Synergies among extinction drivers under global change

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If habitat destruction or overexploitation of populations is severe, species loss can occur directly and abruptly. Yet the final descent to extinction is often driven by synergistic processes (amplifying feedbacks) that can be disconnected from the original cause of decline. We review recent observational, experimental and meta-analytic work which together show that owing to interacting and self-reinforcing processes, estimates of extinction risk for most species are more severe than previously recognised. As such, conservation actions which only target single-threat drivers risk being inadequate because of the cascading effects caused by unmanaged synergies. Future work should focus on how climate change will interact with and accelerate ongoing threats to biodiversity, such as habitat degradation, overexploitation and invasive species.

Introduction

The extinction of species caused by direct perturbation, such as broad-scale tropical forest clearance for agriculture [1] or the elimination of island populations by introduced predators [2], constitutes the primary driver of biodiversity loss in the modern context [3]. Yet even when these systematic threats do not result in immediate extinction, a suite of pervasive secondary processes and synergistic feedbacks can eventually cause extinction [4–7]. The term 'synergistic' describes the simultaneous action of separate processes (extrinsic threats or intrinsic biological traits) that have a greater total effect than the sum of individual effects alone (i.e. positive and multiplicative interactions; Figure 1). For instance, habitat loss can cause some extinctions directly by removing all individuals over a short period of time, but it can also be indirectly responsible for lagged extinctions by facilitating invasions, improving hunter access, eliminating prey, altering biophysical conditions and increasing inbreeding depression [2,8–10]. Together, these interacting and self-reinforcing systematic and stochastic processes play a dominant role in driving the dynamics of population trajectories as extinction is approached [4,11], a concept we henceforth refer to as 'extinction dynamics.'

Research on extinctions has followed two complementary and overlapping approaches, focussing on (i) the patterns of extinction and (ii) the processes leading to extinction. Pattern-based research has compiled and analysed the extent and selectivity of past and current extinctions. Process-based studies aim to derive theory of the extinction process and fit models to empirical data to predict future biodiversity scenarios and guide conservation management (Table 1; also see online Supplementary Material Tables S1–3 for a tabulation and précis of 120 extinction-related syntheses published in books and ISI-ranked journals between 1988 and 2007). Our objectives in this review are to consider the generalities of extinction dynamics that have emerged from, or been reinforced by, recent observational and experimental work. By linking results from the latest and most innovative research, we demonstrate the increasing focus on the synergies among

Glossary

Allee effect: a decline in individual fitness at low population size or density [34].
Background extinction: extinction that normally occurs because of gradual environmental change, newly established competitive interactions (by evolution or invasion) and occasional chance calamities.
Coextinction: extinction of a species triggers the loss of another mutualistic species.
Declining population paradigm: the identification and management of the processes that depress the demographic rate of a species and cause its populations to decline deterministically [4].
Ecological chaos: nonlinear deterministic variation in the abundance of a population over time.
Ecosystem services: products (e.g. timber) and services (e.g. flood control) provided by the assemblage of species in an ecosystem.
Evil quartet: the four principal causes of modern extinctions are (i) habitat loss, (ii) introduced species, (iii) extinction cascades (chains of extinctions) and (iv) overexploitation [14].
Extinction debt: extinction of species or populations occurring long after the causative perturbation.
Extinction vortex: as populations decline, a mutual reinforcement occurs among biotic and abiotic processes that drives population size downward to extinction.
Extirpation: extinction of a local population, rather than of an entire species.
**Minimum viable population (MVP)**: the number of individuals in a population required to have a specified probability of persistence over a given period of time. Usually, a 99% probability of persisting for 100 years (or 40 generations) is used.
Small population paradigm: the study of the dynamics of small populations that have declined owing to some (deterministic) perturbation and which are more susceptible to extinction via chance (stochastic) events [4].
Synergistic processes: various perturbations can interact positively to increase the extinction risk of a species. For example, habitat loss might increase the vulnerability of some species to global warming by further stressing their physiological tolerance and making range shifts impossible (Figure 1).
Trophic cascade: a reciprocal predator–prey effect which alters the abundance or productivity of a population, community or trophic level across multiple links in a food web.

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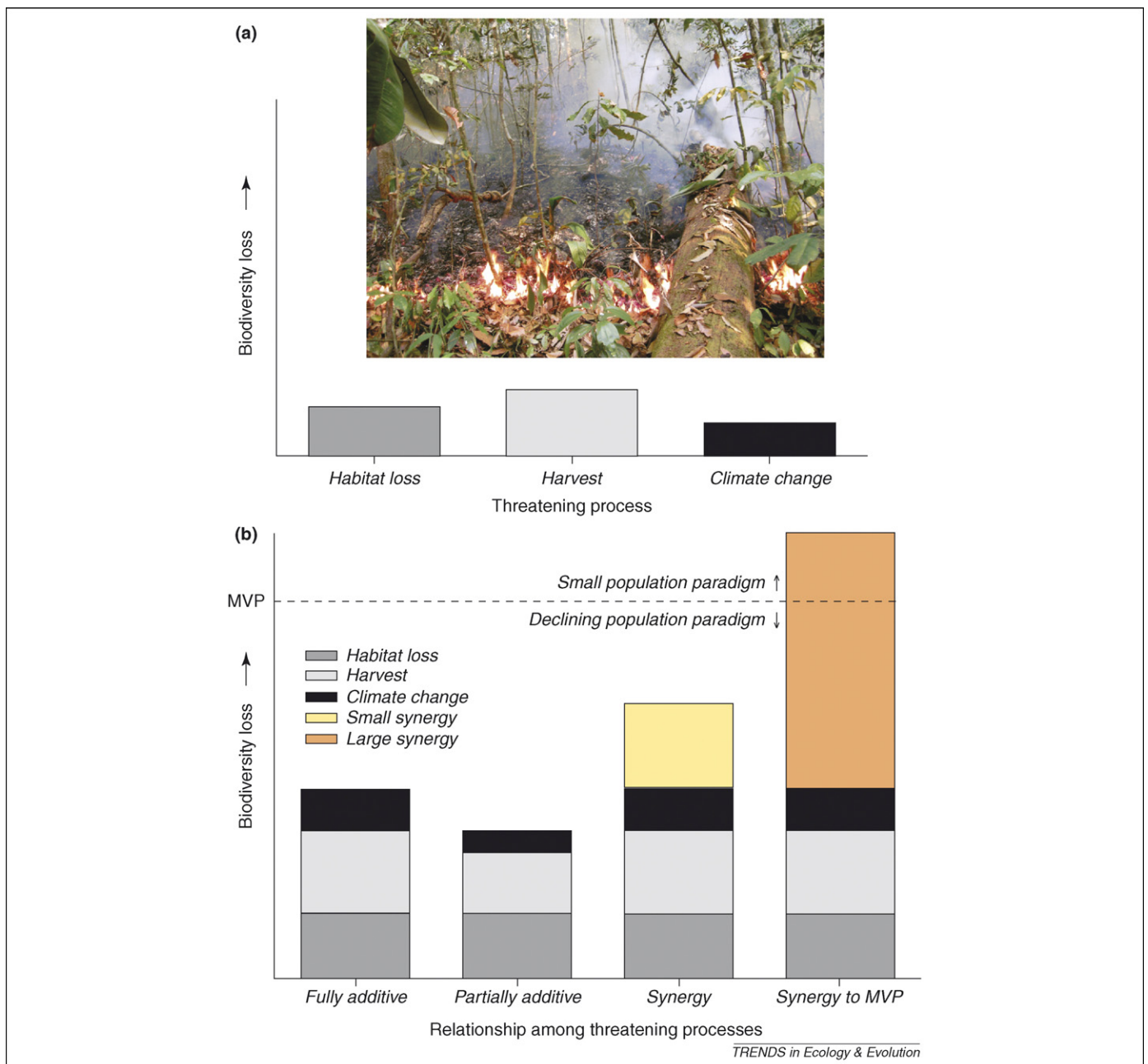
Figure 1. Threatening processes can cause biodiversity loss (either through declines in species' abundance or loss of species from communities), and they can act alone or in combination. The schematic shows three examples of threatening processes: habitat loss, harvest and climate change. **(a)** Acting singularly, each process has varying negative effects on biodiversity such as a reduction in carrying capacity (habitat loss), direct decline in abundance (harvest) or reduction in range size (climate change). Inset: a fragmented forest reserve in the northeast Brazilian Amazon in 2004 succumbing to fire (photo credit: Jos Barlow). **(b)** Many systems show multiple threatening processes acting together. A fully additive model predicts that the combined negative effects are simply the sum of each process's individual effects, whereas combinations might result in only partial additivity (e.g. further range restrictions from habitat loss encompass those predicted from climate change). A synergy among processes implies a positive interaction (feedback) whereby the total negative effect on biodiversity is greater than the sum of each threatening process's individual contribution. Small synergistic interactions will result in population decline (i.e. the declining population paradigm); however, only when large synergies occur that push populations below their minimum viable population (MVP) size does extinction risk become nonnegligible (i.e. the small population paradigm).

extinction drivers, rather than just their discrete, additive impacts.

Pinning down the principles of extinction
Extinction research has been successful in providing some broad generalities ('rules of thumb') of practical use to conservation management for avoiding loss of biodiversity and ecosystem function in the face of habitat destruction, overexploitation, introduced species and diseases, pollution and global climate change (Table 1). This has involved

devising novel tests or applications of fundamental principles that underpin biological extinction (e.g. allometry, species–area relationships, climate envelopes, extinction vortices and extinction cascades) [10,12–14]. It has also demanded careful selection of case studies that help determine the context within which rules of thumb are, or are not, relevant.

The broadest generalisations for extinction dynamics, derived from fossil, meta-analytic and experimental studies, are now firmly established [3,14,15]. We argue that

Table 1. Main conclusions on extinction trends, patterns, drivers, processes and predictions, drawn from two decades (1988–2007) of extinction-related reviews. These syntheses are categorised into five major topical themes

Major theme	Main conclusions
Mass extinction events	Varied causes: bolide impact; volcanism; marine anoxia; climate change
	No periodicity observed over geological time
	Extinctions continue through 'recovery' period
	Mass extinctions permit radiation and speciation of previously subordinate taxa
Correlates of extinction	Primary drivers: habitat destruction and fragmentation; overexploitation; pollution
	Secondary drivers of increasing importance: climate change; environmental variability; invasive species
	Evolved traits predispose species to extinction: narrow geographic extent; 'slow' vital rates; natural rarity; specialisation
	Allee effects; inbreeding depression important but poorly quantified
Pattern and process	Modern extinction rates $\gg$ background rate; nonrandom across taxa; lags common
	Causes of decline decoupled from causes of extinction
	Emergence of generalists following major die-offs
	Rapid modern extinctions change processes of evolution
	Biodiversity loss reduces ecosystem function and leads to more extinctions of codependent species
Role of humans	Humans are agents of '6th mass extinction event,' which started ~50 000 years ago and intensified during the past 500 years
	Language and agriculture permitted humans to exceed expected densities for large predators
Predictions	Patterns of past and modern endemicity required for prediction
	Multiple lines of evidence and generalised data required for meaningful predictions

More details and references can be found in Tables S1–3 in the online Supplementary Material.

generalities developed from either modern or ancient evidence are useful if contextualised within the current pace of change and appreciation for synergies among threatening processes. Extinction occurs most often when new threats emerge that are outside of the evolutionary experience of species or occur at a rate that outpaces adaptation (Table 1). Population size matters; small populations are more likely to go extinct as a result of chance effects (known as the small population paradigm [4]), but above a population-specific abundance [5,16], the short- to medium-term risk of extinction due to chance effects is negligible. Long-term persistence is consistently most sensitive to geographical range and dispersal ability [2,7,17]. One of the most comprehensive analyses of palaeo-extinctions demonstrated a consistent association between persistence of Phanerozoic marine invertebrates and geographic range size under successive bouts of global change [18]. The effect was strongest for background extinctions and weakest for mass extinctions. Widespread species, buffered against local environmental disturbances, experience far fewer range-wide catastrophes and so have lower extinction probabilities [17,18]. Traits such as ecological specialisation and low population density act synergistically to elevate extinction risk above that expected from their additive contributions, because rarity

itself imparts higher risk and specialisation reduces the capacity of a species to adapt to habitat loss by shifting range or changing diet [11]. Similarly, interactions between environmental factors and intrinsic characteristics make large-bodied, long-generation and low-fecundity species particularly predisposed to anthropogenic threats given their lower replacement rates [9,12,13].

Recent work has emphasised the importance of the biological (e.g. life-history traits and ecological relationships among species) and environmental setting (e.g. severity of regional threatening processes and local stochasticity) [2,3] within a framework of self-reinforcing feedbacks [11,19] for predicting extinction risk. For instance, species that are most vulnerable to habitat loss can be different, ecologically and evolutionarily, from those that suffer most from overexploitation. Forest-dependent tropical birds suffer disproportionately greater losses than do those species which select, or at least tolerate, open grassland and rain forest edge habitats [20]. Conversely, novel hunting pressure by invading humans in Pleistocene Australia left now-extinct megafauna marsupial species more vulnerable than arboreal species occupying closed forests [9]. Only those large ground-dwelling mammals that had high per-capita replacement rates, such as red and grey kangaroos (*Macropus rufus* and *M. giganteus*, respectively), persisted [9].

As such, it is usually only under the most intense selection pressures, or when multiple stressors interact [10,21], that context becomes irrelevant [12,22] for predicting the fate of species. This is the most parsimonious explanation for the different rankings of the relative explanatory power of extinction correlates among taxa and systems published in the peer-reviewed literature [16]. However, extinction models suffer from a tradeoff between generality and predictability because it is often difficult to quantify threats coherently and objectively. For example, models describing the effects of human hunting require data that are time consuming to collect, so generality is typically limited [23]. Conversely, global-scale models that are forced to adopt proxy measures of hunting intensity such as human density [8] cannot identify specific populations at risk. Balancing this tradeoff is challenging and will depend, in part, on the conservation objectives.

Commonalities among studies identifying the most consistent drivers threatening species serve as pointers to the most important general processes [2,13], and thus help to direct conservation management resources. Future research needs to focus on whether across-taxa generalities can be applied to local systems, such that any predictions are made with the type of threat, the rate of change and the environmental context clearly quantified. Some progress is already being made: a collation of data on 22 800 fish species showed that large-bodied marine fishes are disproportionately more threatened by commercial fishing, whereas habitat degradation and loss are the primary threats to smaller-bodied marine fishes [24]. A meta-analysis of the response of primates to forestry, agriculture and hunting showed that the relative vulnerability of particular species to the different threats were uncorrelated [25], indicating that the response of a species to one threat type cannot predict its potential response to others.

Extinction proneness and population viability

Establishing predictors of extinction is important for applying ecological principles to improve management efficiency and prioritise efforts to recover threatened taxa [2]. Empirically, the best-supported correlates of extinction include body size, geographical range, dispersal ability, reproductive rate and specialisation [3,15]. For instance, widespread species suffer fewer range-wide catastrophes than more geographically restricted taxa [18]. However, the processes that initially provoke population declines (the declining population paradigm) often do not deliver the coup de grâce because stochastic processes can then take over (the small population paradigm) [4,6]. Even though strong correlates of threat risk as indicated, for instance, by International Union for Conservation of Nature and Natural Resources (IUCN) status (http://www.iucnredlist.org), have been found for many taxa [3,13,26], only a few studies have used records of actual extirpations to predict extinction proneness [26–28]. This means that our ability to predict extinction (as opposed to threat) risk is limited. The point at which a population declines below a minimum viable population (MVP) size and is drawn into the extinction vortex [6] is therefore the threshold where the relative importance of different threatening processes is altered (Figure 1). MVP reflects the stochastic hazards encountered by a population that has already been reduced in size, rather than the sensitivity of a species to deterministic threats [4]. As such, recent simulation [5] and meta-analytic studies [16] have found little evidence for a correlation between MVP estimates and ecological or life-history traits (including body size). The only generalisation to emerge thus far from the collation of almost 1500 species-specific estimates is that MVPs follow a log-normal distribution among species, with median values of a few thousand, rather than tens of thousands of individuals [5,16]. In other words, there are no easy short-cuts to estimate the MVP of a population because it depends more on environmental context than the evolved traits of a species.

Extinction might not happen quickly once a population has been reduced – the death throes of a species often take decades to millennia to conclude. These are timescales beyond the reach of practical ecological monitoring. Therefore, controlled and replicated laboratory microcosms are useful for providing a manipulative and experimental basis for testing predictions based on extinction theory. For instance, the frequency distribution of the time to extinction for 281 replicate populations of water flea *Daphnia magna* under conditions of low and high environmental variability was considerably more peaked (leptokurtic) and had a longer tail (right-skewed) than current theory predicts [29]. This means that populations can sometimes persist by chance beyond expectation even though they are ultimately committed to extinction. Similarly, a spatially distributed network of ciliate *Tetrahymena thermophila* populations provided experimental evidence to support the premise that marine reserves reduce the extinction risk of harvested species [30]. The diffusion of individuals from high-density populations within harvest refugia (reserves) offsets the extinction of adjacent populations exposed to constant harvest rates [30], so even reduced populations might persist if buffered by the influx of individuals from less threatened populations.

It has long been understood that increased ecological chaos can result in population densities falling below an MVP more frequently, thus increasing extinction risk via demographic stochasticity [5,31]. However, ecological chaos is itself a complex combination of stochastic processes operating on both density-independent and density-dependent components of population dynamics, making assessments of extinction risk highly complex emergent properties of these interactions. Experiments with brine shrimp *Artemia franciscana* [32] and *Tribolium* flour beetles [33] indicate that inherent oscillations resulting from deterministic nonlinear population dynamics can be as or more important for determining extinction risk than initial population size or environmental drivers. Likewise, factors that cause a reduction in the growth rate of small populations as they decline, known collectively as Allee effects, are also an important determinant of extinction [34]. Maternal fitness of wild radishes *Rhaphanus sativus*, measured as a fruit set, was reduced from inbreeding depression beyond that expected by a reduction in population size alone [35]. Likewise a combination of laboratory and field experiments on an intertidal polychaete *Galeolaria caespitosa* demonstrated that environmental pollutants can act synergistically to reduce fertilisation success at low densities, thereby exacerbating Allee effects and extinction probability [19]. In other words, the form and intensity of density regulation (both negative feedback and Allee effects) are essential considerations in any model constructed to predict extinction risk.

Given the difficulty of detecting individuals at low densities, the reality of the Allee effect-driven extinction vortex has, until recently, been difficult to demonstrate. Fagan and Holmes [6] compiled a small time-series database of ten vertebrate species (two mammals, five birds, two reptiles and a fish) whose final extinction was witnessed via monitoring. Matching predictions from dynamical models [36], they confirmed that time to extinction scales to the logarithm of population size. They also found greater rates of population decline nearer to the time of extinction than earlier in the time series. This confirms the previously theoretical expectation that the combination of genetic deterioration [35] and associated Allee effects contributed to a general corrosion of population dynamics, driving an increasingly negative per-capita replacement rate as extinction was approached. Variability in abundance was also highest as populations approached extinction, irrespective of population size [6], thus demonstrating indirectly how chaos-induced demographic stochasticity [37] drives the final nail into a species' coffin.

Coextinctions and cascading losses

Beyond the focus of single-species extinctions, ecological processes disrupted by extinction or species decline can lead to cascading and catastrophic coextinctions, also called 'chains of extinction' [14]. Until recently, however, we have lacked appropriate data to test comprehensively the importance or generality of this phenomenon. Recently, the extirpation of Southeast Asian butterfly species has been positively linked to the decline and loss

of their specific larval host plants [38]. More broadly, Koh *et al.* [39] compiled a large database of interspecific systems (pollinators and plants, larval hosts, parasites) and used a fitted probabilistic host-specificity model to estimate that 6300 non-Red-Listed species could go extinct alongside their listed symbiont. The extinction of large predators can also, ironically, have devastating ecological consequences for codependent species complexes. Localised eradication of dingo *Canis lupus dingo* correlates strongly with an expansion of introduced meso-predators (cat and fox) and competitors (rabbits) in Australia. This has, in turn, led to large numbers of extinctions of native mammals in the arid regions of the continent [40]. In the marine realm, large predatory sharks have an analogous role in top-down control of medium-sized elasmobranchs (rays, skates and small sharks). Declines in six apex shark species (blacktip, bull, dusky, sandbar, tiger and great white sharks) over the past 35 years were linked to the collapse of a valuable scallop fishery in North Carolina owing to increased abundance and predation by cownose rays *Rhinoptera bonasus* [41]. Such trophic cascades leading to local extinctions are common [40,42].

Extinctions also disrupt or alter essential ecosystem services. A striking example of functional extinction-related breakdown in tropical forest ecosystems comes from dung beetles, which provide an essential nutrient-recycling role, act as vectors for seed dispersal and probably control the spread of parasites to vertebrates through the removal of dung [43]. Overhunting of mammals in tropical forests and the subsequent reduction in their dung has led to the local elimination of dependent dung beetles [44]. Worse still, heavier beetle species, capable of recycling the largest quantities of dung, are relatively more extinction prone [43]. With the loss of avian and mammal frugivores in degraded and fragmented forests, mid- and late-successional trees lose their primary long-distance dispersers and fail to replace themselves [45,46]. This eventually leads to the collapse of mature forest stands that support many specialist species [47]. A similar problem for rain forest trees has been reported in areas where seed-dispersing primates are overexploited [46,48]. In recognising that preserving ecological function reduces the risk of cascading extinctions, Kareiva and Marvier [49] argue that better conservation outcomes are only possible if human health and welfare are linked to the maintenance of ecosystem services rather than just relying on the intrinsic valuing of biodiversity.

### Synergies among extrinsic drivers of extinction

Like interactions within species assemblages, synergies among stressors form self-reinforcing mechanisms that hasten the dynamics of extinction. Ongoing habitat destruction and fragmentation are the primary drivers of contemporary extinctions [45], particularly in the tropical realm [21,50,51] (Box 1), but synergistic interactions with hunting, fire, invasive species and climate change are being revealed with increasing frequency [1,8,10,17,21,23,52].

By using detailed extinction data [20,28] coupled with theoretical species–area relationships, Sodhi and Brook [1] demonstrated that continued deforestation was projected to result in up to 79% of Southeast Asian vertebrates being

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Box 1. Tropical crisis – epicentre for current and future extinctions

Several basic tenets of macroecology predict that tropical species are more numerous [1], more likely to be endemic, more range-restricted and smaller than their temperate counterparts (Rapoport's Rule [61]; but see Ref. [62]); hence, a greater proportion of tropical species could be at risk of extinction than elsewhere. Recent evidence suggests that the humid tropics, encompassing the region between the latitudes of 23.5° north and south, is where the modern extinction crisis will have the greatest effect [20,47,52,55]. Other than the boreal region, tropical areas represent the largest remaining tracts of continuous pristine forested habitats. Indeed, the tropics contain the highest number of threatened species overall; for example, there is approximately an order of magnitude more threatened amphibian species and seven times more bird and mammal species (http://www.iucnredlist.org) within tropical compared to non-tropical biodiversity hotspots (areas of high endemism and rapid habitat change [63]) (Figure I). Coupled with accelerated rates of habitat loss and degradation, global warming, increase in nitrogen deposition and invasive species [50–52], the hypothesised higher innate extinction proneness and greater concentrations of tropical biodiversity predict increasingly severe species losses. This notion is supported by the distribution of the 34 terrestrial biodiversity hotspots worldwide – nearly 60% are found in the tropics.

Unprecedented native habitat loss and synergies among extinction drivers [1,17,52] demand that tropical conservation interventions attempt to mitigate invasive species and counter climate trends (reducing greenhouse gas emissions) in addition to preserving and restoring habitats. For instance, post-Kyoto Protocol international agreements should formally recognise the carbon-offset benefits of retaining primary tropical forests and discourage agricultural expansion for food and biofuel production into remaining forests.

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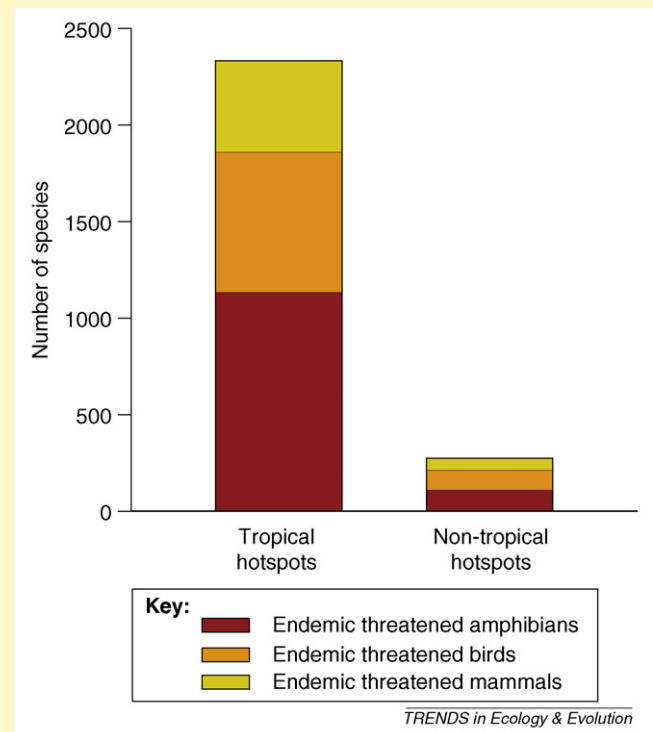
Figure I. The number of tropical versus non-tropical endemic species that are listed as threatened by the IUCN, for the three most speciose terrestrial vertebrate classes (amphibians, birds and mammals).

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consigned to extirpation by 2100, with the time frame of their final loss depending on the lag in their extinction debt. More than half of these losses (over 4000 vertebrate species) are endemics and would constitute global
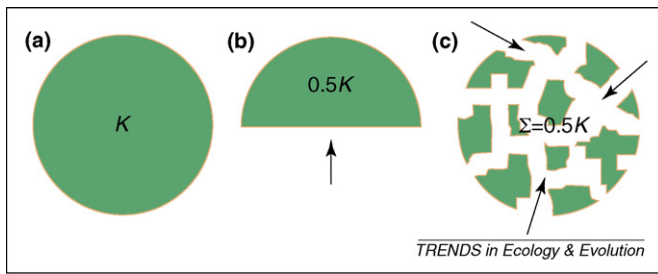
Figure 2. Synergies among threatening processes relative to habitat loss and fragmentation. **(a)** A large population within unmodified, contiguous habitat occupies all available niches so that long-term abundance fluctuates near full carrying capacity (K). **(b)** When habitat is reduced (e.g. 50% area loss), total abundance declines accordingly. **(c)** However, this simple habitat–abundance relationship is complicated by the spatial configuration of habitat loss. In this example, all remaining fragmented subpopulations might fall below their minimum viable population (MVP) sizes even though total abundance is the same proportion of K as in (b). As such, limited connectivity between subpopulations implies much greater extinction risk than that predicted for the same habitat loss in less fragmented landscapes. Further synergies (positive feedbacks among threatening processes; arrows) might accompany high fragmentation, such as enhanced penetration of predators, invasive species or wildfire, microhabitat edge effects and reduced resistance to drought with climate change.

extinctions. Yet this model projection was predicated on the assumption that only a single driver (habitat loss) increases extinction risk. This is likely to be overly optimistic (Figure 2), because deforestation also inevitably causes fragmentation [8,53], which in turn leads to the protracted loss of long-lived taxa such as tropical trees [20], even if some forested areas remain intact [54]. Tree mortality and damage can be as much as three times

higher within 60 m of the forest edge compared with the forest interior [21], with the edge-sensitive species being most vulnerable [53]. Logging trails increase access to forest interiors, facilitating a now-rampant bushmeat trade in central Africa, Southeast Asia and the neotropics that has severely reduced the density and distribution of target species [1,8,55]. Forest clearance and fragmentation also cause localised drying and regional rainfall shifts, enhancing fire risk and curtailing the capacity of species to move in response to shifting bioclimatic conditions (Figure 3; Box 2). Acknowledging these synergies implies that conservation measures designed only to stem the primary threatening process (such as deforestation) are unlikely to be effective in preventing these flow-on extinctions.

Climate change is already beginning to exacerbate other extrinsic threats (Box 2). In an experimental context, habitat fragmentation and overharvesting combined with environmental warming in rotifer zooplankton resulted in populations declining up to 50 times more rapidly when combined than when acting singularly [10] (i.e. a nonadditive effect; Figure 1). An excellent real-world example comes from the highland forests of Costa Rica, where 40% of 50 endemic frog and toad species disappeared following synchronous population crashes during the late 1980s [56]. Recent work has linked these extinctions to an interaction between global warming and disease [57], whereby a retreat of moisture-laden clouds led to a prolonged drying of the montane forest. In a chain of adverse events, this increased the prevalence of pathogenic chytrid fungus
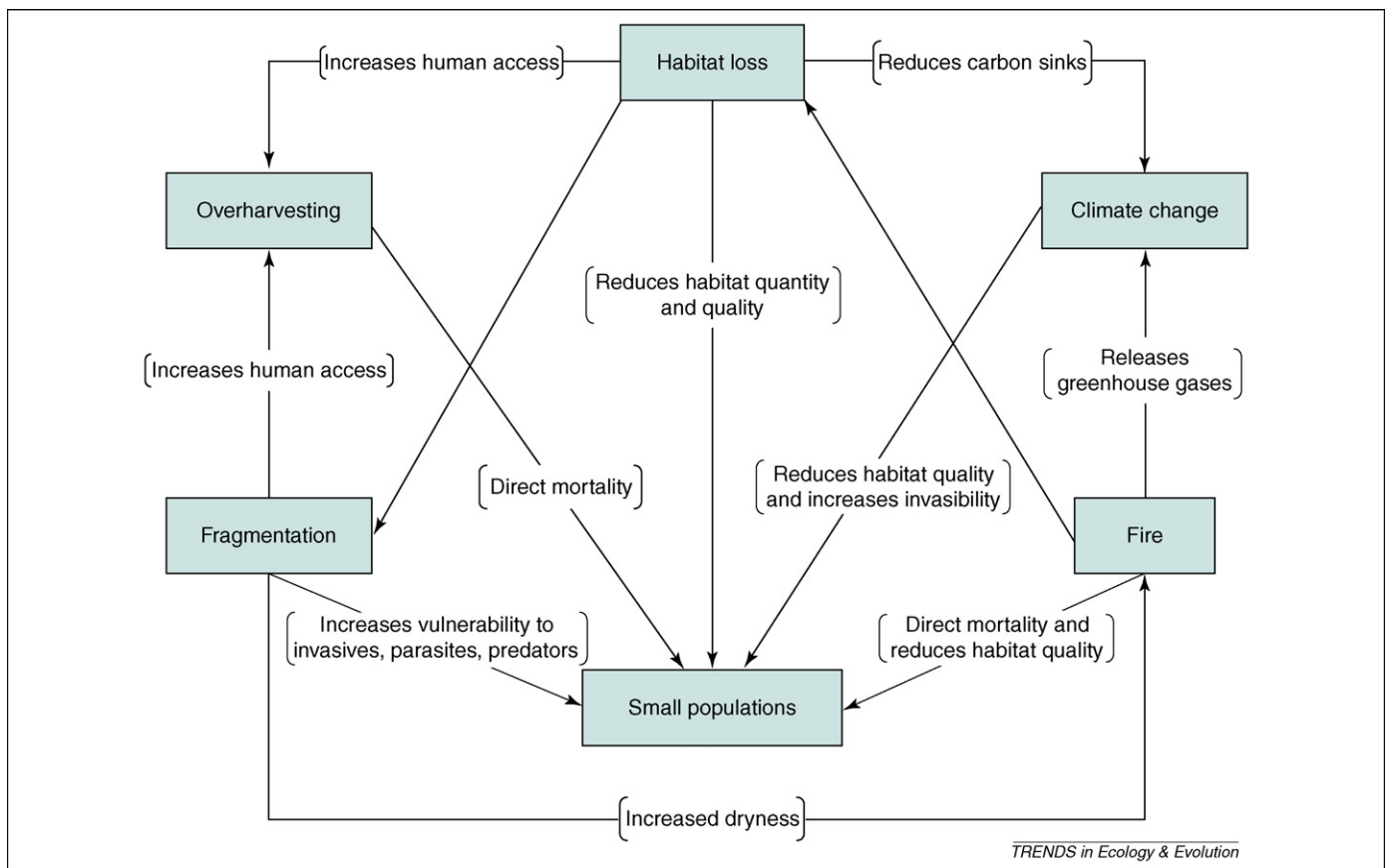
Figure 3. An example of the synergistic feedbacks which threaten species in disturbed tropical rain forests [1,20,28,55].

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Box 2. Climate change and the evil quartet

In a famous synopsis of the sources of human-caused extinction, Diamond [14] defined the evil quartet of drivers: overkill, habitat destruction, introduced species and chains of extinctions. Later work underscored the point that most extinctions involved a synergy of these factors [10,39,64,65], with individual causes being difficult or impossible to isolate [4,64]. We must now add severe anthropogenic interference with the global climate system to this list. The response of biodiversity to past global climate change characteristically unfolded over thousands to millions of years [18,22,66], whereas anthropogenic global warming is now occurring at a greatly accelerated rate. If carbon emissions are not reduced rapidly, the Intergovernmental Panel on Climate Change's Fourth Assessment Report 2007 (http://www.ipcc.ch) projects a rate and magnitude of 21st century planetary heating that is 5–9 times greater than that of the past century. This is comparable to the difference between now and the height of the last glacial maximum. A clear lesson from the past is that the faster and more severe the rate of global change, the more devastating the biological consequences [2,3,15,66].

Compounding the problems associated with the rate of recent climate change is that species trying to shift distribution to keep pace must now contend with heavily modified landscapes dominated by agriculture, roads and urban development [47]. Even in cases where global warming might allow species to expand their range, these benefits can be outweighed by other local threats such as habitat modification [67]. Range sizes are likely to contract along warmer or drier margins (latitudinal or elevational), or even within core areas [23], but will fail to expand in the other direction [17,52]. The new bioclimatic conditions and altered composition of ecological communities might also facilitate invasions by non-indigenous species that act as novel competitors or predators to stress resident species further [1]. Harvest, habitat modification and altered fire regimes will also interact with, and probably enhance, the direct impacts of climate change [1,10] (Figures 1 and 2).

Many questions remain. What can biotic adaptations and extinction in the face of past climate change tell us about likely future responses? Current knowledge suggests some possibility for adaptation via adjustment of the physiological tolerance or range of species [67,68], but even optimistic scenarios predict rates of change that will outpace the adaptation capacity of many species [17,52,69]. Furthermore, is it possible to generalise about which clades and environments will be most vulnerable to climate change, given that it is occurring at unprecedented rates? How much biodiversity will be lost, and will the ecosystem functions of most value to humanity be maintained? Such urgent questions sit squarely within the purview of extinction dynamics, but require greater attention and development [51,65] by focussing on community rather than species-level responses, by coupling physical and biological models and by dedicating more attention to the quantification of ecosystem functions such as nutrient cycling, pollination patterns, decomposition rates and carbon sequestration potential in the face of climate change.

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Batrachochytrium dendrobatidis, which invaded from lower altitudes [58,59]. Yet perversely, a wetting of the lowland Costa Rican forests (more rainy days, although no change in mean rainfall) caused population declines in some species due to an enhanced decomposition rate of leaf litter habitat [60].

Conclusions

Recent research has highlighted the relative strengths and limitations of alternative approaches used to identify and infer cause and effect of extinctions. For example, although it is difficult to extrapolate microcosm experiments [29–33] to broad-scale, real-world processes, when combined with observations of local extinctions [20,26],

meta-analyses [11,16] and statistical inference from correlates and simulation models [5,13,23,28], the mechanisms revealed by experimental extinctions offer powerful explanations for patterns spanning time periods and spatial scales that are problematic for laboratory or field manipulation.

This review shows that extinction research has shifted substantially over the last decade, from studies that focussed primarily on the impact of single drivers to those which have demonstrated a positive interaction (synergies, or reinforcing feedbacks) of more than one threat via a combination of approaches. This view explicitly emphasises how positive feedbacks corrode ecosystem function and energy flow [10,11,39]. The implication of this recent body of work is that only by treating extinction as a synergistic process will predictions of risk for most species approximate reality, and conservation efforts therefore be effective [6,9,45,52,57]. However challenging it is, policy to mitigate biodiversity loss must accept the need to manage multiple threatening processes simultaneously over longer terms. Habitat preservation, restoring degraded landscapes, maintaining or creating connectivity, avoiding overharvest, reducing fire risk and cutting carbon emissions have to be planned in unison. Otherwise, conservation actions which only tackle individual threats risk becoming half-measures which end in failure, due to uncontrolled cascading effects.

Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2008.03.011.

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