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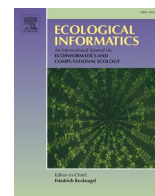
Biological traits interact with human threats to drive extinctions: A modelling study

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ABSTRACT

How a particular threat influences extinction risk may depend on biological traits. Empirical studies relating threats and traits are needed, but data are scarce, making simulations useful. We implemented an eco-evolutionary model to analyse how five threat types influence the extinction risk of virtual organisms differing in body size, maturity age, fecundity, and dispersal ability. The model consisted of observing the evolutionary shift in the mean trait values of an assemblage of organisms when a threat was added into the virtual world where they lived. If a positive shift was found in trait values, we considered that the threat negatively influenced organisms with lower values for that trait. Direct killing mostly affected organisms with slow life cycles (slower-living) and poorly dispersive organisms. Habitat loss caused a reduction in the average dispersal ability of organisms. Habitat fragmentation caused an increase of average dispersal ability, and had a negative effect on larger, less fecund organisms. Habitat degradation and the introduction of invasive competitors had similar effects, mostly affecting large and fast-living organisms, with habitat degradation also affecting highly fecund and poorly dispersive organisms. These results agree with previous empirical studies in which larger, slower-lived, and less fecund organisms are more vulnerable to a greater range of threats. On the other hand, our results challenge two commonly seen hypotheses in the literature: that organisms with high dispersal ability fare well under any high habitat loss scenarios, and that fast-living, highly fecund organisms always do well during environmental change. Our study shows that highly dispersive organisms may be the losers when habitat loss removes large continuous areas of habitat, and fast-living and highly reproductive organisms may be the losers when resources or energy availability dwindle to very low levels. Most importantly, our study underpins the importance of considering the type of threat when analysing the relation between traits and extinction. Even in simple scenarios such as the ones modelled here, different threats lead to different, sometimes opposite, extinction probabilities according to the biological traits of organisms.

1. Introduction

Species are becoming extinct at rates that are unprecedented in human history (Vos et al., 2015). Understanding what drives species to extinction is crucial if further extinctions are to be minimized. However, the mechanisms leading to extinction, both intrinsic (species traits) and extrinsic (environmental threats), and the way they interact remain obscure (Chichorro et al., 2019; Murray et al., 2014).

Much progress has been made recently, with over 150 studies trying to identify similarities in traits between threatened species in the last two decades (synthesized in a recent review, Chichorro et al., 2019).

These studies were both comparative and correlative in the sense that they compared traits of threatened species with those of non-threatened species, often using the IUCN red list categories (IUCN, 2020) as proxies of extinction risk (González-Suárez et al., 2013). Some of the most popularly studied traits include body size, fecundity, longevity, and dispersal ability (Chichorro et al., 2019), although the latter is often assessed using indirect proxies due to a lack of good dispersal data. Additionally, human drivers of risk are often correlated with traits and extinction risk (Murray et al., 2014).

Previous correlative studies indicate that external factors interact in important ways with the relation between intrinsic traits and extinction

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risk (González-Suárez et al., 2013; Murray et al., 2014; Olden et al., 2007). Habitat destruction, pollution, invasive species, over-exploitation, and climate change (Secretariat of the Convention on Biological Diversity (Ed.), 2014) can all influence extinction risk, and some traits can make species particularly vulnerable to some of these threats.

As correlative models of extinction risk become more complex, the amount of data required to test hypotheses (species traits, external drivers, etc.) increases. Additionally, because observations are rarely independent (dispersal ability might relate to body size, fecundity with offspring size, etc.) (Bonte et al., 2012; Ewers and Didham, 2006), it is often difficult to partition this complexity into independent components.

Conceptual models have been suggested to complement correlative models in order to understand mechanistic drivers of diversity patterns better (Murray et al., 2014). Individual-based models (or agent-based models, henceforth referred to as ABMs) are increasingly used as conceptual models to aid understanding of the functioning of species and ecosystems (DeAngelis and Grimm, 2014). Their power derives from the possibility of replicating patterns found at the population and community levels from processes occurring at the individual level (the level at which the basic deciding biological entity exists) (Grimm and Railsback, 2005). Additionally, they allow testing mechanisms independently of natural constraints and partition their contribution into independent components.

In this study, we develop a conceptual ABM to evaluate the influence of different threats, namely direct killing, habitat loss, habitat fragmentation, habitat degradation, and invaders on the risk of population extirpation and the extinction of species, presenting differing body size, maturity age, fecundity, and dispersal ability. The landscape includes organisms competing for resources, which they use to invest in survival, dispersal, growth, and reproduction. These organisms are subject to evolution through asexual reproduction, mutation, and selection. Through these latter mechanisms we may infer the extinction risk by observing the direction of evolution of traits in response to different environments and threats. Since organisms reproduce asexually, variation in traits between organisms can be considered to be intraspecific or interspecific, depending on the threshold used to distinguish species. Thus, simulations can represent a population of a single species or a community of multiple species. Hereafter, we designate both by assemblages to reflect this flexibility across scales and the fact that there are no interactions between organisms apart from competition for resources. After creating virtual organisms adapted to given simulated worlds, we apply the threats and observe how the average trait values of assemblages respond to each threat. These results from in silico experiments are related to real-world knowledge on different organisms and reveal the mechanisms behind population extirpations or species extinctions. Additionally, we hypothesize mechanisms to be tested in the future, which can guide data collection, and can be confirmed or
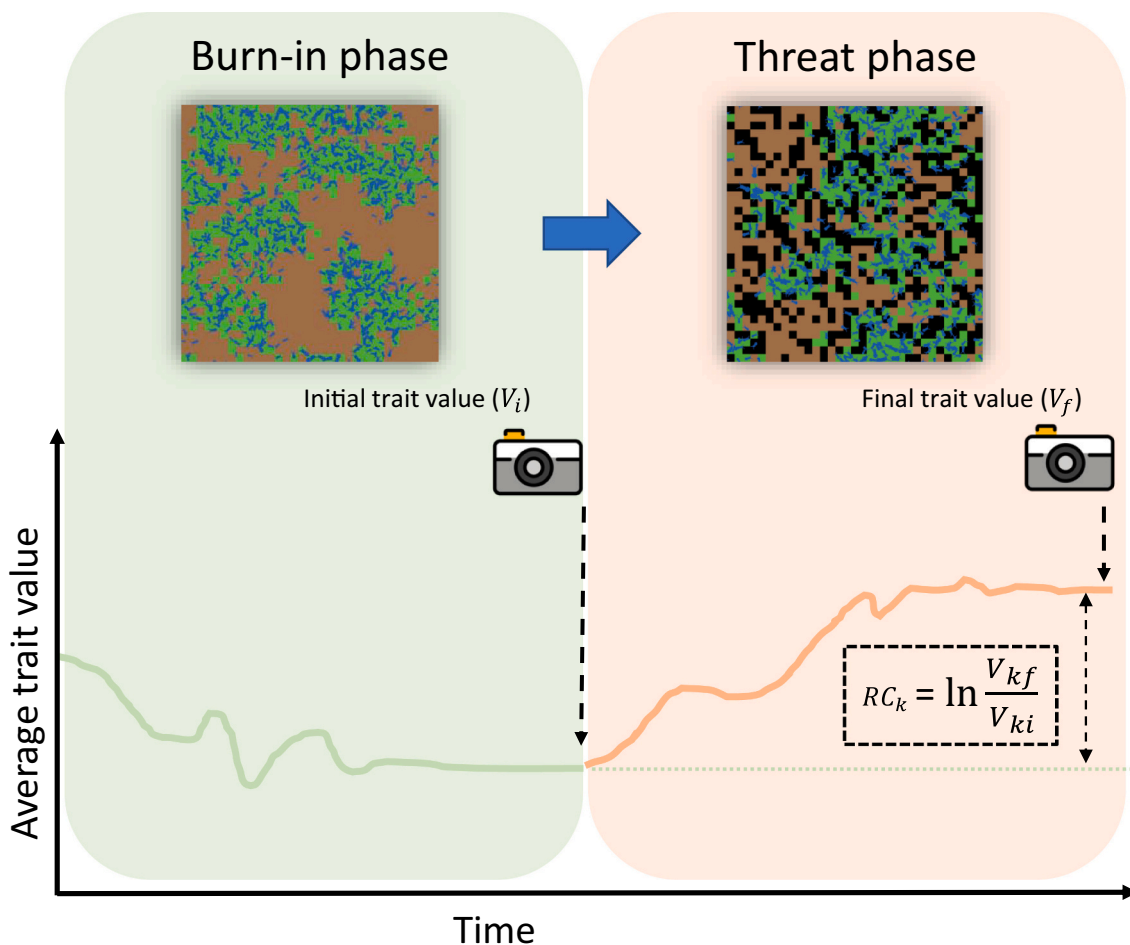

Fig. 1. Schematic representation of the model design. **A)** Average trait value (any of body size, fecundity, maturity age, or dispersal ability) of an assemblage of virtual organisms as a function of simulation time. As the model is initialized at time 0, natural selection and mutation in trait values shift the average trait values up and down, until a local optimum for each trait is attained. This period, in which the trait values are still varying over time, is called the burn-in period. Once the assemblage reaches stable trait values, the burn-in period ends. At the end of the burn-in period, the model takes a snapshot of the mean trait values (initial trait values). The threat is activated, which may change the traits of the assemblage of organisms. Once stable trait values are attained again, the simulation stops and another snapshot is taken. The relative change in trait values of each trait (RC) is calculated as ln (initial value/final value).

disproved as more empirical data become available.

2. Materials and methods

2.1. The model

The purpose of the model was to analyse the shift in mean trait values of an evolving assemblage of organisms competing for resources when an external threat event was introduced into the virtual world where they lived (Fig. 1). We implemented an ABM that simulated a landscape where organisms moved in the environment in order to obtain the required resources to survive and reproduce. The organisms were initialized with a random set of traits. The assemblage then evolved and usually converged towards unimodally distributed trait values around a stable mean. Each stable assemblage (after convergence) was then treated as an experimental unit. We subjected each experimental unit to a range of threats at several intensities. As the assemblage converged to a new set of trait value distributions, we registered the relative change in mean trait values occurring under each threat type and intensity. The model was implemented with no ecosystem or species in mind to increase the generality of results. To ensure tractability, we made several simplifying assumptions in each model component, which reduced the number of free parameters. The ABM model was developed in NetLogo 6.1.1 (Wilensky, 1999). A full description of the model following the Overview Design Concepts and Details (ODD) protocol (Grimm et al., 2020) is available in Supplementary Materials S1.

2.2. The environment

The environment consisted of a continuous 2D space in which organisms foraged in the form of an underlying toroidal matrix of 33 × 33 cells (Fig. 2A). Cells were classified as either resource cells or bare cells. The resource cells were all identical and generated resources linearly every timestep until they reached a maximum number of resources. The number of resource cells and their spatial distribution were defined at the beginning of the simulation (Supplementary Materials S1, submodel "generate-map").

2.3. The virtual organism

Our organisms were abstract, free-living animals that evolved by means of asexual reproduction. Asexual reproduction was implemented due to its simplicity, with no foreseen consequences for the results. The organisms were characterized by an energetic currency, their age, their position in the continuous environment, and their focal traits: body size, maturity age, fecundity, and dispersal ability. We used maturity age as a proxy for longevity, since they are strongly correlated. The organisms competed directly, accessing resources that fuel their maturation, reproduction, and survival needs (Fig. 3). Excess energy was stored in reserves up to a maximum determined by body size. An organism dispersed whenever the intake of resources at the current timestep was lower than its needs for maintenance and maturation/reproduction, which happened for example when a cell was populated with more organisms than it could sustain through resource regeneration. If the amount of energy in the reserves reached a certain ratio of maximum energy and the organism reached maturity age, it reproduced, and part of its energy was allocated to its offspring. The organisms died whenever the energy in reserves fell below 0, if they were killed by perturbation *direct killing*, or due to old age.
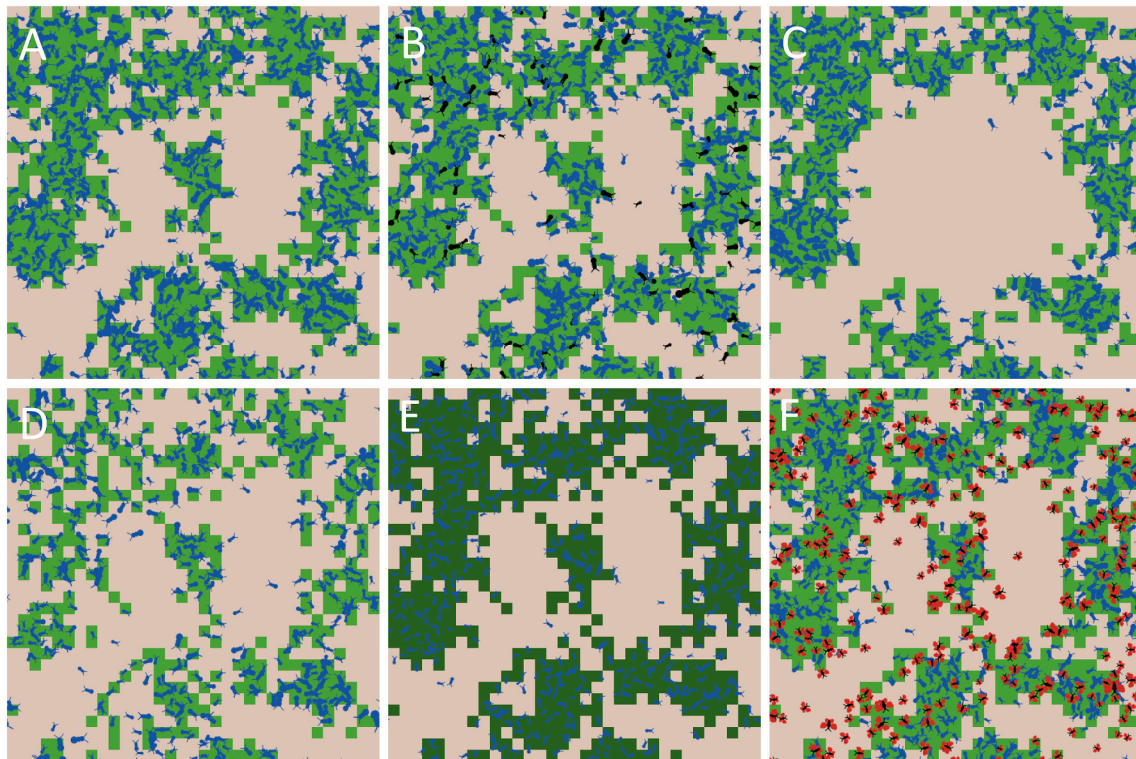

Fig. 2. Visual representation of the same environment under different threats. Blue "bugs" are organisms, green patches contain resources, and light-brown patches contain no resources. A: No perturbation added. Organisms tend to cluster in regions where resources are available. B: Direct killing. Ten percent of organisms die at each round, marked in black. C: Habitat loss. A single fragment covering 30% of the cells was affected by habitat loss, without resources. D: Habitat fragmentation. Thirty percent of cells were randomly assigned without resources. E: habitat degradation. All resource cells had a decrease in resource regeneration rate and in maximum resource value, indicated in dark green. F: Invaders. Invasive competing organisms were added, being immortal, not reproducing, but consuming resources, represented in red and black. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
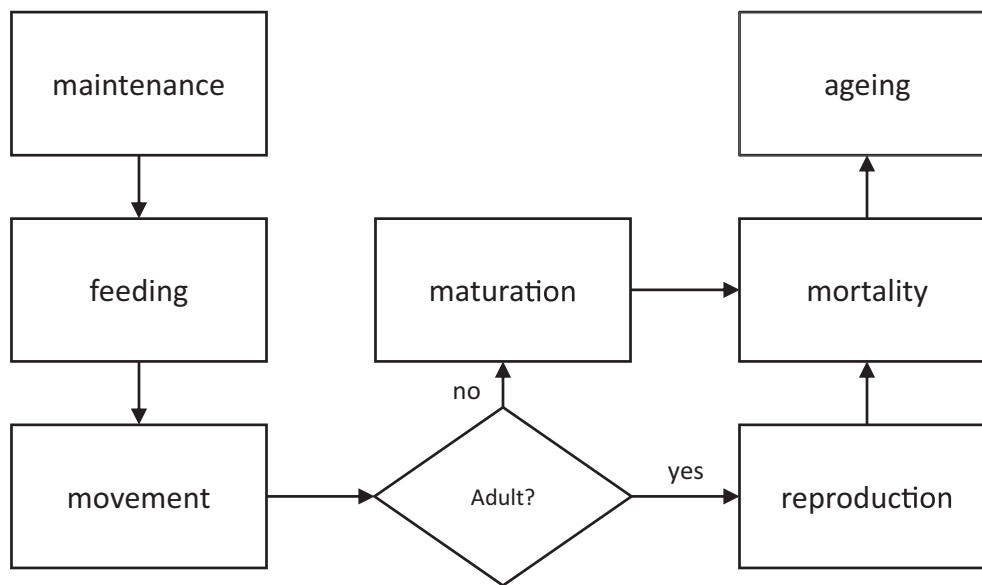
Fig. 3. Functions executed by each organism at every time step. Each function's details can be checked in the ODD protocol in Supplementary Materials S1.

2.4. Traits

The focal traits influenced the fitness of organisms by determining the order by which they foraged (body size), the volume of energetic intakes and expenditures of organisms (body size and dispersal ability), how quickly they reached maturity and died (maturity age), how quickly, and thus how far, they could move in the environment (dispersal ability), and how efficient they were in leaving progeny and spreading their traits in the assemblage (fecundity). The traits were independent, i.e. the values of a trait did not correlate with the values of other traits. This ensured that the underlying mechanisms driving variations in traits were identified. The trade-off governing each trait was selected so as to be realistic across taxa, as detailed in what follows.

2.5. Body size

Being larger than other organisms competing for resources is often a competitive advantage for both animals and plants through access to more resources (Kingsolver and Huey, 2008). On the other hand, energetic expenditure and acquisition scale positively with the body size of organisms (Brown et al., 2004). Therefore, in this model the organisms executed their functions in an energy-sorted order: organisms with more energy (which was positively correlated with body size), had higher chances of foraging first and thus to outcompete other organisms feeding in the same cell. Larger organisms took in and used energy at a faster rate than smaller organisms (Supplementary Materials S1). Larger organisms' mass-specific metabolic expenditures were smaller than those of smaller organisms (Kooijman, 2000), but this advantage was offset in our model by the large organisms' lower mass-specific intake costs than smaller organisms (Kooijman, 2000).

2.5.1. Maturity age

The ability to reach maturity earlier is accompanied by a reduced ability to correct mistakes when replicating DNA, which has multiplicative negative effects on cell functioning, limiting their ability to live longer (Selman et al., 2012). In the model, longevity was proportional to the maturity age of an organism (Supplementary Materials S1, submodel "ageing").

2.5.2. Fecundity

Investment in many offspring has a negative effect on each offspring's survival shortly after birth (Fox and Czesak, 2000). In the model, energy available for reproduction is distributed equitably among each offspring. Consequently, organisms with higher fecundity generated offspring with lower initial energy.

2.5.3. Dispersal ability

Higher dispersal ability may impose energetic, risk, and opportunity costs on organisms that may be expended during the pre-dispersal phase, transfer period, or resettlement phase (Bonte et al., 2012). On the other hand, organisms with higher dispersal ability can move farther away from their current position than poor dispersers. For simplicity, in the model the dispersal cost was debited for every dispersal event, and was proportional to dispersal distance (thus, there are energetic, and opportunity costs to be paid during transfer). The higher mortality risk of dispersers arose as an emergent pattern, as those dispersing had higher chances of dying due to higher energetic expenses during travel and due to landing in unfavourable conditions. Organisms in this model dispersed following a Brownian motion with random orientation, and with distance sampled from a uniform distribution with minimum zero and maximum equivalent to the dispersal ability of the organism (Supplementary Materials S1, submodel "movement").

2.6. Threats

The threats in this model were built to mimic the main biodiversity extinction drivers (Table 1, Fig. 2, Supplementary Materials S1 submodel "add-perturbations"): direct killing, habitat loss, habitat fragmentation, habitat degradation, and invaders. Under direct killing, each round randomly chosen organisms were killed (Fig. 2B), their number being determined by the parameter defining the magnitude of the threat. With habitat loss, a random contiguous fragment of cells was made sterile, meaning that those cells no longer provided resources (Fig. 2C). Habitat fragmentation destroyed cells at random in the map (Fig. 2D), making them sterile. The differences between the effects of habitat loss and fragmentation at the same threat intensity corresponded to the effects of fragmentation per se (Fahrig, 2017). With habitat degradation, all resource cells had their maximum resources and regeneration rates decreased (Fig. 2E). The invaders' threat added competing organisms, inheriting the traits and state variables of random native organisms. Invaders were immortal, did not reproduce, but consumed resources (Fig. 2F). In other words, invasive organisms behaved like normal organisms, in which they competed with other invasive organisms and normal organisms for resources. But since they did not reproduce or die,

Table 1
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, urbanization, etc.
Habitat fragmentation	Destruction of habitat in a non-continuous area	Roads, agricultural landscapes with some remnant forests, edges of a forest being cleared
Habitat degradation	Deterioration of habitat quality	Landscape dominated by invasive plant species, with high nitrogen input from agriculture, affected by sources of pollution such as pesticides and light pollution
Invaders	Introduction of organisms with similar traits, competing for the same resources	Replacement of native species by functionally and phylogenetically similar introduced species.

their traits remained the same throughout the simulations.

2.7. Burn-in phase

A total of 500 organisms were added to the environment, initialized with random values of traits sampled from an exponential distribution. This ensured that a wide range of trait combinations was tested at a simulation start. As time advanced, the number of unique trait combinations started decaying and, due to the evolutionary process (selection and mutation), the simulations tended to stabilize around specific trait values. The model detected when a simulation stabilized by checking if there had been significant changes in trait values and the number of organisms over time (Supplementary Materials S1, submodel "check stopping conditions"). As the model triggered stable conditions, the burn-in phase ended, and the mean trait values of the assemblage were recorded.

2.8. Threat phase

The threat phase started by subjecting a stable assemblage to a threat. The simulation ended when the mean trait values stabilized again (the stopping conditions test was used again). Each threat was applied following a gradient of intensity. We set the maximum threat value as the value at which at least half the simulations did not result in total annihilation of the assemblage. We then created a gradient ranging from no threat (0) to the maximum value of each threat type in 20 steps. In total, we subjected 64 assemblages to each threat type and intensity (64 assemblages, * 5 threats, * 20 gradient values).

2.9. Statistical analysis

The statistical analyses consisted of identifying the trait-threat combinations for which strong changes in trait values were observed along the gradient of threat intensities. We used linear models to determine whether the relationship between the relative change in mean trait values along the gradient of threat intensities was significant either positively or negatively for each trait-intensity combination. We inferred that traits with positive relationships indicate that for that particular threat, lower values of the trait expose species to higher extinction risk. The relative change in trait value (RC_k) was calculated using the following equation:

$$RC_k = ln\frac{V_{kf}}{V_{ki}}$$

where V_{kf} is the mean value of the trait k in the assemblage when the simulation ended, and V_{ki} the mean value of trait k of the initial assemblage (before adding the threat). We ran a linear model for each assemblage using as the response variable the RC_k value, and as explanatory variable the gradient of threat intensities. To check if the overall signal was strong for each (threat, trait) pair, we counted the number of assemblages whose slopes were either negative or positive. We considered that a significant relationship occurred when at least 95% of the slopes were concordant, either positively or negatively.

2.10. Robustness tests

As parameter values of the standard analyses (e.g. initial number of resource cells, energetic intake of organisms, and mutation rates of traits), we chose values that generated both realistic scenarios, and that allowed trait values to increase or decrease after adding threats (values presented in the Supplementary Materials S2). To assess if the results were applicable to a wider range of life-history strategies and landscape conditions, we ran robustness tests. In the robustness tests we changed the parameter values, thus changing the "optimal" organismal phenotype being tested and the environmental conditions. Opposite trends between the standard and robustness tests indicated that the relationship between traits and extinction was strongly influenced by the type of life-history strategy or environmental conditions. Non-significant trends in the standard tests and significant trends in the robustness tests suggested weak effects between threat and traits.

3. Results

By the end of the burn-in period, the simulations converged towards unimodal distributions of the organisms' trait values. The state of the simulation at the end of the burn-in period is presented in Table 2. In general, greater threat intensities led to greater times to reach convergence. The results of the standard tests are summarized in Fig. 4 and the robustness analyses in Table S2.1. We now analyse these results in detail.

Body size and maturity age decreased, and dispersal ability increased with increasing levels of direct killing of individuals. Fecundity did not change significantly but increased in almost half of the robustness tests. No opposite patterns were found in the robustness analyses for maturity age and dispersal ability. In body size, an opposite pattern was triggered once.

As a response to increasing habitat loss, dispersal ability decreased. This result was consistent throughout the robustness analyses. Body size, maturity age, and fecundity did not significantly change. However, body size and fecundity decreased and increased in two and one robustness tests respectively, and maturity age showed significant opposite patterns in three robustness tests.

Body size and maturity age decreased, and dispersal ability and

Table 2
Mean, minimum, and maximum values of several model outputs. With the exception of the burn-in and threat-phase timestep values, all model outputs were observed at the end of the burn-in phase.

| Variable	Mean (min-max)
Burn-in phase (timesteps)	4562 (3155–8461)
Threat-phase (timesteps)	6889 (466–49,409)
Mean body size	0.58 (0.56–0.61)
Mean maturity age (timesteps)	6.3 (5.8–7.0)
Mean fecundity (number of offspring)	1.08 (1.04–1.12)
Mean dispersal ability (maximum distance)	1.9 (1.7–2.1)
Mean number of organisms per cell	1.63 (1.55–1.73)
Mean distance traveled by an organism	1.31 (1.15–1.55)
Mean number of dispersal events	1.47 (1.32–1.68)
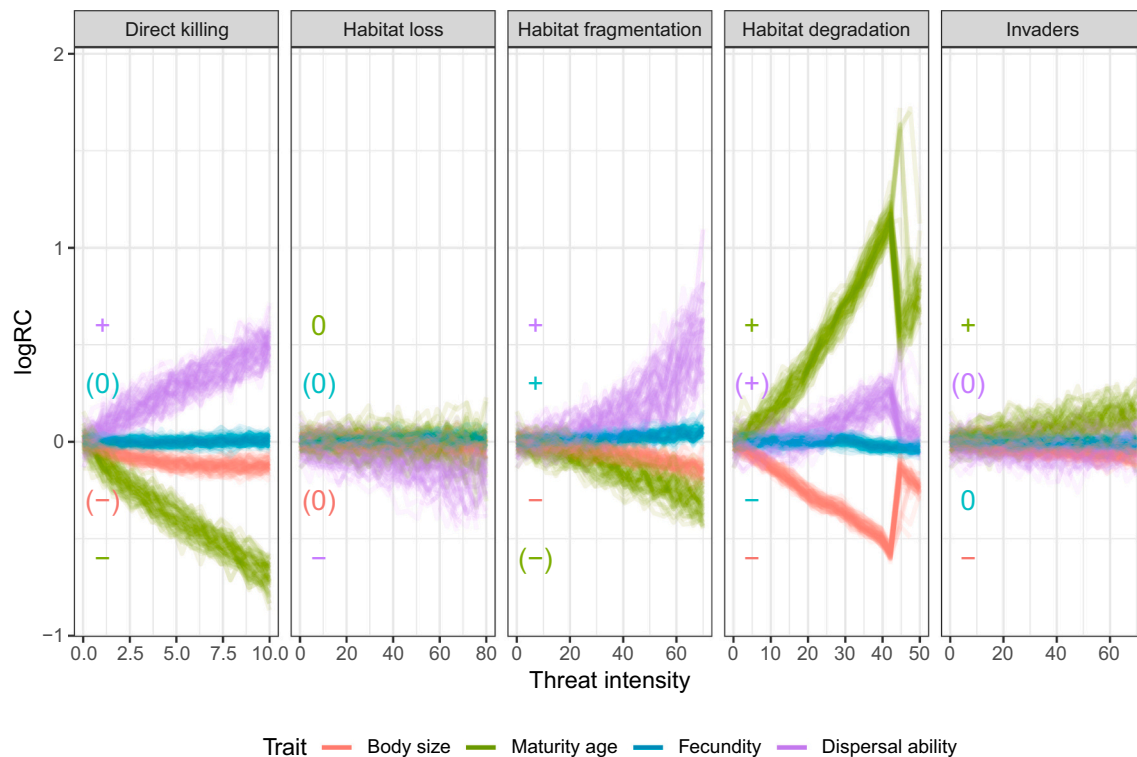
Fig. 4. Evolution of the mean value of each trait as a function of threat intensity per each of the 64 replicate assemblages. The threat intensity was a gradient from zero to the value that allowed at least 50% of the simulations without full extirpation of individuals. Each assemblage is represented 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.

fecundity increased with increasing fragmentation. All patterns were consistent with robustness except for maturity age, which during one robustness test showed a positive response. Although this threat also implied habitat loss, the change in trait values was greater under habitat fragmentation, revealing the direct effects of fragmentation beyond those of loss.

Maturity age and dispersal ability increased with increasing levels of habitat degradation, although there was an inflection point at extreme levels of perturbation (which did not have a qualitative impact on the direction of change). Body size and fecundity decreased, but again with inflection points in the intensity gradient. All patterns were robust to parameter values, except dispersal ability, which decreased under one particular scenario.

Adding competing invasive organisms with traits similar to the native led to increasing maturity age, and to decreasing body size. No change was detected in fecundity or dispersal ability. However, four robustness tests showed strong effects on dispersal ability, two of them increasing, and the remaining two decreasing. Robustness tests were consistent with the standard test for the other traits.

Maturity age and dispersal ability were generally the traits showing stronger signals across threat types.

4. Discussion

Our work confirms in simulated settings that different threat types act differently on organisms depending on their traits (González-Suárez et al., 2013; Murray et al., 2014). By using simulations, we were able to test settings and combinations of traits and threats that have never been studied before, in this way also generating new hypotheses to be tested in the future as adequate data become available. The way that organisms respond to threats or the probability with which species can become extinct may depend on the specific threats to which they are subjected.

Most patterns found were robust to different parameter values, meaning that the underlying mechanism should be consistent across many ecological systems in nature. The stronger responses of maturity age and dispersal ability across threats may indicate that life-history speed and movement patterns of species are expected to be highly selected under a large range of threat types.

4.1. Direct killing

Direct killing negatively affected large, slow-living, and poorly dispersive organisms. While the standard simulations did not find any significant effect on fecundity, the consistent, positive effect on fecundity found among many robustness tests suggests that organisms with low fecundity were also negatively affected by direct killing.

Large-sized organisms were removed from the environment because as organisms were killed at random, competition for resources diminished, which then reduced the need for the competitive advantage that larger size brings. Under some parameter value choices, however, small organisms were instead disfavoured. This seems to be due to the indirect effects of direct killing on resource availability. As organisms die, resources become more abundant. Abundant resources thus allow organisms to become larger under some parameter values.

Direct killing also heavily impacted organisms with slower life cycles. Organisms taking longer to reach maturity faced a greater probability of being killed before they were able to reproduce, and hence, the simulations became dominated by fast-living organisms.

Organisms with poor fecundity were disfavoured for many of the parameter values tested. As direct killing affected all organisms with the same probability, individual survival became less relevant than producing more offspring to compensate for mortality.

Our results also suggest that direct killing disfavours organisms with poor dispersal ability. This effect was again seemingly due to the

increased resources available in each cell; as organisms died more frequently, more resources became available. These resources were better exploited by those organisms that found them first, or those with more dispersal ability.

The widely reported extinction of megafauna before the 18th century has already shown that large-sized, slow-living, low fecund, and less mobile fauna are particularly susceptible, although it must be remarked that human hunting and fishing have long been selective towards large species (Diamond, 1989). The same pattern seems to be occurring in recent times, at least for vertebrate taxa. Among fish and mammal species threatened by overexploitation, larger sizes tend to be more at risk (González-Suárez and Revilla, 2013; Olden et al., 2007), a fact that is typically associated with their slow life cycles in addition to being preferential targets. Additionally, threatened mammals facing overexploitation show lower fecundity independently of size effects than those not threatened (Strauss et al., 2006; Warzecha et al., 2016). Other sources of direct killing, such as the presence of an alien predator species (Matsuzaki et al., 2011) or disease (Murray and Hose, 2005), could have affected organisms with the same traits that we found, but thus far studies examining interactions between threats and traits have been limited (Murray et al., 2014). In some robustness scenarios, small body size was selected against in our model. The increased vulnerability of small-sized individuals also emerged in a model evaluating the impact of predation on the size and maturity age of organisms, showing that prey size often increased when predation had an indirect effect on the resource availability of prey (Abrams and Rowe, 1996).

4.2. Habitat loss

Our model suggests that habitat destruction has a negative impact on organisms with high dispersal ability. Certain life-history strategies or environmental conditions may also lead to negative effects on large-sized organisms and to slow- or fast-living organisms.

Decreases in body size in some robustness tests could be explained by the reduction of total resource area in the environment. As habitat loss decreased the number of suitable habitat cells, it decreased the area of continuous suitable habitat, threatening larger size individuals that require abundant resources. Lower population sizes due to resource scarcity also incur a greater probability of local stochastic accidents (Pimm et al., 1988). Edge effects further exacerbate this due to high spatial resource unpredictability seen through the organism's point of view.

In some scenarios, the higher spatial heterogeneity may have negatively affected slow life cycles, because these organisms attain reproductive age more slowly, and thus reproduce less often, not compensating for mortality losses due to movement into the matrix of unsuitable habitats. On the other hand, slow-lived populations typically survive local extinction better at lower population densities than fast-lived populations (Pimm et al., 1988), and with less stochastic fluctuations, thus possibly conferring higher resilience in spatially heterogeneous landscapes.

Organisms with larger dispersal ability were negatively affected by habitat loss. As habitat decreases in size without alternatives where to move, individuals that invest in long-distance dispersal incur higher mortality.

The impacts of habitat loss on species' traits have not been studied extensively. Conceptually, larger sizes are thought to be the most susceptible to decreases in fragment area (Ewers and Didham, 2006). However, empirical evidence supporting the higher risk faced by larger organisms is very limited due to the existence of many confounding factors under the umbrella of body size (Ewers and Didham, 2006); large size may correlate with other traits that increase (e.g. dispersal ability (Warzecha et al., 2016)) or decrease (e.g. trophic level (Henle et al., 2004)) the organism's capability of surviving in areas with increased habitat loss. Likewise, the effects of habitat loss on lifespan have not been conclusive. Plants with greater longevity (and thus, high maturity age) were hypothesized to be better at coping with habitat isolation (Lindborg, 2007) as they face less fluctuations in their population levels, but fast life cycles have been shown to survive well in isolated fragments, probably because fast life cycles were also characterized by being very fecund (Lindborg et al., 2012; Marini et al., 2012). In a grassland that has faced extensive habitat loss, surviving plants in isolated habitat patches had greater seed output than the original species population prior to the habitat loss event (Saar et al., 2012), which the authors associated with their probable better ability to find microsites than species with lower seed output. A meta-analysis indicates that butterflies with poorer fecundity are more affected by habitat fragmentation (Öckinger et al., 2010). As for dispersal ability, evidence shows that when patches of remaining habitat are very isolated, organisms with reduced dispersal ability often cope better (Ewers and Didham, 2006; Henle et al., 2004; Saar et al., 2012). However, isolation and no dispersal may have consequences for genetic drift and erosion for organisms reproducing sexually (Zambrano et al., 2019), and for species' ability to respond and shift their geographical ranges in the face of climate change (Hodgson et al., 2011).

4.3. Habitat fragmentation

Habitat fragmentation had a negative effect on large, slow-living, and poorly fecund organisms, but a negative effect on poor dispersers. At the same proportion of habitat removal, the effect of habitat fragmentation on traits was stronger than that of habitat loss, revealing the importance of these two effects combined to drive population declines. Slow-moving organisms, being favoured under the pure habitat loss scenario, were disadvantaged under habitat fragmentation, as they could not move among a complex matrix of suitable and unsuitable cells.

With increased fragmentation, organisms with higher dispersal that could move to new, relatively easy-to-find cells, were likely to benefit, also avoiding the dangers of low population size and stochasticity in very small fragments.

Studying the impact that habitat loss and fragmentation have on species traits is challenging. First, because traits often correlate with each other. Second, because the literature on the effects of habitat loss and habitat fragmentation on species' traits is fuzzy, since the terms used are often interchangeable (Fahrig, 2017; Tscharntke et al., 2012; Zambrano et al., 2019). Third, because the effect of habitat loss and fragmentation on life-history traits may depend on the spatial configuration (Ewers and Didham, 2006). For example, the decrease in fragment area is thought to negatively affect mostly intermediate dispersers, whereas long-distance dispersers can find suitable patches elsewhere and poor dispersers do not incur unnecessary dispersal events that lead to increased mortality (Ewers and Didham, 2006; Henle et al., 2004). On the other hand, increasing fragmentation has been shown to benefit good dispersers. For example, species of butterflies and moths in fragmented landscapes were characterized by greater dispersal ability (Öckinger et al., 2010). Differences in dispersal ability among landscapes can be found even within species, whereas isolated patches in fragmented landscapes were more frequently visited by larger, more mobile wild bees (Steffan-Dewenter and Tscharntke, 1999; Warzecha et al., 2016).

4.4. Habitat degradation

Habitat degradation in our model largely equates to resource scarcity. Larger organisms require more resources, and are therefore especially vulnerable to reductions in resource quantity. In the model, organisms that mature more quickly survive for a shorter time as adults. Under these settings, the chances that they may be able to accumulate enough energy to reproduce are smaller. Therefore, greater maturity age is favoured, as it gives an opportunity to accumulate the energy required for reproduction. In the same way, by concentrating more energy on only a few offspring, organisms increase the odds that their offspring

will survive famine during the juvenile stage. Organisms that are poorer dispersers are disfavoured. As resources become less abundant, the necessity to rapidly find them elsewhere increases.

The effect of habitat quality as related to resource availability on biodiversity variables at a landscape level has been poorly studied, despite the fact that along with habitat loss and fragmentation, habitat degradation is one of the major drivers of species extinction (Mortelliti et al., 2010). Furthermore, isolating the effect of habitat degradation per se from other landscape-level drivers of change is difficult, as it often comes as a side-effect of habitat loss and fragmentation (Fischer and Lindenmayer, 2007; Mortelliti et al., 2010). Temperate ungulates are examples of animals that have developed slower life cycles in response to lower resource density, while minimizing their reproduction (Ferguson, 2002; Skogland, 1985). For instance, when food is scarce, pregnant wild deer abandon their fetuses in preference for their own survival (Skogland, 1985). Plants living in nutrient-poor scenarios usually have traits that confer low growth rates, such as high root-to-stem ratios and low specific leaf area (Grime, 1977). Likewise, cave organisms survive extreme resource-depleted scenarios. They are invariably long-lived, with low fecundity, and large organisms simply cannot survive entirely in caves due to lack of resources. All of these traits were favoured by our simulations, which replicate similar circumstances to those frequently occurring in degraded habitats. Our understanding of the mechanisms through which habitat degradation affects species is far from clear as we do not understand the types of traits that are selected (Mortelliti et al., 2010), even though habitat quality may typically outweigh the importance of habitat loss and fragmentation to species extinctions, as suggested by other agent-based simulations (Heinrichs et al., 2016).

4.5. Invaders

The effect of invaders was somewhat similar to habitat degradation, namely a reduction in body size and an increase in maturity age (but no effect on fecundity or dispersal ability).

Invasive organisms added competition for the same resources, reducing the number of resources available and causing similar outcomes for most traits. Organisms become smaller as a direct response to decreasing resource availability, compromising their ability to access resources due to their size being smaller than invasive organisms. To compensate for lower resource intake, organisms become longer-lived so as to accumulate resources over a longer period of time before reproducing. Invasive species had, however, no effect on the dispersal ability of natives. Under habitat degradation, the population density of organisms is reduced. Therefore, higher dispersal may be useful to find other cells of suitable habitat. Such is no longer the case with the addition of an invasive species. The density of native and invasive organisms combined does not change much in relation to the pre-invasive event, and therefore, if an organism disperses to another cell it may find the same density of organisms, curtailing the advantage of moving fast.

The impact of invasive species as competitors for the resources on the traits of native species has not been examined thoroughly. A previous study that examined plant plots invaded by alien species showed that the traits of successful native species were identical to those of alien invaders competing in the same plot (Loiola et al., 2018), namely their fast growth capacity, which is in disagreement with our results. Because plants are sessile, their only available strategy could be an increase in growth speed, while in our model the mobility of organisms may make other strategies plausible. Other studies, though, may provide indirect evidence that successful native species may be slower lived, with decreased size. For example, a study compared the traits of freshwater invasive, threatened native, and non-threatened native fish species, and found that threatened natives had significantly faster life cycles and higher fecundity than those of non-threatened native species (Liu et al., 2017). The authors suggested that the reduced fecundity and faster lives could be related to higher environmental stochasticity, and hence

reduced resilience in the face of environmental change. River systems are especially threatened by the presence of invasive species; in many regions the number of invasive fish species surpasses a quarter of the total species richness (Leprieur et al., 2008), and in this system in particular they could be the number one cause of extinctions (Light and Marchetti, 2007). Therefore, the faster life cycle of threatened fish species could be a consequence of the presence of alien competitors. Likewise, a meta-analysis of trait differences between invasive and non-invasive plant species has shown that natives are on average smaller and have lower growth rates than invaders (Kleunen et al., 2010). Oceanic islands are often even more impacted by invasives (Borges et al., 2020), with most extinctions worldwide being reported for isolated systems (Whittaker et al., 2017). However, the effects on the traits of native organisms were, to our knowledge, never studied and our simulations open an avenue for future research in the area.

5. Conclusions

In this study, we explored how widely the examined drivers of extinction can differently affect individuals (and species) with contrasting traits. Notably, we have shown that different threats lead to different outcomes, even in such simple scenarios as the ones we tested. Threats that directly induce increased mortality to assemblages are detrimental to species with slow life cycles and poor dispersal ability. Threats that decrease the amount of habitat in large contiguous areas are harmful to organisms with high dispersal ability. Habitat loss accompanied by fragmentation is harmful to large, poorly fecund organisms with low dispersal ability. Threats that reduce the quality and quantity of resources in a landscape are harmful to species with a reduced capacity to compete under low resource conditions, such as those that are large sized, or have rapid life cycles and high fecundity. Our work highlights the importance of considering both the type and intensity of any threat when studying the influence of biological traits on the extinction risk of species. We also open new avenues for future research as data become available, by predicting the unexpected effects of particular interactions between traits and threats.

Author contributions

FC, LC and PC designed the study, FC implemented the model and ran the statistical analyses. FC and PC wrote the first draft, and all authors contributed substantially to further revisions.

Data availability

The data and scripts required to reproduce the results of this manuscript are available in Figshare (https://doi.org/10.6084/m9.figshare.19195838).

Declaration of Competing Interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoinf.2022.101604.

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