogenic threats to species.

In addition to anthropogenic threats, the vulnerability of species to extinction may further be exacerbated by their intrinsic life-history characteristics, such as their morphological, physiological, behavioural or ecological traits (Bennett & Owens, 1997; Cardillo et al., 2008; Carmona et al., 2021; González-Suárez et al., 2013; McKinney, 1997; Owens & Bennett, 2000; Purvis et al., 2000; Purvis et al., 2005; Munstermann et al., 2021; Toussaint et al., 2021). Certain biological traits of species may disfavour them if they naturally predispose them to demographic perils. For example, species with slow life strategies, such as those that produce few offspring per reproductive event and delay maturity may be affected by threats that increase mortality rates due to their limited capacity to increase birth rates (Carmona et al., 2021; Pimm et al., 1988; Richards et al., 2021). Likewise, species adapted to a narrow ecological niche have long been hypothesised to be more at risk of extinction since they are likely not to find optimal conditions in view of environmental change (Botts et al., 2013; McKinney, 1997; Richards et al., 2021; Shuai et al., 2021; Slatyer et al., 2013). During the past 20 years, multiple studies tested many of these hypotheses (Table 1).

**Table 1.** *Examples of traits studied in the literature, definition, examples of proxies, and hypotheses.*

| Trait | Definition | Examples of traits | Hypothesis | References |
|---|---|---|---|---|
| Body size | Typical size of an adult organism. | Body mass, body length, plant height, plant mass, shell length | Larger organisms are more vulnerable because 1) they tend to have lower population densities, 2) require more resources; and 3) have slower life cycles. | Carmona et al., 2021; Purvis et al., 2000 |
| Offspring size | Typical size of an offspring. | Size at birth, egg size, seed size | Organisms with larger offspring than expected by body size are more vulnerable to extinction because offspring size is often correlated with lower fecundity and slower life cycles with less capacity to adapt to new conditions. | Purvis et al., 2000 |
| Fecundity | Reproductive output. | Number of offspring per reproductive event, number of reproductive events in a year | Species with larger fecundities can compensate for the effects of higher mortality rates, particularly in the face of changing environments. | Purvis et al., 2000; Richards et al., 2021 |
| Generation length | Typical length of the life cycle, from birth until reproduction. | Generation length, age at maturation, max longevity | Species with slow life cycles are more vulnerable to extinction, due to their weaker capacity to recover normal population numbers after a disturbance. | Carmona et al., 2021; Purvis et al., 2000; Richards et al., 2021 |

| | | | | |
|---|---|---|---|---|
| Diet breadth | Degree of narrowness of diet or of substrate used. | Number of food types ingested, diversity of prey, breadth of soil conditions | Species with narrow diet breadths are more vulnerable because they are less able to shift diets when resource abundance fluctuates or decreases. | Di Marco et al., 2015; González-Suárez et al., 2013 |
| Trophic level | Trophic position. | Herbivore/omnivore/carnivore | Organisms at higher trophic levels are more vulnerable because biomass available is reduced. Furthermore, they are affected by disturbance at lower trophic levels. | Atwood et al., 2020; Purvis et al., 2000 |
| Dispersal ability | Capacity to disperse. | Migrant? or not, dispersal speed, dispersal distance | Organisms with low dispersal ability are more vulnerable because they do not have the mechanisms to find suitable habitat around a changing environment. | Bartonova et al., 2014; Benscoter et al., 2013; Parlato et al., 2015; Saar et al., 2012 |
| Microhabitat | Typical vertical stratum occupied in a habitat. | Nest position, foraging stratum, vertical position in the water column | Organisms that occupy lower strata in a habitat are more likely to face less extinction risk because they are less dependent on other species providing them verticality (like trees, bushes, etc.). On the other hand, species living on the ground may face higher predation pressure or have less dispersal ability. Benthic organisms may be more vulnerable than those in the water column due to loss of good quality substratum and benthic vegetation. | Giam et al., 2011; Johnson & Isaac, 2009; Munstermann et al., 2021 |
| Habitat breadth | Range of habitat types occupied. | Number of habitat types | Species capable of occupying a broad range of habitats are less likely to become extinct, because they may use alternative habitats when one is reduced. | Böhm et al., 2016; Richards et al., 2021; Shuai et al., 2021 |
| Altitudinal range | Range of altitude levels occupied. | Vertical distance between lower and higher limits | Species with broader altitudinal ranges are able to adapt to different altitudinal strata (corresponding to different climatic conditions)  and shift or survive in different altitudes when conditions change. | Keane et al., 2005; Rocha-Ortega et al., 2020 |

Despite the abundance of studies on the topic, our understanding of which traits predispose species to extinction is still fragmentary and biassed. The relative importance of each trait has shown to be affected by multiple factors, which confound relationships between traits and extinction risk, such as the taxonomic group. For instance, large body size has been identified as a significant correlate of extinction risk across mammal orders such as the Carnivora and Primata (Purvis et al., 2000), and to some extent, across all mammals (Atwood et al., 2020; Cardillo et al., 2008; Carmona et al., 2021; González-Suárez et al., 2013), birds (Atwood et al., 2020; Bennett & Owens, 1997; Keane et al., 2005; Owens & Bennett, 2000; Richards et al., 2021), and some insect groups (Desender et al., 2010; Rocha-Ortega et al., 2020; Seibold et al., 2015; Sullivan et al., 2000). In these groups, their large body size is very highly correlated with other traits hypothesised to decrease resilience, such as slow life cycles (Purvis et al., 2000). But body size has also been shown to be negatively related to extinction risk in some other taxa, such as in grassland plants (Powney et al., 2014), cycads (Mankga & Yessoufou, 2017), or dragonflies (Powney et al., 2015). That is due to the association of body size with higher competitive ability for light in plants (larger plants often better compete for light), and higher dispersal ability in some insect groups (Warzecha et al., 2016).

Finally, threat type and intensity have been mostly ignored so far (Munstermann et al. 2021; Murray et al., 2014; Purvis et al., 2005). Threats and traits have long been hypothesised to interact with each other, and thus ignoring threats compromises the search for meaningful predictors. In addition, we have been looking only at the interaction term of the equation, even though the intensity of each threat is equally important, otherwise today's extinction rates would not be 1000 times higher than background rates (Purvis et al., 2005). When threats are included in extinction risk analyses, not only the explanatory power of statistical models increase, but also mechanistic pathways to extinction may be identified (Murray et al., 2014). However, the difficulty to identify and quantify threat types and their intensity has impeded their use in past studies (Murray et al., 2014; Purvis et al., 2005). High-resolution maps of human threat intensity are available at increasing detail, and thus may be used as correlates (Di Marco et al. 2018; Hansen et al., 2013; Venter et al., 2016).

There is an urgent need to synthesise the existing knowledge so that general trait-based pathways to extinction are identified. All past work has been limited in the number of putative traits influencing extinction risk, and geographical or taxonomic scopes. As for other disciplines, past research was focused on traits and settings with abundant readily available data such as geographical range size, vertebrates and the holarctic region, but the numerous gaps were never identified or quantified. A comprehensive review and identification of knowledge gaps is therefore urgently needed. A first step towards that synthesis is to identify and to quantify the gaps in research: the extent to which our knowledge may be biassed towards certain taxa or taxonomic groups, and traits. A previous review performed this exercise within mammals (Verde Arregoitia, 2016), and found biases even within this well studied group. Furthermore, meta-analytic approaches (Gurevitch et al., 2018) could be used to quantify the degree to which the different traits have shown a significant relationship with extinction risk, controlling for taxonomy and space.

Going one step further, and given the hypothesised numerous gaps in past research, general testing of trait and extinction vulnerability across multiple taxa are urgently needed. To achieve such a goal, statistical models should include data from a selection of species unbiased both in terms of taxonomic coverage and geographical location. Comprehensive analyses should also cover a wide variety of traits previously hypothesised or identified as important drivers of extinction in an integrated way, so that results are comparable across taxa. Given the recent growth in number of global trait database initiatives in recent years (Kattge et al., 2011; Madin et al., 2016; Myhrvold et al., 2015; Parr et al., 2017; Pekár et al., 2021; Soria et al., 2021; Tobias et al., 2022; Wilman et al., 2014), it is now possible to perform analyses with less biases in both taxonomic and geographical representation.

The next step, to quantify the interactions between traits and threats, requires even more unbiased data, as of now yet largely incomplete for most taxa and regions. To achieve this third goal, simulation-based approaches could be useful to complement existing empirical data and statistical models. Agent-based or individual-based models (ABMs) are a promising tool for this type of simulation, as they explicitly model individuals' functions, and ways of interaction with the environment and other individuals. ABMs have been increasingly used in ecology (Zakharova et al., 2019), and due to efforts to make their implementation (Wilensky, 1999) and documentation (Augusiak et al., 2014; Grimm et al., 2006, 2010, 2014, 2020) more transparent, they are promising tools even for generic, theoretical scenarios (Lorscheid et al., 2019). In conservation science, agent-based models have been applied multiple times, although mostly to study the effects of threats and conservation actions of individual species (McLane et al., 2011). They have also been applied to predict the environmental, genetic, and demographic factors leading to extinction (Birand et al., 2012; Mashayekhi et al., 2014) or speciation (Birand et al., 2012).

## 1.1 RESEARCH AIMS:

In this work, I attempt to find biological traits that make species more prone to population decline and extinction. Specifically, I want to answer three questions:

1. **Which traits, taxa, and regions have been most studied in the literature? (Chapter I)**

Since some traits, taxa, and biogeographical regions have historically been more studied than others, I suspect that the literature on the relation between these and extinction risk may be biassed. If a large bias exists, the ability to find general trends in trait-based prediction of extinction risk may be limited. I addressed this question in **Chapter I**, where I compiled an extensive list of publications that focused on the relation between traits and extinction risk. I quantified past effort focusing on each trait, taxon, and geographical region, and identified research gaps for future work.

2. **Which traits can be good predictors across taxonomic groups? (Chapter I, II)**

I addressed this question in two ways. First, in **Chapter I**, I counted the proportion of statistical tests in which each trait was significant in the literature. Because this only provides a rough estimate of a trait's importance, without informing whether or not the trait was positively or negatively related to extinction risk, I also estimated how good each trait predicted extinction using a meta-analytical approach, which quantifies the strength and direction of the relationship. As past research was found to be both fragmentary and biassed, I compiled an extensive dataset of species-level trait and extinction risk data, spanning multiple terrestrial taxa (vertebrates, invertebrates and plants, **Chapter II**). While some traits may be correlated with extinction risk across all taxa, some others may be only good at explaining extinction risk within certain taxa, or with contrasting effects depending on the taxon. These traits may not be useful to predict extinction for poorly known taxa, but they are nonetheless useful for taxon-focussed conservation efforts and were also identified.

3. **How do traits interact with threats in predicting extinction risk? (Chapter III)**

Models including the interaction between traits and threats are scarce, as these models are more data thirsty. To tackle this question, I implemented an agent-based model, in which virtual species were subjected to a range of simulated anthropogenic threats (**Chapter III**). In doing so, I also explored how proposed mechanisms underlying each trait and extinction risk behave under each simulated threat.

# 2 MATERIALS AND METHODS

## 2.1 CHAPTER I: LITERATURE SYNTHESIS

My objective was to retrieve from the literature an extensive list of publications that had explicitly compared traits of species to a proxy of extinction risk. First, I obtained a list of potential publications to be included in the review. The potential list originated from a search using wide-scope terms: “trait* AND extinct*” in Web of Science, as well as all papers included in two previous, related reviews (Murray et al., 2014; Verde Arregoitia, 2016), and those already known to me. Each of the potential papers was screened to check its eligibility to be included in the review. Several criteria had to be met, namely that the study compared multiple species, that it had at least one biological trait being studied, and that for each species there was a proxy of extinction risk (such as a Red List threat status, or population trend). From each of these publications, I then collected, among other information, their geographical and taxonomic scope, as well as the list of all traits tested, the statistical test used, the test statistic and the degrees of freedom or number of observations, whether they were univariate or multivariate tests, and whether the trait was significantly related to extinction risk or not.

I analysed the collected data in two steps. First, I compared the number of studies per taxon, geographical realm, and trait, as well as the proportion of significant measurements for each trait. For the second step, I ran several meta-analyses for each trait. Meta-analyses allow the comparison of outcomes from different studies by converting the test statistics into the same measurement – the effect size. I used Fisher’s Z because it allows very diverse statistical methodologies into the same effect size measurement (Rosenthal, 1991). In this case, I converted each test statistic into Pearson’s product moment correlation coefficient and then converted to Fisher’s Z using the R package metaphor (Viechtbauer, 2010). To ensure comparability of outcomes between studies, I only selected univariate tests. To detect the overall effect size for each trait, I ran linear mixed models. Fisher’s Z was used as the response variable, weighed against the inverse of sample sizes, tested against the intercept term only and with random effects being the taxon and study.

## 2.2 CHAPTER II: CORRELATES OF EXTINCTION FOR TERRESTRIAL TAXA

In chapter II, the aim was to find general correlates of extinction for multiple terrestrial taxa. I started by building a dataset that encompassed the maximum number of taxa with extinction risk data, as well as a set of traits generalizable across taxa.

I restricted the selection to species already assessed for the global IUCN Red List, excluding Data Deficient taxa, since the IUCN provides the most comprehensive source of knowledge and data on species' extinction risk across the world. Within taxa that had a sufficient number of species assessed, I selected 5 groups of vertebrates (mammals, birds, reptiles, amphibians, freshwater fishes), invertebrates (dragonflies, grasshoppers, butterflies, spiders, snails), and plants (bryophytes, ferns, gymnosperms, legumes, and monocots). From each group, I selected 60 species, and whenever possible 10 species from each of the six main geographical realms *sensu* Olson et al., 2001: Afrotropic, Australasia, Indo-Malay, Neotropic, Nearctic, Palearctic. Each of these 10 species were randomly selected with the condition that there were five threatened and five non-threatened. Since the selection was performed at random, it was not biassed towards species with better known traits, an issue that has shown to influence results in the literature (González-Suárez et al., 2012; Verde Arregoitia, 2016; Etard et al., 2020). In some groups the geographical extent was smaller due to lack of IUCN assessments, namely butterflies, grasshoppers, spiders, snails, and bryophytes.

The selection of intrinsic and extrinsic traits followed previous work on which traits were hypothesised or tested for their relationship with extinction risk, as reviewed in **Chapter I**. The selected traits were body size, offspring size, fecundity, generation length, diet breadth, trophic level, dispersal ability, microhabitat verticality, habitat breadth and altitudinal range. Intrinsic trait data were compiled from the literature, existing trait databases, measurements of photographs of pinned species, or expert knowledge. Since each different taxonomic group differs in their life-history and ecological strategy, I selected trait proxies which serve as trait analogous, as they serve the same function depending on the group (Weiss & Ray, 2019). For example, body size in mammals was represented by body mass, by hind wing length in dragonflies and by plant height in gymnosperms.

Other traits were obtained and had the same units across taxa, such as the habitat breadth (IUCN habitat categories) (IUCN, 2022) and altitudinal range (IUCN, 2022). When no data was available for a species, the value of a closely related species or genus or family average was used (except for habitat breadth, altitudinal range, and geographical range data). Certain groups lacked data completely for some traits, and for some groups the proxy used was coarser or invariant (e.g. trophic level in dragonflies, spiders, plants).

To identify congruent predictors of extinction risk, I first fit generalised-linear mixed models for each taxon, and then synthesised effect sizes across vertebrates, invertebrates, and plant groups. Generalised-linear mixed models were fit using the threatened status as a binary response variable, z-transformed trait values as the predictor variable and taxonomy as random effect. The latter was used as a proxy of phylogeny to control its possible non-independence. The slope coefficients were then used as effect sizes, and the standard errors were used to derive the standard errors in the meta-analyses. For each trait, I then calculated the overall effect sizes for vertebrates, invertebrates, and plants.

## 2.3 CHAPTER III: SIMULATION APPROACH: INTERACTION BETWEEN TRAITS AND THREATS

In **Chapter III**, the objective was to understand the impact that the interaction between traits and different threats has on the extinction of species. The threats selected were direct killing, habitat loss, habitat fragmentation, habitat degradation, and invaders (Table 2); all of which are among the major drivers of extinctions worldwide. The selected traits were body size, maturity age, fecundity, and dispersal ability. These traits have been hypothesised to be important predictors across taxa, and they can be quantified for all taxa.

Each simulation developed in this chapter consisted of a virtual landscape with organisms competing for resources. Organisms had different trait values due to mutation after reproduction. The introduction of a threat could therefore have an impact on the average trait values of organisms within a simulation due to natural selection. Each trait influenced the life-history strategy of the organism. Larger organisms had greater energetic expenditures and intakes following metabolic theory (Brown et al., 2004; Glazier, 2005, 2010) and had better chances at obtaining resources before smaller organisms, to reflect the competitive advantage that large size brings (Hone & Benton, 2005; Kingsolver & Huey, 2008; Kingsolver & Pfennig, 2004). Maturity age influenced the age at which organisms were able to reproduce, as well as the maximum longevity. The maturity age of an organism was proportional to its longevity, as fast growth typically limits organisms' ability to live longer (Dowling & Simmons, 2009; Kirkwood, 1977; Selman et al., 2012). The number of offspring produced by an organism was determined by the trait fecundity. Because investing in many offspring has a negative effect on each offspring's survival (Fox & Czesak, 2000), the amount of energy received by each organism was inversely proportional to fecundity. Finally, the distance travelled by an organism was proportional to its dispersal ability. Greater distance of dispersal incurred, however, in greater energetic costs (Bonte et al., 2012).

I simulated 64 random landscapes, populated them with organisms with random trait values and I let them run without threats (a replicate). After these replicates converged to stable trait values due to natural selection (burn-in phase), I subjected each of them to a gradient of each of five threats (64 replicates * 5 threats * 20 gradient values). For each replicate and for each threat type/threat intensity/trait combination, I calculated the log relative change in trait value between the beginning of the simulation (end of burn-in phase) and the end of the simulation (end of threat-phase). Thus, positive values indicated positive changes in trait values, and negative values negative changes in trait values. For each replicate and combination of threat and trait, I ran a linear model using as the response variable the log relative change in trait value and as explanatory variable the threat gradient value. To check whether each trait/threat combination had a significant positive or negative response, I counted the number of assemblages with positive and negative slopes. A significant deviation from the mean was considered when at least 95% of the slopes were either all positive or all negative.

In addition to the standard analyses, I also ran robustness tests to check if changing the parameter values had a qualitative influence on the model results. Whenever a change in the parameter value had a significantly opposite signal to that of the standard parameter's simulations, I considered that trait-threat combination not to be robust to parameter changes.

**Table 2.** *Types of threat studied, their description, and real-world equivalents.*

| Threat | Description | Examples |
|---|---|---|
| Direct killing | Removal of organisms from the environment | Fishing and hunting, introduced predators, lethal effects of pollution |
| Habitat loss | Destruction of habitat in a continuous area | Clearing of natural ecosystems for agriculture, urbanisation, watersheds, etc. |
| Habitat fragmentation | Destruction of habitat in a non-continuous area | Roads, damns, fences, agricultural landscapes with some remnant forests, edges of a forest being cleared |
| Habitat degradation | Deterioration of habitat quality | Landscape dominated by invasive plant species, lakes with high nitrogen input from agriculture, affected by sources of pollution such as pesticides and light pollution, trawling of sea floor |
| Invasives | Introduction of organisms with similar traits, competing for the same resources | Replacement of native species by functionally similar introduced species. |

# 3 RESULTS AND DISCUSSION

## 3.1 TRENDS AND BIASES IN THE LITERATURE

The literature review showed that the most studied taxa were mammals and birds (Fig. 1). On the other end, fungi, despite their very high diversity of life-forms, were only studied in one manuscript. Plant and vertebrate studies analysed species from around the globe, with a special focus in the Palaearctic (for plants) and the Australasian (for some vertebrate groups) realms. Insect studies are almost exclusively focussed on the Palaearctic. The focus on vertebrates is probably due to the greater accumulated knowledge in these groups (Titley et al., 2017; Troudet et al., 2017), as is the greater focus on the Palaearctic region (Boakes et al., 2010; Etard et al., 2020; Titley et al., 2017). The lack of representativeness of some taxa (insects, plants, fungi) and realms (notably the tropical regions) seems to be due to both the lack of global trait database initiatives (Aguilar-Trigueros et al., 2015) and of extinction risk assessments (Cardoso et al., 2011; Dahlberg & Mueller, 2011).

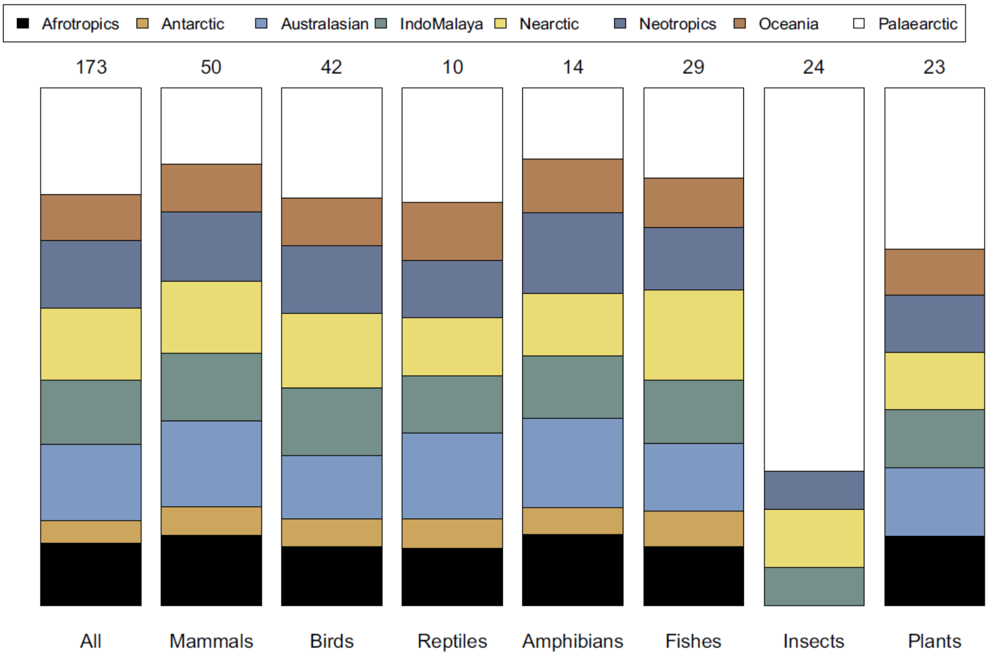

**Figure 1** Proportion of articles focusing on the different biogeographical regions by taxonomic group. Numbers above columns are the total number of studies per taxon.

Body size was the most studied among 189 traits identified in the literature, followed by geographical range and fecundity (Fig. 2). Most traits were not studied across all taxa (only biogeographical range and body size were so). This is due to some traits being not applicable for some groups (such as brain size, torpor behaviour of mammals), or more often trait data not being available. Body size is one of the traits that is most collected, from species descriptions to field guides, and is thus easy to find across all groups. Other traits are either not documented or not easily available in literature or online databases. The investment in global-trait initiatives should be a priority to facilitate rapid advancements in analyses and knowledge in this area. Basic funding for these groups to better understand their traits and increasing the number of extinction risk assessments (e.g., using the IUCN criteria) is fundamental to fill the many existing gaps in the near future.

Because the large majority of traits was scarcely studied (**Chapter I**), it was difficult to determine how consistent they were at predicting extinction across studies. Among the most popular 10% of traits, the percentage of statistical tests showing significant relationships to extinction probability varied from 21% (nest microhabitat) to 74% (geographical range size) (Fig. 2).

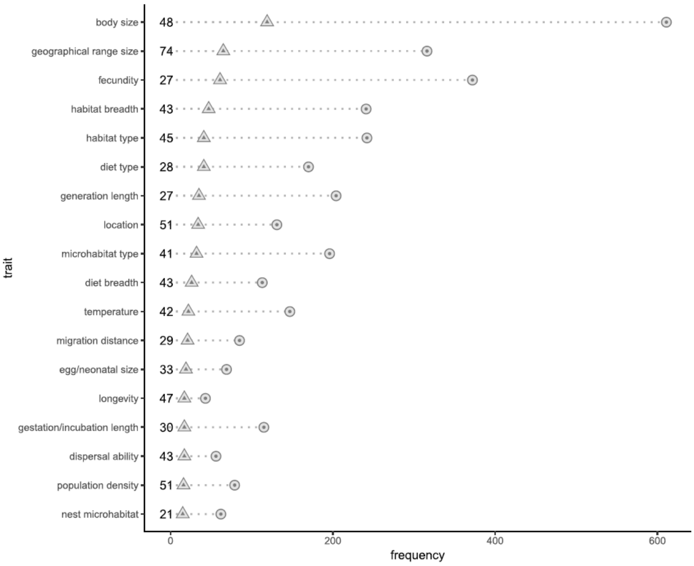

**Figure 2** Summary information on variable use among all studies, depicting only variables included in at least 17 (10%) studies. The numbers before the dotted lines indicate the percentage of measurements in which the variable was significant. Triangles: number of studies in which the variable appears. Circles: total number of measurements for that variable.

Whether or not the relationship was the same across studies for a given trait was only inspected for geographical range size, habitat breadth, and body size, due to data availability. The former two were consistently negatively related to extinction risk, indicating that species at risk tend to have smaller ranges and narrower habitat breadths while the latter showed no consistency among studies (**Chapter I**).

## 3.2 DRIVERS OF EXTINCTION RISK

The results of **Chapter II** suggest traits may be grouped into four categories depending on the consistency of their relationship with extinction risk across multiple taxa. In the first category I identify universal traits, which can be confidently used to predict extinction risk across all taxa (habitat breadth). The second category comprises traits for which current data suggests they could also be universal traits, but for which further data on missing taxa should be collected in the future (traits related to slow life-history and altitudinal range). The third category comprises traits relating with extinction risk across many but not all taxa (dispersal ability). And the last category comprises traits that are good predictors within certain taxa (body size, diet breadth, trophic level, and microhabitat).

The only clear universal predictors of extinction risk were geographical range size and habitat breadth (**Chapter I**), furthermore, the latter was consistently negatively related to extinction risk among vertebrate, invertebrate, and plant groups (Fig. 3) (**Chapter II**). Indeed, habitat breadth and geographical range size are two of the three dimensions of rarity, together with population size (Rabinowitz, 1981). Species occurring in fewer habitat types may have less opportunities to expand and survive in alternative suitable conditions in view of any threats such as habitat loss. With increasing habitat loss occurring across all biomes, those more able to use alternative habitats will inevitably fare better.

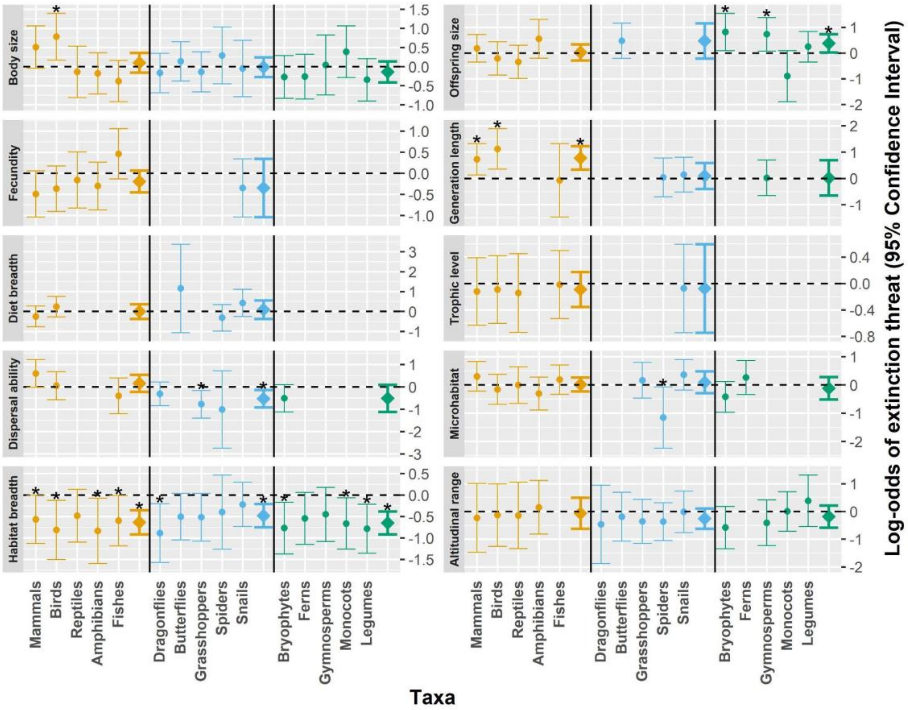

**Figure 3** Effect sizes (log-odds of extinction threat) for each trait and within each taxonomic group studied (GLMMs, thin bars), and overall effect sizes among vertebrates, invertebrates, and plants (bold bars). Error bars represent lower and upper bound 95% confidence intervals. Positive values indicate a positive relationship between the trait and extinction risk, and vice-versa. Confidence intervals not overlapping with 0 (marked with an asterisk *) indicate a smaller than 5% probability that the slope of the relationship is zero.

Traits indicating slow life cycles – large offspring size, low fecundity, long generation length –, as well as narrow altitudinal range were identified as potential universal traits. Offspring size was significantly positively correlated to extinction risk across plant groups, and marginally so in invertebrates (Fig. 3). In vertebrates, generation length was positively related to extinction risk, and fecundity marginally negatively correlated. The higher vulnerability faced by species with slow life cycles could be due to their limited capacity to compensate for higher mortality rates in the face of demographic threats (González-Suárez et al., 2013; Pimm et al., 1988), or to find new sites due to low abundance (Saar et al., 2012). Investing in few offspring, even if well-adapted to certain circumstances, is also detrimental in the face of increasingly unpredictable threats and changes. Larger progenies ensure larger variability and the capacity of a species to adapt to a fast-changing environment. Altitudinal range was only marginally negatively related to extinction risk in invertebrates and plants (Fig. 3), but the inclusion of more data in mammals and birds in a robustness test (**Chapter II**) suggested that this trait was also relevant among vertebrates. Altitudinal range can be interpreted as a surrogate for climatic tolerance, and species with low tolerance have fewer chances to be able to exploit new ranges for survival (Botts et al., 2013; Keane et al., 2005). Given the current climate emergency, species with reduced capacity to adapt to present and future changing temperature and precipitation patterns should fare worse.

Poor dispersal ability was a congruent predictor among invertebrates and marginally so in the sole plant group tested (Fig. 3) but not for vertebrates despite extensive data available. When threatened locally, species with greater capacity to colonise new areas will have a lower probability of extinction (Benscoter et al., 2013; Reinhardt et al., 2005). Unsurprisingly, taxonomic groups with high dispersal ability such as birds and dragonflies have a lower number of threatened species than less dispersive groups according to the IUCN Red List criteria (IUCN, 2022). With climate change, the importance of dispersal as a predictor will only likely increase (Mattila et al., 2011; MacLean & Beissinger 2017; Santini et al., 2016). However, the effect on vertebrates may not be as strong as for invertebrates and plants: many vertebrates are able to cross linear barriers such as roads, or to move much farther than most invertebrates or plants, for which even small fragmentation levels may pose a challenge (Bartonova et al., 2014; Saar et al., 2012).

Other traits had responses dependent on taxa. In our study, body size deserves special attention given its ubiquity in past studies. It was positively correlated with extinction risk in birds and mammals, but in other groups, such as in in cycads (Mankga & Yessoufou, 2017) or amphibians (Ripple et al., 2017; Ruland & Jeschke, 2017), smaller body sizes were related to higher extinction risk. Body size relates, in first instance, to the resource needs of species (Brown et al., 2004). Everything else being equal, larger species require more resources (Brown et al., 2004). Additionally, large mammals and birds tend to be targeted by human exploitation (Diamond, 1989; Owens & Bennett, 2000; Purvis et al., 2000; Smith et al., 2019). Yet, body size can also be related to many other traits, such as the speed of the life cycle, fecundity, dispersal ability, and therefore its effect on species' survival should depend on the relevance of each particular trait to each group (Madin et al., 2016). Finally, several studies in vertebrates suggest that the influence of body size on extinction should depend greatly on the threat type (González-Suárez et al., 2013; Ruland & Jeschke, 2017).

## 3.3 INTERACTION BETWEEN TRAITS AND THREATS

The five simulated threats had contrasting effects on the four studied traits of organisms (Fig. 4). For most trait-threat interactions, the increase in threat intensity led to monotonic increases or decreases in trait values.

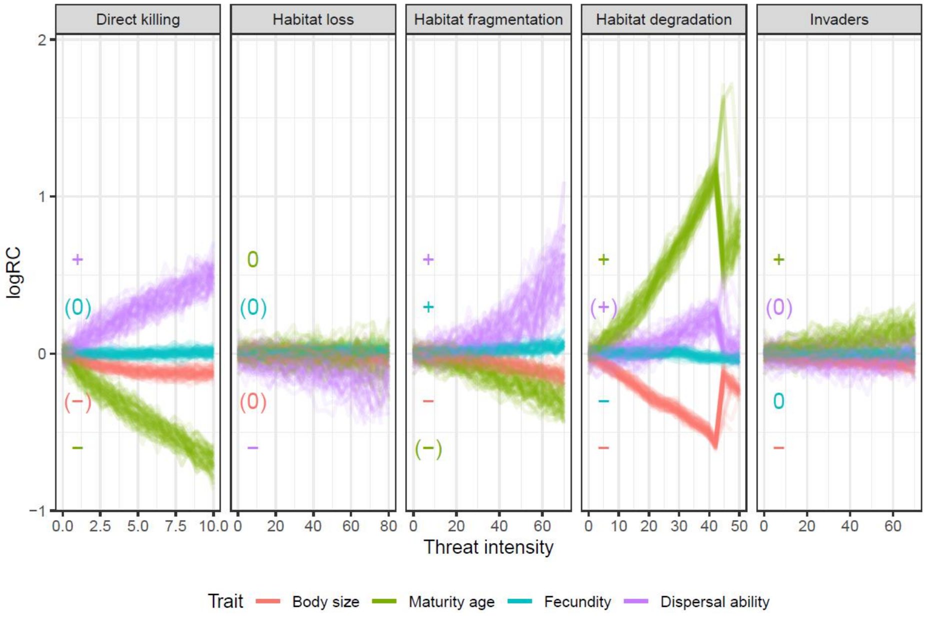

**Figure 4** Evolution of the log relative change (logRC) in mean trait value of each trait as a function of threat intensity per each of the 64 replicate assemblages. The threat intensity was a gradient from zero to the value that allowed at least 50% of the simulations without full extirpation of individuals. Each assemblage is represented by a single curve. Pre-threat intensity can be assessed in the zero value of threat intensity (values obtained at the end of the burn-in phase). For each threat-trait combination, "+" and "-" indicate strong positive or negative relationships. Parentheses "()" may indicate opposite patterns found in one or more robustness tests in relation to the standard tests, or significant trends found in the robustness tests where no significant trends were found in the standard test.

Direct killing of organisms decreased the (mean) body size and maturity age and increased the dispersal ability of organisms in relation to pre-threat values, with greater threat intensity leading to the greatest differences in trait values. Despite not changing significantly in the standard test, fecundity increased significantly in almost half of the robustness tests. The other traits were robust to changes in parameter values, except for body size which increased under one robustness scenario. The widely reported extinction of slow-lived, low-dispersal megafauna before the 18th century due to human hunting and prosecution attests our results (Diamond, 1989). Furthermore, recent studies comparing threatened with non-threatened species have shown that the larger, slow living species are particularly threatened by direct killing, at least in mammals (González-Suárez et al., 2013), fishes (Olden et al., 2007), and birds (Owens & Bennett, 2000).

Habitat loss led to the decrease of average dispersal ability of organisms and no significant changes were observed for the remaining traits. However, the robustness analyses showed that body size and fecundity decreased and increased in two and one robustness tests respectively, and that maturity age showed significant opposite patterns in three robustness tests. Conceptually, larger sizes are typically perceived as being more susceptible to decreases in fragment area (Ewers & Didham, 2006), but empirical support of that idea is lacking, as this trait is usually strongly correlated with other traits perceived to increase (dispersal distance) (Warzecha et al., 2016) or decrease (trophic level) (Henle et al., 2004) an organism's capability to survive in a landscape with high habitat loss. The positive effects of habitat loss on fecundity are well supported in plants (Lindborg et al., 2012; Marini et al., 2012; Saar et al., 2012) and Lepidoptera (Öckinger et al., 2010). As for dispersal ability, evidence also shows that if the remaining habitat patches are very isolated, organisms with reduced dispersal ability often cope better (Ewers & Didham, 2006; Henle et al., 2004; Saar et al., 2012), but note that isolation may also have negative consequences for genetic drift and erosion in organisms reproducing sexually (Zambrano et al., 2019) or for species ability to shift their geographical ranges in the face of climate change (Hodgson et al., 2011).

When random patches were removed from the environment, body size decreased, while fecundity and dispersal ability increased in response to increased habitat fragmentation. Maturity age also decreased, but under some particular robustness scenarios maturity age significantly increased. Our results are in accordance with empirical studies that suggested that good dispersers tend to respond better to increased fragmentation (Öckinger et al., 2010; Steffan-Dewenter & Tscharntke, 1999; Warzecha et al., 2016).

In response to habitat degradation, body size and fecundity decreased, and maturity age and dispersal ability increased. However, dispersal ability decreased under some robustness scenarios. Despite being perceived as one of the major drivers of species extinctions (Mortelliti et al., 2010), this threat has been poorly studied due to the difficulties of isolating its effect from other landscape-level threats, such as habitat loss and fragmentation (Fischer & Lindenmayer, 2007; Mortelliti et al., 2010). In any case, supporting evidence for our results can be found in many natural systems. Temperate ungulates (Ferguson, 2002; Skogland, 1985), songbirds (Martin & Mouton, 2020), and plants (Grime, 1977) living in resource poor or drought-prone landscapes have adapted to greater longevity and low fecundity. An extreme example is provided by caves and troglobiont organisms, which are almost invariably small, with long life and low fecundity compared with the closest surface relatives.

In response to invader intensity, body size decreased, and maturity age increased, while no significant changes were observed in fecundity or dispersal ability. However, two robustness tests showed increases in dispersal ability, while two others showed decreases. The impact of invasive competitor species on the traits of native communities has not been studied thoroughly. In fishes, threatened natives had significantly faster life cycles and higher fecundity than non-threatened native species (Liu et al., 2017), which could indicate that successful natives may need slower life cycles and lower fecundities to resist invasion. Native plant species have shown to be on average smaller and with lower growth rates than invaders (Kleunen et al., 2010), which confirm our results, but another study also showed that native and alien successful species share the same traits across many habitats in Central Europe (Loiola et al., 2018). Ultimately, the outcome of invaders on native species traits will depend on their own traits and our simulation tested only one of the possibilities.

# 4 CONCLUSIONS AND PROSPECTS

The main contribution of the thesis is a much-needed global synthesis on which biological drivers predispose species to extinction. Despite the literature and knowledge bias against non-vertebrate taxa (Donaldson et al., 2017; Troudet et al., 2017), the Southern Hemisphere (Donaldson et al., 2017, Titley et al., 2017), and the very low data availability for many potentially good predictors of extinction risk (**Chapter I**), several traits could be identified as predictors of extinction regardless of the taxon (**Chapter I and II**).

Species characterised by a narrow geographical and habitat breadth are more threatened with extinction. Species characterised by slower life cycles - large offspring sizes, low fecundity, and long generation lengths -, have reduced population replacement rates, are less likely to be able to compensate for demographic accidents due to stochastic events (Pimm et al., 1988), and thus face higher extinction probability. Likewise, species with a low climatic tolerance as measured by altitudinal range are more prone to becoming extinct, as they cannot adapt to new conditions. Poor dispersal ability was a predictor of extinction among invertebrates and plants: as the environment changes, poor dispersers may not be able to move to better conditions. The remaining studied traits are important predictors of extinction, but their influence on extinction varies between taxa.

This thesis furthermore shows the importance of considering the threat type and intensity, and of the interplay between traits and threats (**Chapter III**) (González-Suárez et al., 2013; Murray et al., 2014; Munstermann et al., 2021; Purvis et al., 2005). Threats that directly increase mortality in populations are detrimental to slow life cycles and low dispersal ability. Threats that increase spatial unpredictability in the availability of resources are likely to affect large species with poor fecundity, and either good or poorly dispersive species depending on the spatial configuration of habitat loss. Threats reducing the quality and quantity of resources strongly affect large, fast life-histories with high fecundity. Most of these patterns find support in studies performed with different taxa and regions.

We are experiencing an era of dramatic change in the restructure of biodiversity patterns worldwide and extinction rates that are orders of magnitude larger than background rates (Carmona et al., 2021; Cowie et al., 2022; De Vos et al., 2015). Monitoring of declines and extinctions of species is critical and the object of global (e.g., Convention on Biological Diversity) and regional (e.g., EU Habitats Directive) agreements and policies. Yet, monitoring instruments in these agreements are biassed towards few charismatic taxa, with little relation with biodiversity at large. Using increasingly available trait data as surrogate information for extinction risk can and should be considered in the future, and here I demonstrate how it can contribute to monitoring initiatives.

To predict future trajectories towards extinction, more data and assessments are needed for underrepresented taxonomic groups and geographic regions. National and international funders of biodiversity conservation and research infrastructures should consider this in their future goals and efforts. Likewise, extinction risk drivers and their usefulness as predictors can and should in the future account for the type and intensity of human threat involved. This work is the first to take an unbiased view of the relation between traits, threats and extinction risk and builds the foundation for future work that tries to go beyond using the usual suspects to monitor these relations. With increasing data available on traits and threats to biodiversity, the future looks promising to trait-based understanding and prediction of extinction risk across the tree of life.

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