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Interactive effects of habitat modification and species invasion on native species decline

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Different components of global environmental change are often studied and managed independently, but mounting evidence points towards complex non-additive interaction effects between drivers of native species decline. Using the example of interactions between land-use change and biotic exchange, we develop an interpretive framework that will enable global change researchers to identify and discriminate between major interaction pathways. We formalise a distinction between numerically mediated versus functionally moderated causal pathways. Despite superficial similarity of their effects, numerical and functional pathways stem from fundamentally different mechanisms of action and have fundamentally different consequences for conservation management. Our framework is a first step toward building a better quantitative understanding of how interactions between drivers might mitigate or exacerbate the net effects of global environmental change on biotic communities in the future.

Multiple causal agents of decline

An explicit goal of global change research is to better predict and manage human impact on biodiversity [1], ecosystem functioning [2] and, ultimately, human welfare [3]. Meeting this objective will demand more than the current focus on the independent effects of land-use change [4], atmospheric CO₂ increase [5], climate change [6], anthropogenic nitrogen deposition [7] and increasing biotic exchange [8]. It is becoming clear that the impact of one global change driver (see Glossary) can be strongly dependent on the effects of other drivers acting in concert [9]. There is growing recognition that we lack even a basic understanding of how the interactive effects of global change drivers might mitigate or exacerbate total ecosystem effects in the future [1,9].

Here, we explore the ecological implications of interactive effects between multiple drivers of global change, and discuss appropriate management strategies for mitigating native species decline when interactive effects are operating. We do not attempt to describe the effects of all possible pairwise interactions between drivers or to provide

a complete synthesis of empirical evidence across such a broad topic. Rather, our goal is to develop an interpretive framework that will enable global change researchers to identify and discriminate between the different causal pathways of interaction between multiple drivers. We hope this will stimulate increased research emphasis on interactive effects that transcend traditional discipline boundaries.

To illustrate our arguments, we focus on selected examples of interactive effects between land-use change and biotic exchange. These are widely considered to be the

Glossary

Antagonistic interaction: Non-additive, emergent property of the interaction between multiple factors that diminishes the impact of the factors below what would be predicted from the simple additive effects of these processes operating independently.

Driver: A variable that is causally linked, through direct or indirect pathways, to a measured change in a response variable.

Interaction chain: A term used in an analogous manner to indirect interaction chain effects in food-web ecology. It describes a chain of direct linkages between the effects of habitat modification (or other factors) on invasive species abundance/numerical dominance, which, in turn, has a direct effect on native species decline. This results in an apparent indirect correlation between higher order factors and native species decline.

Interaction modification: A term used in an analogous manner to indirect interaction modification effects in food-web ecology. It describes how the direct per capita impact of invasive species on native species is dependent on the context of another indirect causal agent of decline (in this case, the landscape disturbance context).

Invasion impact: Positive or negative effect of invasive species on the environmental, social or economic conditions in the invaded location, resulting from the product of the geographical extent of invasive populations, the abundance or biomass per unit area, and the per capita or per unit biomass effect on native species.

Invasive dominance: The degree to which the abundance or biomass of invasive species outnumbers or outweighs that of native species. Used synonymously with 'numerical dominance', rather than as reference to the outcome of interspecific interactions.

Invasive species: Non-native organisms (excluding humans) that become established in a location outside their natural geographical range and cause, or have the potential to cause, environmental, social or economic change.

'Main effects' conservation management: Consideration of multiple causal agents of native species decline in an implicitly additive manner (if at all), often followed by selection or acceptance of the single dominant factor that explains the greatest proportion of the effect size.

Non-additive: Emergent property of the interaction between two or more factors that cannot be predicted or explained by adding together the individual effects of the factors considered in isolation.

Synergistic interaction: Non-additive, emergent property of the interaction between multiple factors that magnifies the impact of the factors beyond what would be predicted from the simple additive effects of these processes operating independently.

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two most important contemporary drivers of biodiversity loss [1] and yet they are most often studied independently. Of 11 588 studies on land-use change ('habitat loss' or 'habitat fragmentation' or 'land use') and 3528 studies on species invasion ('invasive species' or 'species invasion' or 'introduced species' or 'alien species' or 'exotic species') published between 2002 and 2007 (ISI, March 2007), only 178 (1.2%) investigated both land-use change and species invasion simultaneously, and only 4 (0.03%) also used the term 'interaction'. Moreover, we found examples of interactive effects that were not recognized as such and therefore not reported. Finally, we explicitly recognize that these are only two of many possible interacting factors, and briefly discuss potential interactions between climate change, CO₂ increase and nitrogen deposition.

A framework to assess interactive effects

"The search for a single invasive strategy is illusory" [8]

Early progress in invasion biology was divided along strongly defined lines of invader traits [10] versus invasibility of the recipient ecosystem [11,12]. However, the emerging realization is that these two components of invasion success are not independent [8,13]. Instead, the answers to the most important 'invasion' questions depend on the degree of interdependence with other global change drivers [8]. Principal amongst these factors is the strong correlation between loss of native habitat and increase in abundance of invasive species [11,14,15], which makes it difficult to identify causal pathways of native species decline [14,16,17]. In some instances, habitat modification might drive increases in the local abundance or regional distribution of invaders, with total invasive impact scaling in direct proportion to invader abundance (a numerically mediated process). In other instances, habitat modification might change the mode of action or functional response of invasive species, with total impact scaling disproportionately with invader abundance (a 'per capita' or functionally moderated process) [18]. Although both of these processes can lead to increased impact in modified habitats, we formalise the distinction between numerical and functional effects, and adopt terminology from the study of indirect interactive effects in food-web ecology [19] to describe two types of interaction pathways (Box 1). First, we define an 'interaction chain effect' as the indirect mediating effect that habitat modification has on native species decline by altering the numerical abundance or geographic range size of an invasive species (Box 1, Figure 1a). Second, we define an 'interaction modification effect' as the direct moderating effect that habitat modification has on the per capita impact of invasive species on native species (Box 1, Figure 1b). Although the two interaction pathways might both result in changes in total invasive impact that are superficially indistinguishable from each other (Box 1), we show that it is important to discriminate between the two pathways because they stem from fundamentally different mechanisms of action and have fundamentally different consequences for conservation management strategies.

Interaction chain effects

The simplest interaction between habitat modification and invasion occurs when habitat modification drives increased invader abundance, but per capita invasive impact remains constant (Box 1). Interaction chain effects are likely to be common, as invader abundance typically increases following all forms of natural and anthropogenic disturbance [11,15,20]. Moreover, the landscape-level context to disturbance can enhance these local site effects [21,22]. For example, forest edges are important local foci for invasion of Amur honeysuckle *Lonicera maackii* into woodlots in Ohio, USA, but landscape factors controlling propagule pressure, such as distance to nearest town, are more important determinants of geographic spread [21]. Empirical studies are strongly supported by simulation models showing that the local density of invasive species is determined not only by local habitat quality, but also by the spatial structure of the habitat in the surrounding landscape [22,23]. Increasing the amount of suitable habitat for invasive species increases total population size in the landscape [23], which drives an increase in local density due to increased propagule pressure.

The non-linear response of invasive potential to habitat availability in model simulations [23] suggests that even a comparatively small increase in habitat change over time can lead to an abrupt increase in invader abundance. In practice, whether the relationship between habitat modification and invasive abundance is linear or non-linear is species and context dependent, but the distinction is of management importance because invasive potential might not be predictable from ecosystem response below a habitat loss threshold [23]. Such landscape-scale threshold effects on the density of invasive species [23] might explain abrupt shifts in exotic dominance beyond a threshold of habitat cover [24], often following prolonged lag phases [8]. For example, after coexisting for 125 years, habitat destruction led to a sudden shift from native *Mytilaster*-dominated to invasive *Brachidontes*-dominated mussel communities in the Mediterranean Sea, stemming from a change in the relative importance of competitive ability versus stochastic colonisation success in disturbed habitats (Box 2) [25].

Another landscape-scale mechanism explaining invasive impact is that generalist invasive predators reach high densities in modified habitats by utilizing food resources in matrix habitats [26–28] and then 'spill over' [27,29] into native habitats. Spatial resource subsidies represent a fundamental mechanism by which habitat modification interacts with invasion to increase the mortality of native organisms within habitat remnants [26,27,29]. For example, the invasive predatory beetle *Coccinella septempunctata* was more than three times as abundant in native grasslands embedded within cropland-dominated landscapes than at control sites in more pristine grassland-dominated landscapes [29]. Consequently, habitat modification magnified predation pressure on native aphid *Bipersona* sp. through invasion of coccinellid predators from the surrounding matrix [29].

Habitat modification can also drive insidious sublethal effects of invasive species [30,31]. For example, invasion of

Box 1. A framework for interpreting interactive effects

Interactions between global change drivers can be divided into two major types, based on their broad mechanism of action. First, there are numerically mediated effects, which we call interaction chain effects, because the per capita or per unit effect of one global change driver is constant across all levels of effect of other drivers. Total impact only increases because of a numerically scaled response to a second driver variable. For example, abundance of invasive species might increase with habitat modification, possibly leading to greater total impact on native species in disturbed areas (Figure 1a). Interaction chains can be quantified effectively using path analysis [16,17]. Second, there are functionally moderated effects, which we call interaction modification effects, because the per capita or per unit effect of one driver variable increases or decreases with the level

of effect of a second driver (Figure 1b). Quantifying interaction modifications might require more judicious use of experimentation [55].

Both interaction types represent non-additivity in the combined effects of the two interacting factors, such that the net outcome of the two processes is significantly more (a synergistic effect) or less (an antagonistic effect) than the sum of the two processes operating independently. In Figure 1b, a synergistic interaction is shown only for the effect of habitat modification on the interaction between invasive and native species. However, species invasion might also alter the impact of habitat modification on native species (e.g. [39]) or interactive effects between the two factors might be antagonistic (e.g. [40,41]).

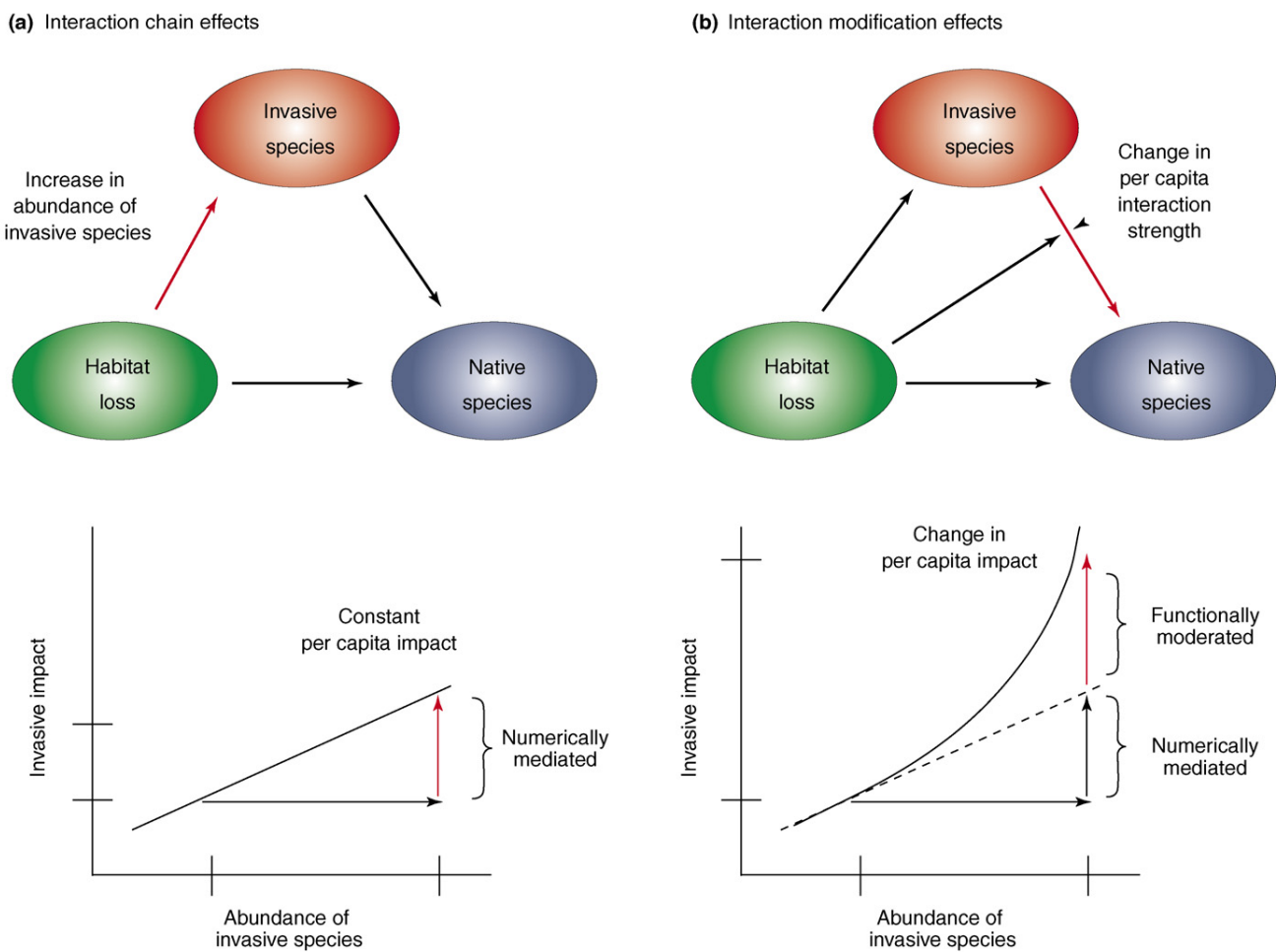


Figure 1. Two major pathways by which habitat modification can interact with species invasion to increase the total impact on native species. (a) In an interaction chain effect, total invasive impact on native species is increased by the indirect effect of habitat modification on invader abundance, but the per capita invader impact (i.e. the slope of the abundance/impact relationship) remains constant at all levels of habitat modification. (b) In an interaction modification effect, total invasive impact is dependent not only on invasive abundance, but also on the degree to which habitat modification alters ecological interactions between invasive and native species (indicated by the opposing arrow-head symbols). For clarity, no feedback effects are shown between species invasion and habitat modification, and the direct impact of habitat modification on native species is not represented in the graphs. The positive curvilinear relationship between invasive abundance and impact (b) is only one of many possible relationships [56].

flowering Siam weed *Chromolaena odorata* into logged forests in Thailand attracted butterfly pollinators away from native *Dipterocarpus obtusifolius* flowers, leading to a seven- to eight-fold reduction in pollinator visitation in modified habitats [31].

Interaction modification effects

There are a growing number of examples in which invasive impact cannot be explained without recourse to the moderating influence of habitat modification on the per capita interaction strength between native and invasive species.

Box 2. Empirical examples of interactive effects**An interaction chain effect: mussel invasion in the Mediterranean**

The mussel *Brachidontes pharaonis* colonised the Mediterranean Sea via the Suez Canal in 1869, but remained rare before 1995 (Figure 1a) [25]. Early studies predicted that it would not become invasive because it was an inferior competitor to native *Mytilaster* in near-shore habitats [25]. However, a recent increase in habitat degradation led to *Brachidontes* dominance of offshore platforms, providing large source populations for propagules, which saturated near-shore beachrock habitats. This caused a dramatic shift from *Mytilaster*-dominated to *Brachidontes*-dominated communities on near-shore beachrock [25], which might otherwise have been a sink habitat for invasive species. Therefore, habitat destruction altered the population-level outcome for native species by increasing the relative importance of stochastic colonisation by invasive propagules, even in undisturbed habitats [25,57].

An interaction modification effect: earthworm invasion in California

In California, USA, the native earthworm *Argilophilus marmoratus* is restricted to relatively undisturbed grasslands, following displacement by the invasive earthworm *Aporrectodea trapezoides* in areas converted to livestock grazing (Figure 1b) [32]. In an elegant set of competition experiments, Winsome and colleagues [32] showed that native *Argilophilus* were outcompeted by invasive *Aporrectodea* in high-productivity disturbed habitats because of the greater absolute and relative growth rate per unit resource consumption and earlier onset of reproduction of *Aporrectodea* [32], even though *Argilophilus* grew faster in disturbed than undisturbed grasslands when *Aporrectodea* was excluded [32]. However, in less productive natural grasslands, *Aporrectodea* failed to acquire enough resources to maintain its rapid growth rates or reach reproductive maturity [32].

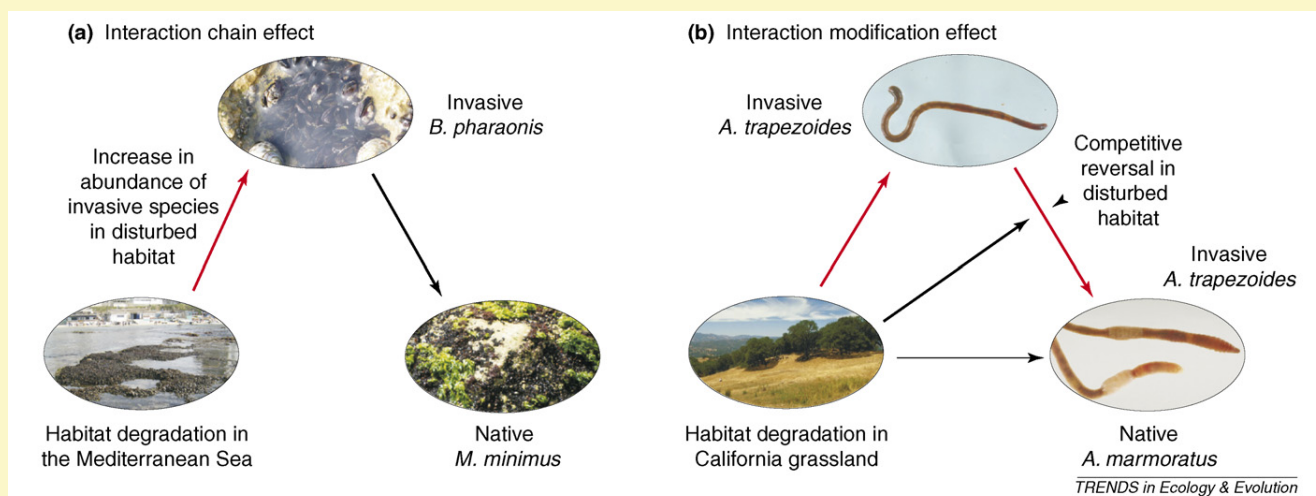


Figure 1. Empirical examples of interactive effects. (a) Interaction chain effect, in which habitat degradation in the Mediterranean Sea caused an increase in abundance of the invasive mussel *B. pharaonis*, displacing the native mussel *M. minimus* in near-shore habitats through increased propagule pressure. In this example, habitat degradation occurred on offshore platforms, so there is no direct effect of habitat change on native decline in near-shore bedrock. Photos reproduced with permission from Gil Rilov. (b) Interaction modification effect, in which grassland conversion to agriculture in California increased productivity, driving both an increase in abundance of the invasive earthworm *A. trapezoides* and a competitive reversal over the native earthworm *A. marmoratus*. In this example, native earthworms had higher growth rates in high-productivity conditions typical of disturbed habitats, so the direct effect of habitat change on native earthworms is likely to be small, and potentially positive, in the absence of invasive earthworms. Photos reproduced with permission from Thais Winsome.

In semi-natural grasslands in California, the native earthworm *Argilophilus marmoratus* outcompeted the invasive earthworm *Aporrectodea trapezoides* because of its greater ability to acquire resources in low-productivity conditions [32]. However, a competitive reversal occurred in disturbed habitats because of the higher relative growth rates of invasive *Aporrectodea* in high-productivity conditions (Box 2). Similarly, under natural salt marsh conditions in Rhode Island, USA, native plants outcompeted invasive *Phragmites* for soil nitrogen [33]. However, loss of woody vegetation in adjacent coastal habitats increased surface nitrogen runoff and the consequent amelioration of nitrogen limitation allowed *Phragmites* to dominate native species in aboveground competition for light [33]. In Washington State, USA, disturbance allowed invasive dwarf eelgrass *Zostera japonica* to rapidly replace native eelgrass *Zostera marina* on tidal mudflats, even though experimental field transplants showed that native eelgrass was the superior competitor under natural conditions [34].

Habitat modification might also affect per capita interaction strength between native and invasive species via alteration of predator–prey interactions in disturbed

landscapes [26,28,35]. Invasive brown-headed cowbirds *Molothrus ater* caused higher rates of nest predation on neotropical migrants at forest edges than in forest interiors in the USA, but only in landscapes with moderate to high levels of habitat modification [28]. The majority of *Molothrus* studies can be considered to be reporting numerically mediated interaction chain effects [36]. However, a range of mechanistic explanations for the alteration of per capita *Molothrus* impact have also been proposed [36], including changes in prey apparency following structural vegetation change, prey switching or changes in foraging activity due to clumping of spatial subsidies in the surrounding landscape [26,36].

Analogous effects of spatial subsidies are known in epidemiology, whereby non-native reservoir hosts in matrix habitats maintain high rates of pathogen transmission to native populations in habitat fragments [37,38]. For example, incidence of barley yellow dwarf virus (BYDV) in native blue wildrye *Elymus glaucus* doubled when exotic wild oats *Avena fatua* were present in a Californian landscape [37]. Increased infection rate represents an interaction chain effect, but recent studies suggest that the associated increase in mortality is due to an interaction

modification effect arising from BYDV-moderated competitive inhibition of native grasses by invasive grasses [38].

Our focus has been on the moderating effect of habitat modification on per capita invasion impact, but invasive species might also moderate habitat loss effects. For example, increased dispersal-related mortality caused a four- to five-fold increase in subpopulation extinction rates of the native planthopper *Prokelisia crocea* in native prairie cordgrass *Spartina pectinata* patches surrounded by an invasive smooth brome *Bromus inermis* matrix, compared to *Spartina* patches surrounded by natural mudflats [39]. This is potentially an important class of invasive impact, as non-native plants represent the predominant matrix land use in many regions.

A final important point is that not all interaction modification effects necessarily involve synergistic interactions. There might also be mitigating (antagonistic) effects of habitat disturbance on invasion impact. For example, habitat disturbance resulting from water abstraction for agriculture facilitated coexistence of native round-head galaxiids *Galaxias anomalus* with invasive brown trout *Salmo trutta* in New Zealand, because trout are substantially more sensitive to low flow conditions [40]. Although an interaction modification effect was not distinguished from an interaction chain effect in this study, a 34-year study of competitive coexistence between brown trout and bullheads *Cottus gobio* in their native habitat in England showed that low flow conditions altered the relative competitive advantage of trout [41].

Conservation management: the case for addressing interactive effects

Arguably the most pressing reason to consider interactive effects between global change drivers is to enable better prediction and management of native species decline [42]. Within conservation management, the issue is not that multiple threat criteria are ignored, but that current approaches lack explicit consideration of the interaction terms between factors. Even in advanced multifactor approaches, such as multicriteria decision making, the assumption is often one of simple independence and additivity between factors [43]. We liken this to a 'main effects' model of conservation management, in which multiple causal factors are considered in an implicitly additive manner, often followed by acceptance of the single dominant factor that explains the greatest proportion of the effect. In reality, the strength of interaction between drivers can be visualized as a gradient from completely additive to strongly non-additive. In the former scenario, 'main effects' conservation strategies are appropriate, and the decision about whether to focus on factors such as eradication of invasive species or mitigation of habitat modification will be based on the relative impact of each factor (within socioeconomic and logistical constraints). However, scant data exist with which to evaluate the relative importance of dominant threats to native species [44], much less their interactions. Nevertheless, correctly establishing causality through a mechanistic understanding of impact is crucial for achieving conservation goals. In cases in which multiple causes of species decline interact,

we argue that sustainable long-term management strategies must consider 'interactive effects' models of native species decline to be successful and cost-effective (Box 3) [42,45–47].

As an example, the invasive fire ant *Solenopsis invicta* is widely believed to competitively displace native ant species, lending weight to its status as one of the world's '100 worst' invasive species. However, recent research has shown that experimental elimination of fire ant colonies does not lead to increased abundance or diversity of native ants [48]. Instead, conservation of native species requires mitigation of the habitat disturbance that simultaneously drives fire ant invasion and native decline [48]. Of course, the reverse situation might also occur, in which habitat restoration is unsuccessful in recovering native populations without removal of invasive species. In the presence of invasive grasses, physical restoration and revegetation of dune habitat in California [49] was ineffective at boosting seedling emergence of the threatened Antioch Dunes evening primrose *Oenothera deltoidea howellii* to levels similar to those found in semi-natural habitat. Successful recruitment through to one-year-old plants only ever occurred in 'restored' habitats following removal of invasive grasses [49].

Naturally, there will be many situations in which neither habitat restoration nor invasive species control alone eliminates invasive impact [14,33,42], which is to be expected if habitat modification changes the per capita impact of invasive species via an interaction modification effect. In these cases, conservation management will demand multiple, context-dependent solutions to invasive species problems, based on a more detailed understanding of the mechanisms underlying invasive impact. For instance, habitat manipulations that improve habitat quality through the provision of refuges, mitigate changes in abiotic conditions that drive competitive reversals, or increase the available area of natural habitat can be effective management strategies to reduce the per capita impact on native populations (Box 3) [50].

Generalising the framework across global change drivers

Habitat modification and species invasion are just two of many inter-related and interacting global change drivers. Attributing native species decline to one or more drivers becomes increasingly difficult as the number of potential drivers and their interactive effects increases [9]. Although a complete summary of the extensive global change literature is outside the scope of this article, we illustrate briefly some important interactive effects below.

Interaction chains are well known in global change research. In addition to the direct effects of CO₂ on plant physiology, elevated CO₂ can drive climatic change, which affects a great variety of species across trophic levels [6]. However, measuring the independent effects of CO₂ or climate change on native species decline will not enable prediction of the net combined effects of both drivers. This is analogous to habitat modification enhancing the population size of invasive species. One driver (CO₂) increases the extent or frequency of another driver (climate change), with the 'per unit' (e.g. degree of temperature increase)

Box 3. How to manage interactive effects

Managing interaction chain effects: feral cat invasion in New Zealand

Explicit recognition of interaction chains that promote invasive abundance has prompted the use of habitat manipulation as a tool to limit invasive abundance or distribution indirectly [42,58], while facilitating native re-establishment (e.g. [53]). In New Zealand, invasive mammals such as cats *Felis catus* exert greater predation pressure on native skinks *Oligosoma* spp. in agriculturally modified grassland than in semi-natural grassland (Figure 1a). Heavily grazed grassland supports a greater abundance of alternative prey, such as rabbits *Oryctolagus cuniculus*, providing a resource subsidy that increases cat densities. Controlling wide-ranging, elusive predators presents particular challenges for conservation management. However, controlling the interaction chain leading to elevated cat densities, by restoring disturbed habitats or removing resource subsidies, might be a viable management alternative for reducing impact on native species [50,59]. For example, reduction of rabbits in the matrix surrounding natural habitats has been shown to prevent cats from attaining densities sufficient to threaten native lizard populations [59]. In these situations, reserve-level management schemes to control invasive species are unlikely to be effective if

landscape-scale habitat modification produces continued propagule pressure in restored habitats [25,57]. Successful conservation strategies will require an explicit focus on restoration or management of surrounding matrix habitats.

Managing interaction modification effects: fox invasion in Australia

Total impact on native species might be a function of both increased predator abundance and increased prey susceptibility in modified habitats, such that the per capita impact of invasive species depends on habitat quality. For example, habitat degradation in Australian *Eucalyptus* woodland reduces the number of structural refuges for native marsupials [60], making them more susceptible to mortality or sublethal behavioural modification effects from invasive predators such as foxes *Vulpes vulpes* (Figure 1b) [50,60]. Consequently, provision of refuges or restoration of habitat structural complexity can be effective management actions to reduce the per capita impact [60]. One advantage of this approach is that expensive ongoing predator control becomes unnecessary, because refuges enable native species to achieve positive intrinsic rates of population increase, even in the presence of the predator [50].

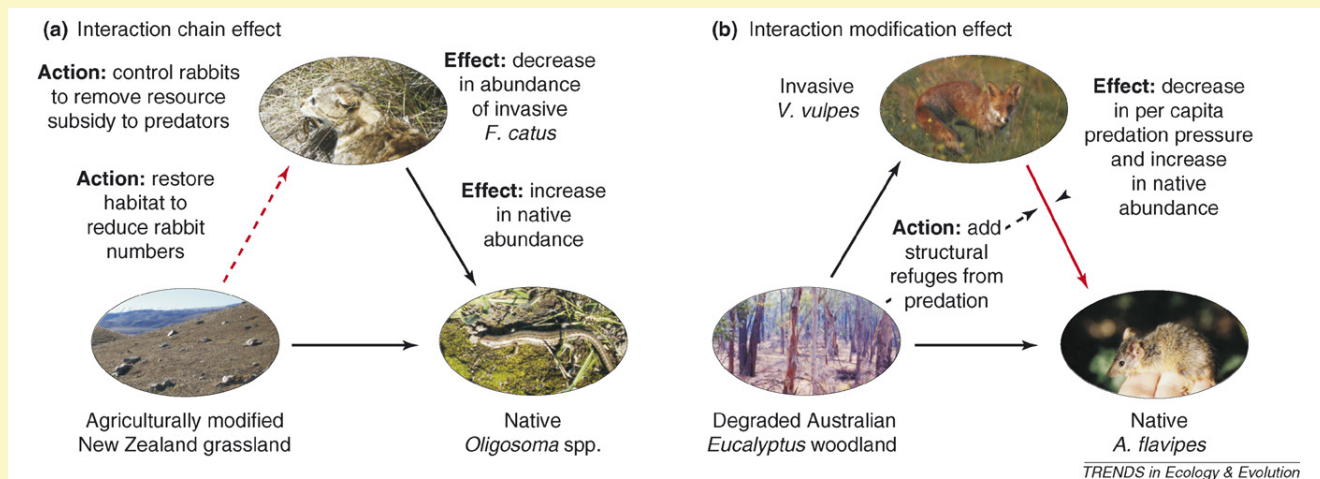


Figure 1. Examples of how to manage interactive effects. (a) Using a numerically mediated interaction chain effect to indirectly control feral cat predation on native lizards by removing alternative prey or restoring habitat. Photos reproduced with permission from Grant Norbury. (b) Using a functionally moderated interaction modification effect to control fox predation on native marsupials by manipulating habitat structural refuges. Photo at lower left reproduced with permission from Paul Sunnucks; photo at upper centre reproduced with permission from iStock Photo (www.istockphoto.com); and photo at lower right reproduced with permission from Ashley Herrod.

effect of the latter remaining constant. Similarly, future climate models predict range expansions of invasive ants [51] and other species (e.g. [52]). In these cases, the per capita effect of invasive species on native species might remain constant, but their abundance or geographic range increases as a result of another global change driver.

In contrast to interaction chains, the per unit effect of one driver can be modified by another, in an interaction modification effect. For example, the geographical distribution of butterflies tracks climate warming [9], but in fragmented landscapes the movement of habitat specialists is restricted by adverse conditions in the matrix [9]. In this case, direct responses to either climate change or habitat fragmentation do not change in intensity. Yet, one driver (fragmentation) increases the impact of a given change in climate on native biota. Similarly, when invasive plants are nitrogen limited [20,53], atmospheric nitrogen deposition could alter competitive dynamics in favour of invasive species [33], such that the per capita competitive ability of invasive plants increases. Climate change and

elevated CO₂ can also alter interspecific dominance patterns in favour of invasive plant or vertebrate species, with long-term negative effects on native species (e.g. [54]). Habitat disturbance might even act synergistically with nitrogen deposition to facilitate invasive species dominance in a three-way interaction. For example, habitat modification can remove buffers against nitrogen runoff from adjacent managed land into coastal salt marshes, leading to competitive dominance of invasive over native plants [33].

Conclusions

Rather than suggest prescriptive formulas for how conservation management can deal with interactive effects between specific global change drivers, we have emphasized that appropriate management will depend on the underlying mechanisms driving native species decline. Successful sustainable mitigation will require clear delineation of interaction chain versus interaction modification effects. If the effect of one driver scales in proportion to the effect

of other drivers (i.e. an interaction chain effect), then this opens up unique opportunities for mitigating negative impact via indirect pathways, such as managing invasive impact by improving habitat quality or quantity. In cases in which two or more factors have truly synergistic effects (i.e. interaction modification effects), simultaneously addressing all interacting drivers will probably be important. This will require system-specific information and will probably present more challenges than opportunities for conservation management. To better inform conservation management, ecologists need to routinely incorporate multiple factors into sampling designs or at least specify the environmental (global change) context in which a single factor is being addressed. Ecologists should clearly identify the pathway and mechanism of interaction, distinguishing interaction chain effects from interaction modification effects by quantifying per capita or per unit rate changes in functional and numerical responses of native species, across the full range of variation in global change drivers. Despite recent progress, ecological understanding of the interactions between multiple drivers of global change is still in its infancy and presents an important future challenge for conservation management.

Acknowledgements

We thank Tamsin Braisher, Laura Fagan, Ana Rodrigues, postgraduate students and colleagues at the School of Biological Sciences, University of Canterbury, and four anonymous reviewers for helpful comments on the article. Thanks to Gil Rilov (Department of Zoology, Oregon State University), Thais Winsome (Biology Department, Mission College, California), Grant Norbury (Landcare Research, Alexandra, New Zealand), Paul Sunnucks and Ashley Herrod (School of Biological Sciences, Monash University, Australia) and iStockPhoto.com for kindly providing photographs that were used in this article, and to Tony Arthur, Geoff Baker, Robert Bugg, Mac Callahan, Paul Hendrix, Trish Kendal, Hania Lada, Roger Pech and Andrea Taylor for further assistance in obtaining illustrations.

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