Body size and trophic position determine the outcomes of species invasions along temperature and productivity gradients

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Abstract

Species invasions are predicted to increase in frequency with global change, but quantitative predictions of how environmental filters and species traits influence the success and consequences of invasions for local communities are lacking. Here we investigate how invaders alter the structure, diversity and stability regime of simple communities across gradients of habitat productivity, temperature, and community size structure. We examine all three-species trophic modules (apparent and exploitative competition, trophic chain and intraguild predation) with empirically derived temperature and body mass scaling of vital rates. We show that the success of an invasion and its effects on community stability and diversity are predictably determined by the effects of environmental factors on each species and the relative strengths of trophic interactions between resident and invading species. We predict that successful invaders include smaller competitors and comparatively small predators, suggesting that species invasions may facilitate the downsizing of food webs under global change.

Introduction

Human-induced global change is transforming local communities and ecosystems through five main drivers: climate change, pollution, overharvesting, land and sea use change, and invasive species (Isbell et al. 2017; IPBES 2019). Invasive species threaten biodiversity (Sala et al. 2000) and persistence of local communities worldwide (Gurevitch & Padilla 2004; Bellard et al. 2016). Shifting species ranges to higher elevations and latitudes in response to climate change (Parmesan & Yohe 2003; Sunday et al. 2012), combined with increased tourism, pet trade and commodity transport (Chan et al. 2019; McCarthy et al. 2019; Essl et al. 2020), are expected to accelerate species invasions globally over the next century (Seebens et al. 2021; Sentis et al. 2021). Species invasions can exacerbate or mitigate the pressures that ongoing environmental change exerts on local communities by altering biodiversity and community resilience to abiotic stressors (Walther et al. 2002; Wardle et al. 2011; Hong et al. 2022).

Warming and nutrient enrichment are two pervasive aspects of global change that structure local communities in aquatic (Fussmann et al. 2014; Boukal et al. 2019) and terrestrial systems (Meyer et al. 2012; Clark et al. 2017). They modulate food web dynamics (Binzer et al. 2012; Sentis et al. 2017) and can facilitate or prevent species invasions. However, a general consensus on how invaders influence community structure and persistence along temperature and habitat productivity gradients is currently lacking. In particular, the mechanisms underlying community-level responses to species invasions in future environments affected by global change remain incompletely understood (Sentis et al. 2021).

Exploring the nexus between invasibility, diversity and stability of communities (Rooney & McCann 2012; Catford et al. 2019) can help us better understand the impacts of global change on local ecosystems (Francis

et al. 2014). The effects of species invasions on the diversity-stability relationship have been studied in different types of animal, animal-plant and plant interaction networks (Rooney & McCann 2012; Brose et al. 2017; Tomiolo & Ward 2018). However, previous studies considered relatively species-rich communities with many direct and indirect effects; focusing on food web modules could allow for more mechanistic, causal insights.

One promising avenue towards a better understanding of these mechanisms is to disentangle the role of environmental filters and species traits in biological invasions (Chesson 2000; Kraft et al. 2015). Environmental filters constrain the invader per se but also structure the local community, which is a biotic filter that restricts the invader's realised niche (Kraft et al. 2015). The roles of both filters are therefore closely linked (Thompson et al. 2018a, b). This link is often neglected in studies that estimate future shifts in species distributions caused by climate based on the expected performance of invading species in new habitats (Bellard et al. 2013; Buckley & Csergo 2017; Seebens et al. 2021), but ignore the accompanying impacts of environmental change on resident communities.

The invader's realised niche is constrained by its trophic position and the topology of the local food web. Available niches may be occupied by resident species that interact with the invader directly through consumptive interactions or indirectly through competition (Dueñas et al. 2018). Classic work on species coexistence has proposed general rules for community assembly (Chesson 2000; Shea 2002). The 'R* rule' for exploitative competition states that the species with the lowest resource requirements is competitively superior (Tilman 1985). An analogous 'P* rule' for apparent competition states that the prey that can withstand the highest predation pressure will prevail (Holt et al. 1994). Both rules can also inform when species invade and how they affect resident communities in the context of global change.

Among species traits, individual body mass can be used to predict invasibility because it affects individual fitness, species interactions and energy flows (McCann & Rooney 2009; Brose et al. 2017; Dijoux & Boukal 2021). For example, larger species tend to prey on smaller species, especially in aquatic habitats (Ou et al. 2017) and warming-induced metabolic meltdown is more likely for larger consumers than smaller ones (Rall et al. 2010, 2012). Food webs may therefore be simpler in warmer habitats, with fewer species at higher trophic positions (Brose et al. 2012). This could create niches for future invaders, which could subsequently attenuate or alter food web responses to global change through cascading effects (Reynolds & Aldridge 2021). However, little is known about how the body mass and trophic position of the invader affect community responses to invasions under climate change, and simple predictions are difficult to make. For example, previous models have shown that high consumer-resource mass ratios associated with large consumer species can either confer a higher extinction risk for top predators under warming or buffer the effects of eutrophication by dampening population fluctuations (Binzer et al. 2016; Sentis et al. 2017).

Here, we investigate in detail how consumer-resource systems respond to species invasions along temperature and habitat productivity gradients. To this end, we develop biomass-based models (Yodzis & Innes 1992) with mass- and temperature-dependent biological rates parameterised using empirically estimated relationships (Binzer et al. 2012; Fussmann et al. 2014). We simulate all possible invasions in a consumer-resource system that can lead to the four baseline three-species food web modules (apparent and exploitative competition, food chain, and intraguild predation). Our aim is to decouple the influence of the invaders and abiotic drivers. We explore (i) how temperature, nutrient levels and body mass ratios between the resident and invading species influence invasion success and (ii) how invasion-induced changes in species composition, diversity and stability of local communities vary across different food web topologies and environmental gradients.

Our main expectations are: (1) all else being equal, community responses to invasions (Box 1) follow known mechanistic processes from community ecology (Box 2); (2) based on the R* and P* rules and the higher susceptibility of larger species to metabolic meltdown at warmer temperatures, smaller invaders are more successful at warmer temperatures, especially in less productive environments, while larger invaders are more successful in more productive environments, especially at lower temperatures; and (3) invasions that result in larger and smaller consumer-resource size ratios will tend to stabilise and destabilise the community dynamics.

Methods

Community structure and dynamics

We consider a resident consumer-resource system and examine five scenarios that differ in the trophic position of the invader, including another basal resource, another consumer, a top predator, an intraguild predator feeding on both resident species, or an intraguild prey feeding on the (shared) resident resource while being consumed by the resident consumer (Fig. 1a-e). This corresponds to apparent competition (hereafter AC), exploitative competition (EC), tri-trophic chain (TC) and intraguild predation (IGP) (Tables S1–S3).

We simulate the dynamics of each module for each combination of temperature between 0°C and 40°C (step size 0.1°C) and nutrient levels (I_K) available to the basal resource species the between 0.1 g.m^{-2} and 20 g.m^{-2} (step size 0.1 g.m^{-2}), yielding 80,200 combinations of temperature and nutrient levels as in Binzer et al. (2012) and Sentis et al. (2017). We also vary the body masses of species in each module, constraining consumers to be at least as large as their resources, which is true for most predator-prey pairs (McCauley et al. 2018). For simplicity, we set the body mass of the basal resource species to 1 mg and express the other masses in relative values (Fig. 1a-e).

We denote the body mass ratio between competing resources $R_{INV}:R_{RES}$ (AC module) and the consumer:resource ratio $C:R$ (TC and IGP modules) as a, the mass ratio between competing consumers $C_{INV}:C_{RES}$ (EC and IGP modules) or between predators and intermediate consumers $P:C$ (TC and IGP modules) as β, and the mass ratio between resident resource and consumer $C_{RES}:R_{RES}$ (AC and EC modules) and between the top predator and resident basal resource ($P:R$; TC and IGP modules) as $\gamma = a\beta$. Furthermore, we quantify the asymmetry in size ratios between adjacent trophic levels with a ratio parameter $\delta = \beta / a$ (Table S4). We consider module-specific sets of mass ratios to reflect the different trophic positions of the invader: 4 or 15 consumer-resource body mass ratios for the resident system, and 16 or 25 combinations of species mass ratios (i.e., at least all pairwise combinations of a and $\beta = 1, 2, 5$ and 10, Text S1) in each module (Tables S5–S7). All numerical simulations were run in the packages 'deSolve' and 'rootSolve' in the R software (Soetaert & Herman 2009; Soetaert et al. 2010).

Analyses of community structure and stability before and after invasion

We distinguish six mechanisms of invasion-induced change in the community based on the observed changes in local composition and diversity (hereafter *invasion outcomes*, Box 1). The invasion-induced change in diversity $\Delta D = N_{INV} - N_{RES}$ is calculated as the difference between the number of species in the invaded and resident community N_{INV} and N_{RES} present after 5000 years (end of simulation) under the same environmental conditions and species masses.

To assess how invaders affect the stability of the resident system, we first calculate the Jacobian matrix at the equilibrium with the species present after 5000 years (Eqs 10–13, Table S8) and use its dominant eigenvalue to determine the stability of the resulting community. We distinguish three stability regimes for the invaded community (hereafter S_{INV}) and the resident system (hereafter S_{RES}): stable equilibrium (E), population oscillations (O), and a collapsed system with no remaining species (N) (Binzer et al. 2012; Sentis et al. 2017), to which we arbitrarily assign values $v(E) = 2$, $v(O) = 1$ and $v(N) = 0$. We then compare the stability regimes between the resident system and the invaded community under the same environmental conditions and species mass ratios. Nine outcomes (hereafter *regime states*, S_{RES}-S_{INV}) define all possible changes in stability caused by species invasion. Similar to ΔD, we calculate the invasion-induced change in stability as $\Delta S = v(S_{INV}) - v(S_{RES})$. Positive, zero and negative values of ΔS correspond to stabilizing (O-E, N-O and N-E), neutral (O-O, E-E and N-N) and destabilising (O-N, E-O, E-N) effects of the invader on the local consumer-resource system, respectively.

To assess how the body mass of the invader affects the community responses across food web modules and abiotic conditions, we calculate the percentage of each invasion outcome (Box 1) and regime state for a given set of body mass ratios across all 80,200 combinations of temperature (0–40ºC) and nutrient levels (0.1–20 g.m^{-2}) for each combination of body masses in each food web module (Tables S4–S7), and average these

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percentages across all combinations of body masses considered for each module.

Results

Community response to invasion: the role of environmental conditions and food web topology

Temperature, nutrient levels and size structure of the resident community influence its composition, stability (Text S2 and Fig. S1) and response to invasion. We first focus on responses for fixed body mass ratios $a = \beta = 10$ describing invasions by a 10-fold larger resource species in the AC module (Fig. 1a), a 10-fold smaller consumer species in the EC module (Fig. 1b), a large top predator in the TC module (Fig. 1c), and a medium-sized intraguild prey (Fig. 1d) or a large intraguild predator (Fig. 1e) in the IGP module.

The impact of an invader on the resident community varies with temperature, nutrient levels and the invader's trophic position (Fig. 1f-p). The community resists invasion in the following cases: (1) the invading consumer or predator suffers from metabolic meltdown at combinations of relatively high temperatures and low nutrient levels (Fig. 1g-1j, blue area top left), (2) the invading resource (AC module) or consumer (IGP module) is competitively inferior to resident resource or intraguild predator, respectively, at a wide range of intermediate temperatures and nutrient levels (Fig. 1f and 1i, blue area away from top left and bottom right) and (3) the consumer-resource system collapses due to the paradox of enrichment at combinations of relatively low temperatures and high nutrient levels (Fig. 1f-1j, blue area bottom right).

Successful invasion and occupancy of a vacant niche occur at combinations of relatively high temperatures and low nutrient levels that are above the extinction limit (caused by metabolic meltdown) of the local consumer or predator, but also below the extinction limit of the invader for invading larger resource species (AC module), smaller consumers (EC module) and intraguild prey (IGP module; Fig. 1f, 1g and 1i, yellow areas). Invading intraguild predator occupies a vacant niche when the intraguild prey goes extinct due to the paradox of enrichment at sufficiently low temperatures and high nutrient levels (Fig. 1j, yellow area).

Furthermore, a larger resource outcompetes and substitutes the resident resource in the AC module under environmental conditions just below the extinction limit of the resident consumer (Fig. 1f, green area), because a larger resource provides more energy to the consumer due to lower consumer: resource body mass ratio. An invading smaller consumer (EC module) and intraguild predator (IGP module) substitute the competitively inferior resident consumer over a much wider range of intermediate temperatures and nutrient levels; in the latter case, the environmental conditions must be sufficiently below the extinction threshold of the invading predator (Fig. 1g and 1j, green area).

Only invading top predator (TC module) can integrate into the community across a broad range of environmental conditions (Fig. 1h, light brown area). Intraguild prey integrates into the community when environmental conditions are just below the metabolic meltdown threshold of the resident intraguild predator, making the latter a poor competitor for the shared prey (Fig. 1i, light brown area). Intraguild predator integrates into the community when conditions are just below its own extinction threshold (Fig. 1j, light brown area; note that the extinction threshold is higher than in Fig. 1i due to the additional intraguild prey).

Vulnerability to invasion occurs for a smaller consumer in the EC module at low temperatures and sufficiently high nutrient levels (Fig. 1g, black area), where the resulting lower consumer-resource mass ratio triggers population oscillations. Finally, at sufficiently low temperatures and high nutrient levels, an invading top predator (TC module) rescues the resident resource by dampening population oscillations during its temporary presence in the system, so that only the top predator and resident consumer die out (Fig. 1h, ochre area).

These module-specific outcomes of invasions are reflected in different effects on community stability. Invading basal resource (AC module), intraguild prey and intraguild predator (IGP module) does not alter system stability except the invading intraguild predator, which can stabilise the dynamics over a narrow range of combinations of nutrient levels and (low to moderately high) temperatures (Fig. 1l, 1o and 1p). Successful invasion at low temperatures and high nutrient levels in the EC module always destabilises the community

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towards cycles or complete collapse due to the paradox of enrichment (Fig. 1m). Finally, successfully invading top predator may or may not change system stability depending on temperature and nutrient levels (TC module, Fig. 1n).

Community response to invasion: the role of species body mass ratios

We examine the role of body mass ratios in community response to invasion from two perspectives: competition in the AC, EC and IGP$_C$ module and predation in the TC and IGP$_P$ module. To this end, we investigate the role of body mass ratios a and β between competitors and the role of size structure asymmetry between multiple trophic levels given by δ. For brevity, we summarise here only the general patterns of invasion outcomes (Fig. 2) and effects on community regime state (Fig. 3); Text S3 and Table S9 provide further details.

Resistance to invasion and species substitution dominate the results for the three modules with invading competitors (Fig. 2a-c, S2ab and S3a-c), with predominantly neutral effects on the community regime (ΔS = 0; Fig. S2cd, dotted lines in Figs. 3a-c and S3f-j). Invasion-induced increase in stability is less frequent but occurs in all modules except EC (Figs. 2b and S3g). Integration of the invader and rescue of the resident species are rare and limited to TC and IGP modules (Figs. 2a-c and S2ab). Invasion-induced vulnerability occurs only for smaller ($\beta < 1$) or, very rarely, much larger ($\beta \gg 1$) invading consumers in the EC module (Fig. 2b) and promotes system instability (Figs. 2b and S3g).

The predominant outcomes in the AC, EC and IGP$_C$ modules, i.e. resistance to invasion or substitution of the resident competitor, correspond to predictions based on the P* and R* rules (Box 2) and depend strongly on the resident: invader body size ratio (Fig. 2a-c, Text S4). In the AC module, a smaller competitor can sustain a higher equilibrium predator biomass and exclude a larger competitor (P* rule, Figs. 2a, S4a-l and S5a-l). In the EC module, a smaller consumer has lower resource requirements at equilibrium and therefore excludes a larger competitor (R* rule, Figs. 2b, S4s-x and S5s-x). Invading smaller resource in the AC module can stabilise the dynamics and prevent collapse ($\Delta S > 0$ for $a < 1$; Figs. 3a and S3f), while invasion of a smaller consumer in the EC module can destabilise the dynamics, leading to population cycles or collapse ($\Delta S < 0$ for $\beta < 1$; Figs. 3b and S3g). In the IGP module, a smaller intraguild prey is competitively superior to the intraguild predator (Fig. S6g-l) but cannot withstand its predation pressure (Figs. 2c and S6m-o). Intraguild prey therefore collapses immediately after its introduction (Fig. S6m-o) or is displaced by an invading intraguild predator (Fig. S6a-f) as soon as the biomass of the latter becomes too high, with a stabilising effect similar to that in the AC module (for $\beta > 1$; Fig. 3c).

Community responses to an invading top predator in the TC and IGP modules vary predictably with the size-structure asymmetry between trophic levels characterised by δ (Figs. 2de and 3de). Successful invasion of the top predator in the TC module requires the presence of an intermediate consumer, which is more common with large a (Fig. S1) and thus smaller δ values. That is, an invading top predator is more likely to integrate or to rescue a resident species than to fail if it is more similar in size to the resident consumer (for $\delta < 1$, Fig. 2d). In this way, the top predator triggers oscillations more frequently, but prevents community collapse through the rescue effect (Fig. 3d). Changes in community composition and stability decrease when the resident consumer and the resource become more similar in size ($\delta > 1$ in Figs. 2d and 3d). In this case, the invasion of a comparatively large top predator usually fails and the resident system collapses due to the paradox of enrichment driven by the resident consumer-resource interaction (cf. Fig. S1b). On the other hand, the intraguild predator in the IGP module feeds on two prey populations, which explains the independence of community resistance from δ (Fig. 2e). Given the influence of the intraguild prey-resource mass ratio on the dynamics of the resident system (Fig. S3), species substitution occurs more frequently the more similar the size of the intraguild predator and intraguild prey ($\delta < 1$), while niche occupancy occurs more often the more similar the size of the intraguild prey and shared resource ($\delta > 1$, Fig. 2e). Invading intraguild predator stabilises the resident community and prevents its collapse more often as it gets more dissimilar in size to the intraguild prey ($\delta > 1$; Fig. 3e).

Invasion outcomes and the diversity-stability relationship

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The effects of invasion on community stability and diversity observed in our simulations depend on the outcome of the invasion. Invasion-induced destabilisation occurs primarily under vulnerability, where it almost always leads to community collapse (regime states *E-N* and *O-N* ; Figs. 4 and S8, Tables S9–S11). More than half of the invasions leading to integration and some leading to substitutions also trigger a loss of stability, with invasion-induced cycles replacing equilibrium (*E-O*). We do not observe invasion-induced destabilisation under resistance, occupancy and rescue mechanisms. An invasion-triggered increase in stability, which would prevent a complete collapse of the resident community and is characteristic of the rescue (*N-E*), occurs less frequently under occupancy (*N-E* and *N-O*) and integration (*N-O*). An invasion-triggered increase in stability associated with a shift from oscillations to stable equilibria (*O-E*) is rare and occurs only under substitution and vulnerability (Fig. S1a).

As a result, we find that invasion-induced changes in diversity and stability are interrelated, but one cannot be predicted from the other alone (Fig. 4b). Diversity loss ($\Delta D < 0$) is almost always associated with invasion-induced loss of stability ($\Delta S < 0$). No net change in diversity ($\Delta D = 0$) is mostly associated with no change in stability as expected, but loss of stability (invasion-induced cycles in EC) or increased stability (dampen cycles induced by invasion through species substitution in IGP$_P$) also occur as a result of invasion. Interestingly, invasions leading to increased diversity ($\Delta D > 0$) have the most evenly distributed effects on stability. About one third of the simulations each lead to reduced, increased or unchanged stability across species mass ratios, food web topologies and environmental conditions (Fig. 4b).

Discussion

Our study summarises how simple communities respond to the combination of three major drivers of global change: warming, eutrophication and species invasions (IPBES 2019). While these drivers have received considerable attention separately (Bellard et al. 2013; Binzer et al. 2016; Gallien & Carboni 2017), their combined impacts on local communities remain poorly understood despite some recent advances (Latombe et al. 2021; Sentis et al. 2021). We focused on two ubiquitous interactions through which invaders affect resident communities—predation and competition (Gallardo et al. 2016; Dueñas et al. 2018)—to understand how invasion outcomes relate to changes in community composition, diversity and stability (Tilman 1999). We showed that the outcomes depend predictably on the interplay between environmental conditions and differences in body mass and trophic position between the invader and its local competitor or predator/prey (Table S12). This allowed us to (i) identify combinations of environmental conditions, invader traits and community size structure that characterise communities prone to successful invasions, and (ii) describe the community-level consequences of such invasions.

What drives successful invasions and when do they occur?

Environmental and biotic filters underpin invasion success in local communities (Mitchell et al. 2006; Blackburn et al. 2011; Gray et al. 2015). Species living in warm, nutrient-poor environments such as tropical and subtropical seas (Sunday 2020; Trisos et al. 2020) may be at risk of metabolic meltdown (Pörtner & Farrell 2008), while species living in relatively cold, nutrient-rich environments such as shallow lakes at higher latitudes (Janssen et al. 2014; Glibert 2017) are vulnerable to unstable dynamics and community collapse (Oksanen et al. 1981). Previous models have shown that (1) "intermediate" environmental conditions that balance the opposing effects of warming and eutrophication can prevent biodiversity loss and maintain food web structure and that (2) larger consumer-resource body mass ratios mitigate the destabilising effect of eutrophication but tend to increase the vulnerability of top predators to warming (Binzer et al. 2016; Sentis et al. 2017). Our results extend these findings in the context of species invasions. That is, large species cannot invade warm, nutrient-limited habitats because of the risk of metabolic meltdown (Pörtner & Farrell 2008), while nutrient enrichment in colder habitats limits invasions by smaller species due to the paradox of enrichment and community collapse (Oksanen *et al.* 1981).

Size structure of the local community plays an additional filtering role in invasions (Gray et al. 2015). We observed that invasion success was mainly determined by size differences between resident and invading competitors, while asymmetries in size structure between adjacent trophic levels determined the fate of invading

predators. This can be explained by the limiting similarity hypothesis, which states that the coexistence of species sharing the same (trophic) niche requires similar traits (MacArthur & Levins 1967), while this requirement does not hold for invaders in different trophic positions. Apart from competition for resources, we did not consider self-limiting mechanisms that would lead to stronger intraspecific than interspecific competition in our models and favour species coexistence (Holt et al. 1994). In our case, the application of the R* and P* rules (Box 2; Tilman 1985; Holt et al. 1994) can explain why only smaller competitors could successfully invade. We also considered a homogeneous environment, which tends to amplify the impact of invasive species on resident communities through high levels of interspecific competition, leading to limited coexistence due to frequent species replacement or strong resistance to the invader (Melbourne et al. 2007). This is in contrast to heterogeneous environments, where competing species with different traits can coexist through niche partitioning (Ricklefs 1977).

Our results also extend previous theory by showing that successful invasions in the IGP module depend on asymmetric competition between the intraguild predator and prey (Wootton 2017). Intraguild predators have a double advantage over pure competitors (as in the EC module) or specialist predators (as in the TC module): they depend less on a particular food source and can suppress intraguild prey through high predation pressure, even if the latter is a better competitor for the shared resource (Wootton 2017). These results are corroborated by experiments on intraguild predation between poeciliid fishes along a productivity gradient (Schröder et al. 2009), where the larger *Poecilia reticulata* most often successfully invaded the system and drove the smaller *Heterandria formosa* to extinction. Here we found that intraguild prey and predator can only coexist when environmental conditions are close to the metabolic meltdown threshold of the latter species, i.e. when high temperatures are combined with nutrient limitation.

Comparing results between modules, we found that intraguild prey (regardless of body size, IGP module), larger consumer (EC module) and larger resource (AC module) species were the least likely to successfully invade. This contrasts with the frequent successful invasions of intraguild predators (IGP module). Overall, we predict that successful invasions should involve comparatively smaller species, i.e. smaller competitors at lower trophic levels and predators that are not much larger than their prey. Invaders with other traits may need specific environmental conditions to be successful: for example, larger competitors at lower trophic levels and intraguild prey may only invade relatively warm and nutrient-poor environments that are not suitable for their predators.

When and how do invasions change the diversity and stability of resident communities?

Overall, our results were consistent with the classic diversity-stability hypothesis which states that more diverse ecosystems are more resilient to disturbance (Elton 1927; Tilman & Downing 1994; Rooney & McCann 2012). However, we also observed results that deviated from this relationship: invaders could either stabilise communities by increasing local diversity, or they could disrupt initial community stability (e.g. by integrating an invading predator that destabilises the local community) and cause species extinctions. Invaders affected the diversity and stability of resident communities even when their presence was only temporary. These contrasting findings highlight the ambivalent role of invasions as both contributors to and threats to local biodiversity (e.g., Henriksson et al. 2016; Tomiolo & Ward 2018).

The effect of invasion on the diversity-stability relationship depended on the outcome of the invasion in our models. Successful invasions led to variable, outcome-dependent changes in system stability. Our results suggest that one-to-one species substitutions in simple communities rarely alter system stability, while invasions that lead to increased diversity can both destabilise (outcome type: integration) and stabilise (occupancy and, to a lesser, extent integration) community dynamics. We have found that these potential changes in stability occur primarily in relatively cold, nutrient-rich environments in communities that are vulnerable to population fluctuations caused by eutrophication. These communities are sensitive to changes in vital rates, which determine the population dynamics and interactions of their constituent species (Binzer et al. 2012; Fussmann et al. 2014). For example, a long-term study of the plankton community in Lake Washington found that community stability was lowest during a period of increased nutrient loading following a successful invasion by a subsequently dominant cyanobacterium (Francis et al. 2014).

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Surprisingly, our study revealed that failed invasions can still affect the diversity and stability of local communities in cold, nutrient-rich habitats prone to the paradox of enrichment. Diversity could decrease due to increased population cycles after failed invasions of smaller consumers (EC module). Diversity could also increase due to rescue by invading top predators (TC module) if their temporary presence dampened consumer-resource cycles and rescued the basal resource, but not the consumer, from the collapse caused by enrichment. Such feedbacks from transient top predators on resident species might also arise from cascading effects of an invading top predator on lower trophic levels in more complex food webs (Woodward & Hildrew 2002; Gallardo et al. 2016; Reynolds & Aldridge 2021). However, adequate evidence of the rescue effect would require long-term data, ideally from experiments with controlled introductions and subsequent removal of the invading species (Bell et al. 2003).

Conclusion and perspectives

Warming and eutrophication are expected to alter the dynamics and simplify the structure of larger food webs (Brose et al. 2012), facilitating species invasions and increasing their impact on invaded systems (Sentis et al. 2021). We have shown how body size and trophic position determine the fate of species invasions and that species invasions can mitigate or amplify the negative effects of environmental stressors on local communities. Our predictions showed that smaller species are particularly likely to invade communities in warmer, nutrient-limited environments, while communities facing cold temperatures and nutrient enrichment are vulnerable to invasions by larger predators. Invaders can also fill vacant niches when resident species disappear. For example, the predicted poleward shift of smaller zooplankton species may benefit warming Arctic habitats (Evans et al. 2020). Invading predators may also buffer local communities against eutrophic effects at lower temperatures (as in Hughes et al. (2013)). Therefore, invasive species may not always need to be eradicated or controlled (Simberloff 2009; Glen et al. 2013), especially if the associated costs are too high. On the other hand, our findings support active management and eradication of invaders with negative impacts on local communities, including those that destabilise local communities such as small consumers in cold, nutrient-rich habitats (Robertson et al. 2020). Overall, we predict that species invasions may contribute to the downsizing of food webs (Young et al. 2016), as successful invaders will include smaller competitors and comparatively small predators.

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Legends

Fig. 1. Community responses to species invasion along environmental gradients for each food web module. (a-e) Trophic position of the invader (blue circle) relative to the resident species (green circles) under apparent competition (AC, panels a, f and l), exploitative competition (EC, panels b, g and m), trophic chain (TC, panels c, h and n), and intraguild predation (IGP) with invading consumer (IGP$_C$,

panels d, i and o) and with invading predator (IGP$_P$, panels e, j and p). Invasion outcomes (panels f-j) as in Box 1 summarize community changes with gain in diversity (ΔD > 0), no net change (ΔD = 0) or loss in diversity (ΔD < 0) after invasion. Regime states$S_{RES}.S_{INV}$ (panels l-p) summarize all possible combinations of the system qualitative state prior to (S_{RES}) and after (S_{INV}) invasion leading to a gain of stability (stabilizing, ΔS > 0), no net change (neutral, ΔS = 0) or loss of stability (destabilizing, ΔS < 0) after invasion. Regime state abbreviations: N = no species present, O = population oscillations with at least two species present, E = 1 to 3 species in stable equilibrium. Species body mass ratios fixed at $a = \beta = 10$.

Fig. 2. Module-specific effects of species body mass ratios on the averaged proportions of invasion outcomes that drive local diversity change . Body mass ratio given for (a-c) invader and its resident competitor (d, e) and adjacent trophic levels. Food web modules: (a) AC = apparent competition, (b) EC = exploitative competition, (c) IGP = intraguild predation with invading intraguild prey (β [?] 1) and invading intraguild predator (β [;] 1), (d) TC = trophic chain and (e) IGP$_P$ = intraguild predation with invading intraguild predator. Species: R = basal resource, C = consumer,P = predator. Symbols denote gain of diversity (squares), no net change (circles) or diversity loss (triangles) following invasions. Colours as in Fig. 1f-j.

Fig. 3. Module-specific effects of species body mass ratios on the averaged proportions of regime states following invasion. Body mass ratio between (a-c) invader and its resident competitor, and (d, e) between adjacent trophic levels. Food web modules and species as in Fig. 1. Regime state abbreviations: N = no species present, O = population oscillations with at least two species present, E = 1 to 3 species in stable equilibrium. Lines = neutral (dotted lines) and non-neutral (solid lines): influence of invader on local stability regime; symbols = gain of stability (squares), neutral change (circle) and loss of stability (triangles) following invasions. Colours identical to Fig. 1l-p.

Φιγ. 4. Διφφερενςες ιν σταβιλιτψ ςηανγε ($\Delta\Sigma$)βετωεεν (α) ιναςιον ουτςομες ανδ (β) βιοδιερςιτψ ςηανγε ($\Delta\Delta$) following successful species invasions. Values = cumulative proportions of regime states shown in Fig. S1. Biodiversity change in (b) illustrates the cumulative proportions observed across invasion outcomes in (a) broken by their effect on diversity, i.e. $\Delta D > 0$ for integration, occupancy and rescue, $\Delta D = 0$ for substitution and $\Delta D < 0$ for vulnerability. Change in stability: $\Delta S < 0$, loss of stability; $\Delta S = 0$, no change; $\Delta S > 0$, increase in stability. Note that resistance to invasion (with $\Delta S= 0$ and $\Delta D = 0$) is excluded in both panels.

Box

Box 1: Invasion outcomes driving local diversity change. Integration: Invader integrates and coexists with resider

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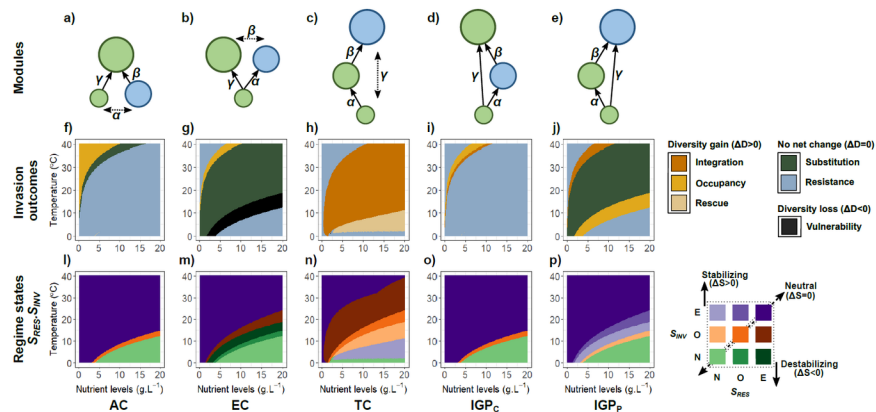**Box 2: Principles of species coexistence and exclusion in trophic modules P* rule (apparent competition):**
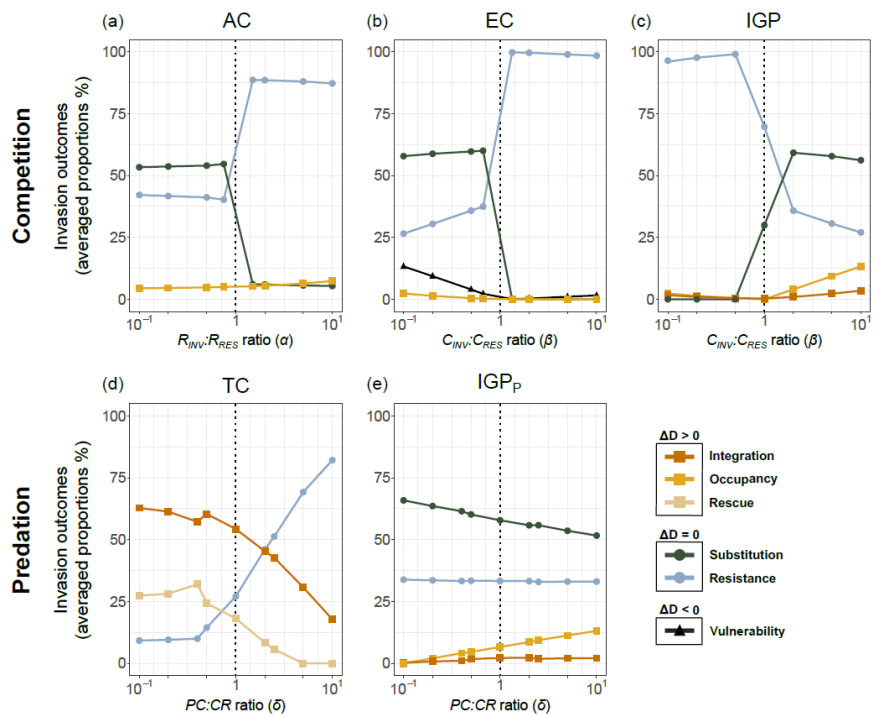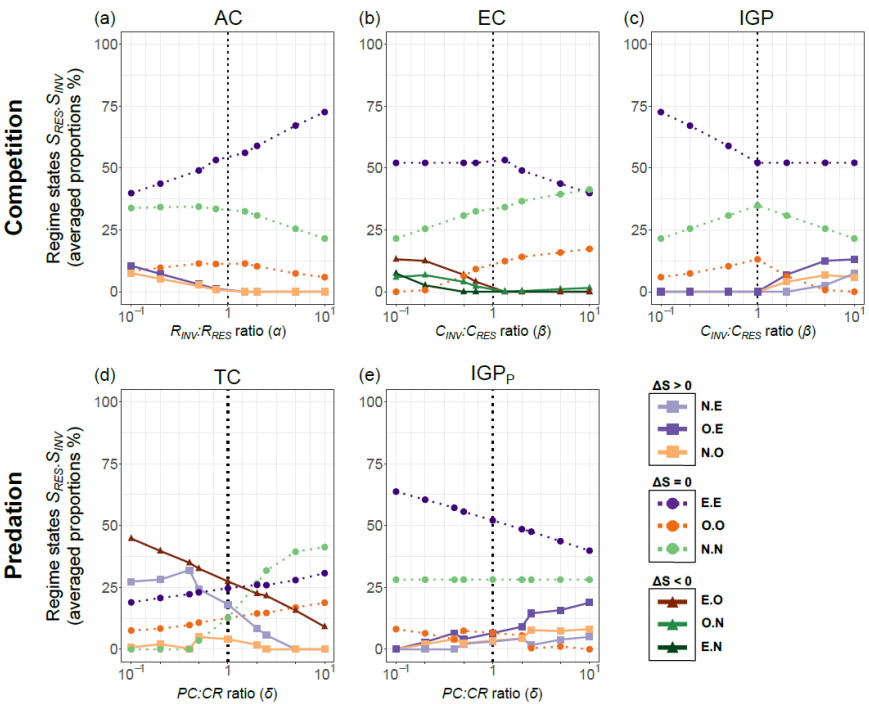
Figures

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Fig. 1
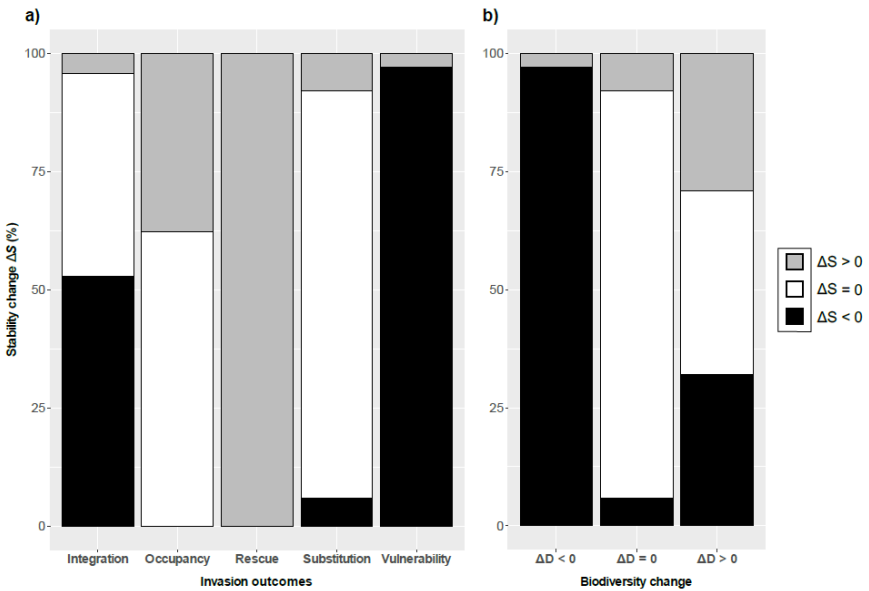

Fig. 2

Fig. 3

Fig. 4