

LETTER

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 environmental gradients (habitat productivity, temperature) and community size structure. We simulate all three-species trophic modules (apparent and exploitative competition, trophic chain and intraguild predation). We predict that invasions most often succeed in warm and productive habitats and that successful invaders include smaller competitors, intraguild predators and comparatively small top predators. This suggests that species invasions and global change may facilitate the downsizing of food webs. Furthermore, we show that successful invasions leading to species substitutions rarely alter system stability, while invasions leading to increased diversity can destabilize or stabilize community dynamics depending on the environmental conditions and invader's trophic position.

KEYWORDS

body size, diversity–stability relationship, eutrophication, metabolic ecology, predator–prey mass ratio, species invasions, trophic modules, warming

INTRODUCTION

Warming, eutrophication and species invasions constitute three major drivers of global change (Bellard et al., 2016; IPBES et al., 2019). While these drivers have received considerable attention separately (Gallien & Carboni, 2017; O'Gorman et al., 2019), their combined impacts on local communities remain poorly understood despite recent advances (Latombe et al., 2021; Sentis et al., 2021). Warming and nutrient enrichment structure local communities in aquatic (Boukal et al., 2019; Fussmann et al., 2014) and terrestrial systems (Clark

et al., 2017; Meyer et al., 2012). They modulate food web dynamics (Binzer et al., 2012; Sentis et al., 2017) and can facilitate or prevent species invasions. 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; Essl et al., 2020), are expected to accelerate species invasions over the next century (Seebens et al., 2021; Sentis et al., 2021).

Species invasions can exacerbate or mitigate the effects of environmental change on local communities by altering

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their composition and resilience to abiotic stressors (Wardle et al., 2011; Hong et al. 2022). However, a general consensus on how invaders influence community structure and stability 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 (Henriksson et al., 2016; Rooney & McCann, 2012) can also help us 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; 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* (Kraft et al., 2015). Environmental filters and traits of an invading species together determine its ability to establish and persist in the community, e.g. through mass and temperature dependence of vital rates (Brown et al., 2004; Dell et al., 2014). Environmental filters also structure the local community, which acts as a biotic filter that restricts the invader's realized niche (Kraft et al., 2015) through competitive and predatory interactions. The roles of both filters are therefore closely linked (Thompson et al., 2018a, 2018b), but the newly formed trophic links and the concurrent impacts of environmental change on the resident community are often neglected in studies that estimate future shifts in species distributions (Bellard et al., 2013; Seebens et al., 2021).

The invader's realized niche is constrained by its trophic position and the topology of the local food web, as resident species 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 & Chesson, 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.

Body mass can be used to predict invasibility because it affects individual fitness, species interactions and energy flows (Brose et al., 2017; Dijoux & Boukal, 2021; McCann & Rooney, 2009). 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 may create niches for future invaders, which could modulate community responses to environmental 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 global change, and simple predictions are difficult to make. For example, high consumer-resource mass ratios associated with large consumer species are predicted to confer a higher extinction risk under warming, but also buffer eutrophication effects 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) that track the biomass dynamics of populations with body mass- and temperature-dependent biological rates parameterised using empirically estimated relationships (see Text S1 for details). 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). 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 the community composition, diversity and stability 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 than at colder temperatures, especially in less productive environments, while larger invaders are more successful in productive environments, especially at lower temperatures; and (3) invasions that result in larger and smaller consumer-resource size ratios will respectively tend to stabilize and destabilize the community dynamics.

METHODS

Community structure and dynamics

We start with 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 and an intraguild prey feeding

BOX 1 Invasion outcomes driving local diversity change.

Integration: Invader integrates and coexists with resident species (Moyle & Light, 1996), leading to increased diversity.

Occupancy: Invader occupies a niche vacated by a species lost from the resident community prior to the invasion event (Herbold & Moyle, 1986), leading to increased diversity.

Rescue: Invader fails to persist in the system but facilitates the persistence of a resident species that would otherwise go extinct (Brown & Kodric-Brown, 1977), leading to increased diversity.

Substitution: Invader replaces its resident competitor (Bøhn et al., 2008), leaving the diversity unchanged.

Resistance: Invader disappears without affecting the resident community. This includes both environmental and biotic resistance to invasion (Moyle & Light, 1996) and leaves the diversity unchanged.

Vulnerability: Invading species permanently or temporarily destabilizes the resident system and triggers diversity loss through extinctions (Downing et al., 2012; MacDougall et al., 2013).

Invasion success: Invading species successfully establishes and persists in the community (this includes the outcomes of integration, occupancy and substitution). Invasion failure occurs when the invader fails to establish or persist in the community (this includes the outcomes of resistance, rescue and vulnerability).

BOX 2 Principles of species coexistence and exclusion in trophic modules.

P^* rule (apparent competition): The basal (or prey) species capable of sustaining the highest predation pressure dominates the competition and can indirectly exclude its competitor due to higher predation mortality (Holt et al., 1994).

R^* rule (exploitative competition): Consumer species with the lowest resource requirements is competitively superior (Tilman, 1985). This can lead to the exclusion of the inferior competitor or its presence at a lower biomass density.

Extinction cascade (trophic chain): A specialist predator cannot persist without its prey. Any species loss within a chain leads to a cascading collapse of all species at higher trophic levels in that chain.

Coexistence in intraguild predation (intraguild predation): Coexistence in the IGP module relies on two principles, i.e. intraguild prey must be competitively superior to the intraguild predator (R^* rule) and must be resilient to predation-induced mortality to avoid its own exclusion (Holt & Polis, 1997; Wootton, 2017).

on the (shared) resident resource while being consumed by the resident consumer (Figure 1a). This corresponds to apparent competition (hereafter AC), exploitative competition (EC), tri-trophic chain (TC) and intraguild predation (IGP with IGP_C and IGP_P representing consumer and predator invasions respectively) modules (Figure 2a–e).

For brevity we only describe here the combinations of environmental conditions and species traits we used across our biomass-based models (Table S1) with empirically derived temperature and allometric scaling of vital rates obtained from Binzer et al. (2016; see Text S1 and Tables S2 and S3 for details). We simulate the dynamics of each module for each combination of temperature between 0 and 40°C (step size 0.1°C) and levels of nutrient input (I_K) available to the basal resource species between 0.1 g m⁻² and 20 g m⁻² (step size 0.1 g m⁻²), yielding 80,200 combinations of environmental conditions 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 ectotherm predator–prey pairs (McCauley et al., 2018). We set the body mass of the basal resource species to 1 mg and express the other masses in relative values (Figure 2a–e). These values can be interpreted as the mean or adult body masses of each species, i.e. we do not consider changes in body mass during ontogeny.

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 α , 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 $\gamma = \alpha\beta$. Furthermore, we quantify the asymmetry in size ratios between adjacent trophic levels with a ratio parameter $\delta = \beta/\alpha$ (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 α 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’ (Soetaert et al., 2010; Soetaert & Herman, 2009) in the R software version 3.6.2 (R Core Team, 2019).

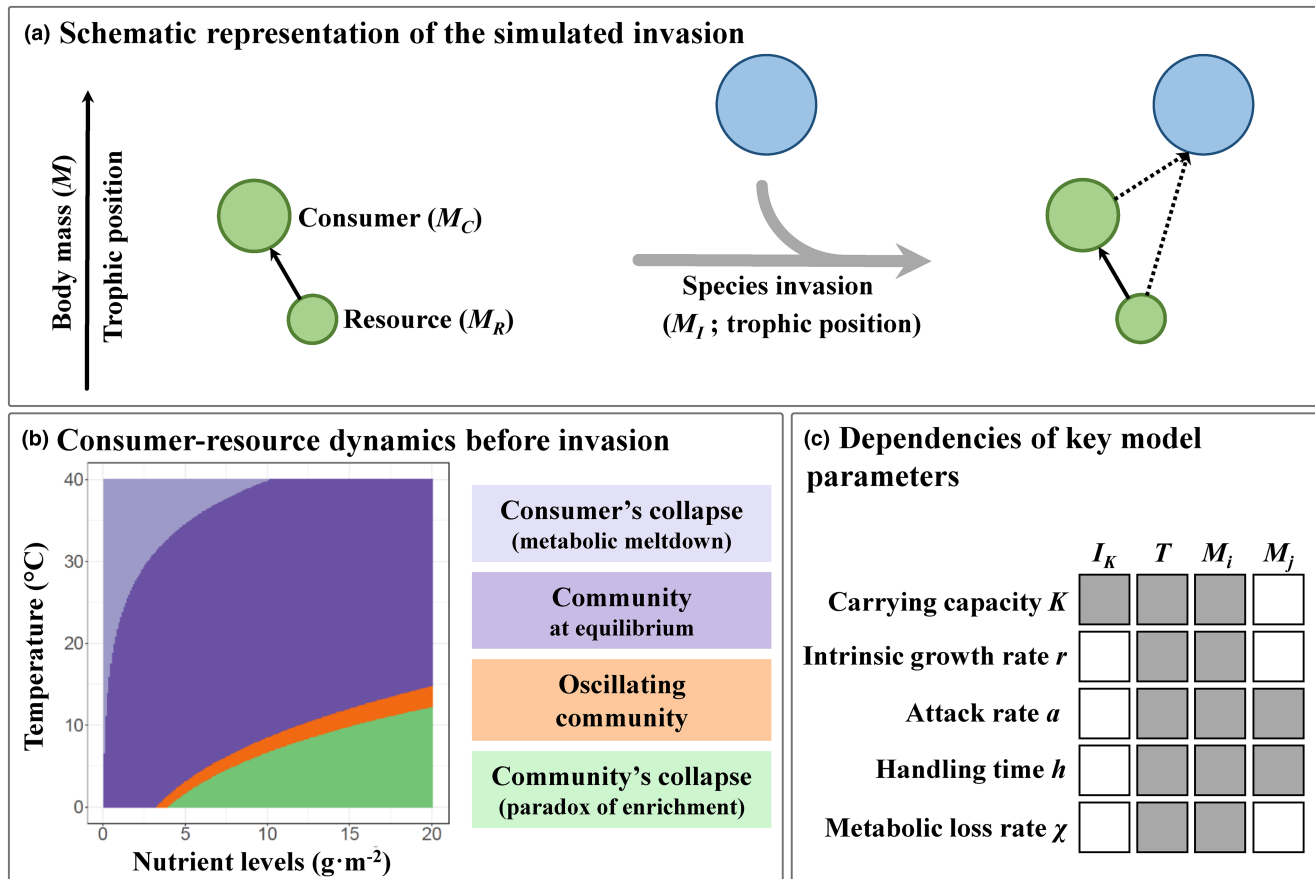


FIGURE 1 Summary of the modelling framework. (a) We model invasions in a simple consumer-resource system along environmental gradients of temperature and nutrient levels. Invaders are characterized by their body mass M_i and their trophic position relative to the resident community. (b) Environmental conditions structure the resident community prior to invasion, with four qualitatively different states (colour coded; see [Figure S1](#) and [Text S2](#) for details). (c) We use biomass-based models in which all biological rates and trophic interactions described by Holling type II functional responses between resident and invading species (Equations 1–5, [Table S1](#); Equations 6–9, [Text S1](#)) depend on nutrient input, temperature and body masses of species i and j , temperature and nutrient input ([Figure S2](#)). We conduct transient and equilibrium analyses (Equations 10–12, [Table S8](#)) for all trophic modules to map all invasion-driven changes in diversity, composition and stability regime of the community along environmental gradients for a wide range of species body mass ratios.

Analyses of community structure and stability before and after invasion

We distinguish six mechanisms of invasion-induced change in the community based on the changes in local composition and diversity (hereafter *invasion outcomes*, [Box 1](#)). The change in diversity $\Delta D = N_{INV} - N_{RES}$ calculates 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 calculate the Jacobian matrix at the equilibrium with the species present after 5000 years (Equations 10–13, [Table S8](#)) and use its dominant eigenvalue to determine community stability. 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 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*, $S_{RES} \rightarrow S_{INV}$) define all possible changes in stability caused by species invasion. 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 ($O \rightarrow E$, $N \rightarrow O$ and $N \rightarrow E$), neutral ($O \rightarrow O$, $E \rightarrow E$ and $N \rightarrow N$) and destabilizing ($O \rightarrow N$, $E \rightarrow O$, $E \rightarrow N$) effects of the invader on the local consumer-resource system, respectively.

To assess how the body mass and trophic position of the invader affect the community responses across food web modules and abiotic conditions, we calculate (1) the percentage of each invasion outcome ([Box 1](#)), (2) percentage of each regime state and invasion-driven changes in (3) community diversity (ΔD) and (4) stability (ΔS) across all 80,200 combinations of temperature (0–40°C) and nutrient levels (0.1–20 g m⁻²) for each combination of body

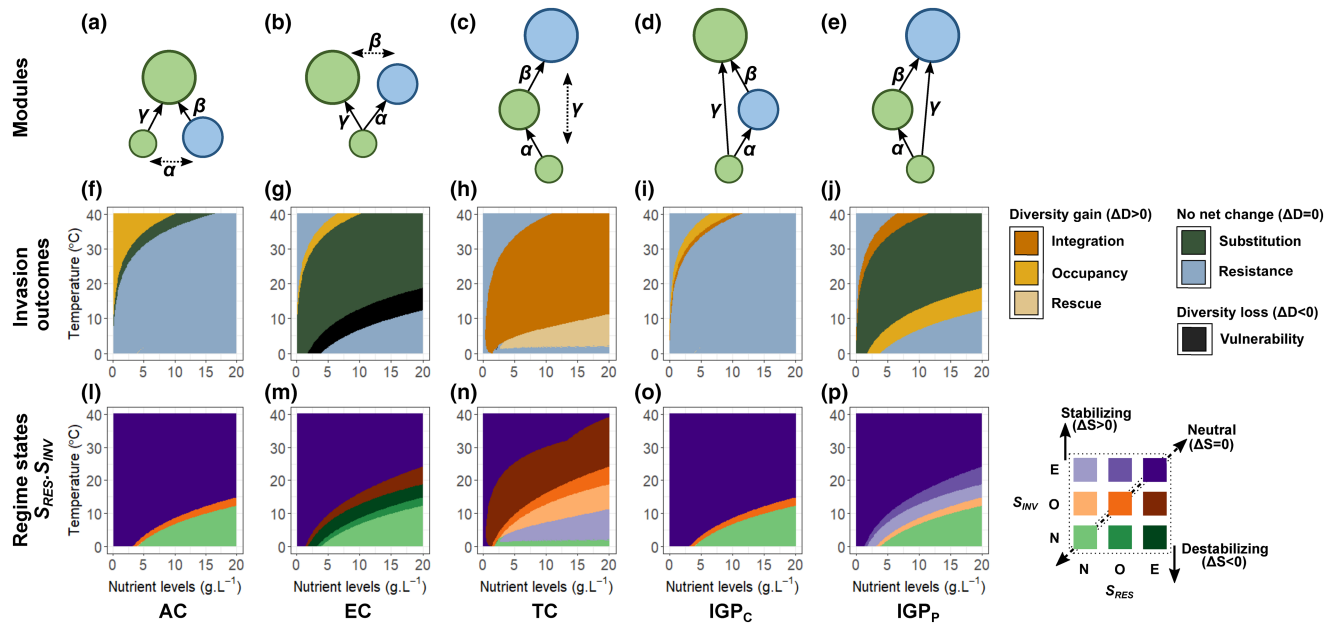


FIGURE 2 Community responses to species invasion along environmental gradients for each food web module. (a–e) Trophic position and body mass of the invader (blue circle) relative to the resident species (green circles) under apparent competition (AC, panels a, f and l), exploitative competition (EC, 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 ($\Delta D > 0$), no net change ($\Delta D = 0$) or loss in diversity ($\Delta D < 0$) 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, $\Delta S > 0$), no net change (neutral, $\Delta S = 0$) or loss of stability (destabilizing, $\Delta S < 0$) 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 $\alpha = \beta = 10$.

masses in each food web module (Tables S4–S7). To highlight the role of environmental conditions, we average the proportion of each outcome and changes in community diversity and stability across gradients of body mass ratios (i.e. between invading and resident competing species and between trophic levels) for low to mid and mid to high values of temperature ($0 < T \leq 20^\circ\text{C}$ and $20 < T < 40^\circ\text{C}$) and nutrient levels ($0.1 < I_K \leq 10 \text{ g m}^{-2}$ and $10 < I_K < 20 \text{ g m}^{-2}$), yielding four types of environment (hereafter ‘cold and nutrient-limited’, ‘cold and nutrient-rich’, ‘warm and nutrient-limited’ and ‘warm and nutrient-rich’).

RESULTS

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

Environmental conditions and size structure of the resident community influence its composition, stability (Text S2 and Figure 1b) and responses to invasion. We first examine the responses for fixed body mass ratios $\alpha = \beta = 10$ describing invasions by a 10-fold larger resource species in the AC module (Figure 2a), a 10-fold smaller consumer species in the EC module (Figure 2b), a large top predator in the TC module (Figure 2c) and a medium-sized intraguild prey (IGP_C, Figure 2d) or a large intraguild predator (IGP_P, Figure 2e).

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

A competitor can successfully invade a vacant niche when environmental conditions, i.e. relatively high temperatures and low nutrient levels, allow the invader to exist above the extinction limit of the resident species but below its own extinction limit caused by metabolic meltdown (AC, EC and IGP module; Figure 2f,g,i, 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 (Figure 2j, 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 (Figure 2f, 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) replace the competitively inferior resident consumer over a much wider range of intermediate temperatures and nutrient levels; in the latter case, environmental conditions must be sufficiently below the extinction threshold of the invading predator (Figure 2g,j, green area).

Only invading top predator (TC module) can integrate into the community over a wide range of environmental conditions (Figure 2h, light brown area). Intraguild prey integrates into the community when environmental conditions are just below the metabolic meltdown threshold of the intraguild predator, making the latter a poor competitor for the shared prey (Figure 2i, light brown area). Intraguild predator integrates into the community when conditions are just below its own extinction threshold (Figure 2j, light brown area; the threshold is higher than in Figure 2i 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 (Figure 2g, black area), where the resulting lower consumer-resource mass ratio triggers population oscillations and may lead to species loss (Figure 2m, dark and medium green areas). 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 (Figure 2h, ochre area).

These module-specific invasion outcomes are reflected in different effects on community stability. Invading basal resource (AC module), intraguild prey and intraguild predator (IGP module) do not alter system stability except the invading intraguild predator, which can stabilize the dynamics over a narrow range of combinations of nutrient levels and (low to moderately high) temperatures (Figure 2l,o,p). Successful invasion at low temperatures and high nutrient levels in the EC module always destabilizes the community towards cycles or complete collapse due to the paradox of enrichment (Figure 2m). Finally, a successfully invading top predator may or may not change system stability depending on temperature and nutrient levels (TC module, Figure 2n).

Invasion success and invasion-driven changes: The role of environment and size structure

Invasion success and changes in the invaded community also depend on the community size structure. We summarize the general patterns along size structure gradients, focusing on differences between the four types of environments (i.e. cold and nutrient-limited, cold and nutrient-rich, warm and nutrient-limited and

warm and nutrient-rich), the role of body mass ratios α and β between competitors in the AC, EC and IGP modules and the role of size structure asymmetry between adjacent trophic levels given by δ in the TC and IGP_p modules.

Invasion success follows two main patterns defined by environmental conditions and community size structure across the trophic modules. For almost any community size structure, successful invasions by a competing species are least likely in cold and nutrient-rich environments and most likely in warm and nutrient-rich environments (Figure 3a–e). Invading species usually succeed when they compete with a larger resident species in the AC and EC modules (α and $\beta < 1$, Figure 3a,b), while larger invaders mostly fail. The P* and R* rules underline these outcomes (Text S3). In the AC module, a smaller competitor can sustain a higher equilibrium predator biomass and exclude a larger competitor (P* rule, Figures 3a; Figures S3a–c and S4a–l). In the EC module, a smaller consumer has lower resource requirements at equilibrium and therefore excludes a larger competitor (R* rule, Figures 3b; Figures S3b–d and S4m–x). In the IGP module, a smaller intraguild prey is competitively superior to the intraguild predator (Figure S5g–l) but cannot withstand its predation pressure (Figures 3c; Figure S5m–o). Intraguild prey therefore cannot invade (Figure S3m–o) and is displaced by an intraguild predator if the latter invades (Figure S5d–f). Successful invasion of the top predator in the TC module requires the presence of an intermediate consumer, which is more common with large α (Figure S1) and thus larger size-structure asymmetry between trophic levels characterized by smaller δ values (Figure 3d). On the other hand, the intraguild predator in the IGP module feeds on two prey populations, which explains the independence of its invasion success from δ (Figure 3e).

Community size structure and environmental conditions also affect invasion-driven changes in community diversity ΔD (Figure 3f–j) and stability ΔS (Figure 3l–p). With some rare exceptions, invasion lowers local diversity ($\Delta D < 0$) only in the EC module when the smaller competitor invades in a cold environment (Figures 3g; Figure S4) and triggers large population oscillation leading to a collapse (Figures S6 and S7). Increasing diversity ($\Delta D > 0$) after a competitor invades is limited to warm, nutrient-limited environments with an empty consumer or resident niche due to its metabolic meltdown or the presence of a consumer that would otherwise suffer from a metabolic meltdown (AC module, Figure 3f; EC and IGP modules, Figure 3g,h for $\beta < 1$). Invasion by an intraguild predator can increase diversity in all types of environments, but especially at cold temperatures (Figure 3h,j). Increased diversity after invasion in the TC module is more common when the top predator and intermediate consumer have more similar sizes ($\delta < 1$, Figure 3i), and this effect of size ratio asymmetry

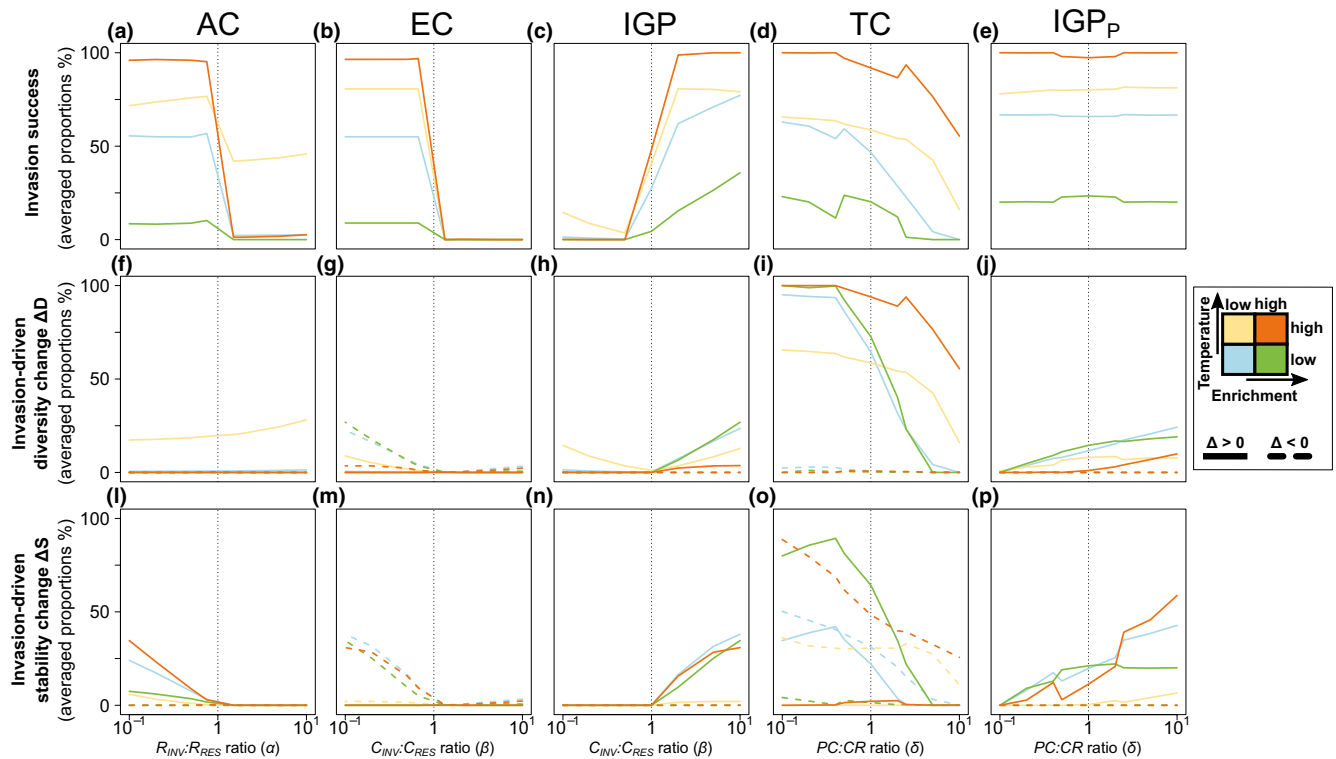


FIGURE 3 Differences in the effects of species body mass ratios and trophic position on the average proportion of invasion successes and changes in diversity and stability across environmental conditions and food web modules. Invasion success (a–e), invasion-driven change in diversity ΔD (f–j) and stability ΔS (l–p) along gradients of body mass ratio, given for (a–c, f–h, l–n) invader and its resident competitor and (d, e, i, j, o, p) adjacent trophic levels. Food web modules: (a, f, l) AC = apparent competition, (b, g, m) EC = exploitative competition, (c, h, n) IGP = intraguild predation with invading intraguild prey ($\beta \leq 1$) and invading intraguild predator ($\beta \geq 1$), (d, i, o) TC = trophic chain and (e, j, p) IGP_p = intraguild predation with invading intraguild predator. Species: R = basal resource, C = consumer, P = predator. Colours denote the averaged proportions in four environment types, defined by combined low and high values of temperatures and levels of nutrient input: blue = cold and nutrient-limited ($T \leq 20^\circ\text{C}$ and $I_K \leq 10 \text{ g m}^{-2}$), yellow = warm ($T > 20^\circ\text{C}$) and nutrient-limited environments, green = cold and nutrient-rich environments ($I_K > 10 \text{ g m}^{-2}$), dark orange = warm and nutrient-rich environments. Solid lines = invasion-driven positive change ($\Delta > 0$), dashed lines = invasion-driven negative change ($\Delta < 0$). Note that invasion-driven neutral change ($\Delta = 0$) is left out for simplicity.

is particularly strong in cold environments in which the size ratios affect the propensity for population cycles and paradox of enrichment (Figures S6 and S7).

Loss of stability ($\Delta S < 0$) is limited to the emergence of population oscillations after an invasion by a small competitor (EC module, Figure 3m) or top predator, especially when it is only slightly larger than the intermediate consumer (TC module, Figure 3o). Invasion-driven gain in stability ($\Delta S > 0$) occurs when a smaller resource species (AC module, Figure 3l), intraguild predator (IGP module, Figure 3n) or the top predator (TC module, Figure 3o) stabilize resident consumer-resource cycles (compare Figures 1a, S6 and S7). This occurs more often with increasing size ratios between the trophic levels (AC module: $\alpha \ll 1$, IGP module: $\beta \gg 1$ and $\delta \gg 1$). The propensity for the change in stability also varies between environments (Figures 3; Figure S5). Loss of stability in the EC module is almost equally likely in all types of environments except for being rare in warm, nutrient-limited conditions (Figure 3m), while in the TC module it is most common in warm, nutrient-rich conditions and almost absent in cold-nutrient rich conditions (as the

resident consumer-resource dynamics are already unstable; Figures 1a and 3o). Increase in stability in the AC, IGP and TC modules is least common in the warm, nutrient-limited environments with the lowest propensity for cycles (Figure 3l,n,o; Figure S9).

Invasion outcomes and the diversity–stability relationship

Invasion outcomes affect the diversity–stability relationship in our simulations. Invasion-induced destabilization occurs mainly under vulnerability, leading to community collapse (regime states $E \rightarrow N$ and $O \rightarrow N$; Figures 4; Figure S10 and Tables S9–S11). About 50% of invasions leading to integration and some leading to substitution trigger population cycles ($E \rightarrow O$; Figure S10). Resistance, occupancy and rescue mechanisms do not destabilize the community. Rescue always increases stability as it prevents the collapse of the resident community ($N \rightarrow E$); the collapse can also be prevented under occupancy ($N \rightarrow E$ and $N \rightarrow O$) and integration ($N \rightarrow O$). Increased stability associated with a shift from

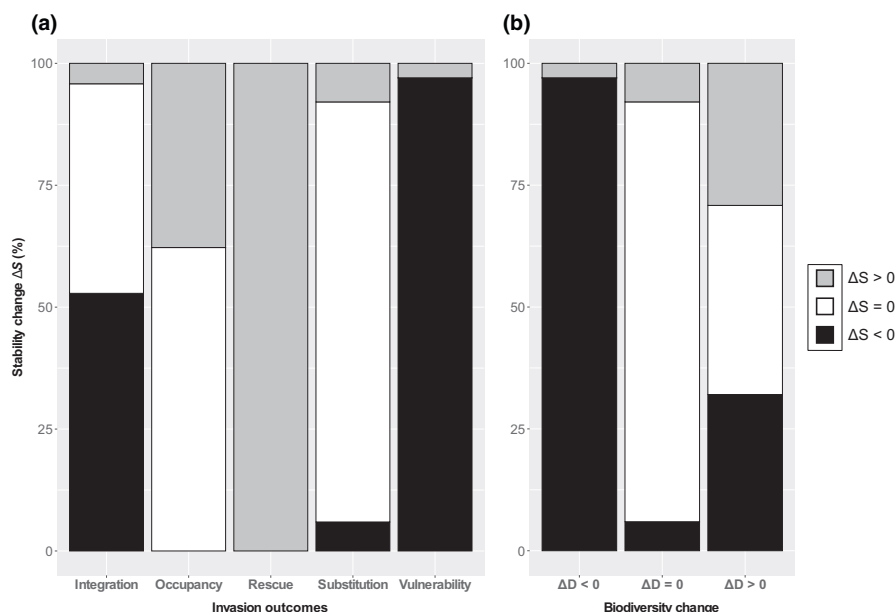


FIGURE 4 Differences in stability change (ΔS) between (a) invasion outcomes and (b) biodiversity change (ΔD) following successful species invasions. Values = cumulative proportions of regime states shown in Figure S1. Biodiversity change in (b) illustrates the cumulative proportions observed across invasion 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.

oscillations to stable equilibria ($O \rightarrow E$) rarely occurs under substitution and vulnerability (Figure S1). Conserved stability regime is the most common outcome for substitution ($E \rightarrow E$ and $O \rightarrow O$), followed by occupancy ($E \rightarrow E$) and integration ($E \rightarrow E$ and $O \rightarrow O$); rescue and vulnerability never maintain the same stability regime (Figures 4; Figure S10 and Table S11).

Invasion-induced changes in diversity and stability are thus linked, but one cannot be predicted from the other alone (Figure 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 (dampened cycles caused by invasion through species substitution in IGP_p) can 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 (Figure 4b).

DISCUSSION

Our study examines the responses of simple communities to the combined effect of three major drivers of global change: warming, eutrophication and species invasions (IPBES et al., 2019). We focused on the impacts of predation and competition by invaders (Dueñas et al., 2018; Gallardo et al., 2016) on resident communities. Our goal

was to understand how invasion outcomes are related to changes in community composition, diversity and stability along environmental gradients (Tilman, 1999). We identified predictable patterns in the outcomes by considering environmental conditions and differences in body mass and trophic position between the invading resident species (Table S12). This allowed us to characterize invulnerable communities and elucidate community-level consequences of successful and transient invasions.

What drives successful invasions and when do they occur?

Environmental and biotic filters underpin invasion success in local communities (Blackburn et al., 2011; Gray et al., 2015; Mitchell et al., 2006). Species living in warm, nutrient-limited 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 (Glibert, 2017; Janssen et al., 2014) are vulnerable to the paradox of enrichment and population collapses (Oksanen et al., 1981). Previous models have shown that (1) ‘intermediate’ environmental conditions that balance the opposing effects of warming and eutrophication prevent biodiversity loss and that (2) larger consumer-resource body mass ratios mitigate the destabilizing effect of eutrophication but increase the vulnerability of top predators to warming (Binzer et al., 2016; Sentis et al., 2017). Our results extend these findings to species invasions.

That is, we predict that invasions will most likely succeed in warm, nutrient-rich environments; positive effects of warming and eutrophication on successful colonization were reported, e.g. for invasive *Corbicula* clams (Basen et al., 2017; Ferreira-Rodríguez et al., 2022). We also predict that smaller competitors, intraguild predators and relatively small top predators (i.e. not much larger than their prey) are most likely to invade.

Size structure of the local community plays an additional filtering role in invasions (Gray et al., 2015). We observed that invasion success of competitors is mainly determined by size differences between resident and invading species, while asymmetries in size structure between adjacent trophic levels determine the fate of invading predators. This can be explained by the limiting similarity hypothesis, which states that coexisting species sharing the same (trophic) niche should have similar traits (MacArthur & Levins, 1967), while this requirement does not hold for invaders in different trophic positions. In our case, the R^* and P^* rules (Box 2; Holt et al., 1994; Tilman, 1985) explain why only smaller competitors could successfully invade.

Apart from competition for resources, we did not consider self-limiting mechanisms in our models that would favour species coexistence (Holt et al., 1994). We also considered a homogeneous environment, which tends to amplify the impact of invasive species through 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). For example, (Burns, 2013) predicted that seasonal succession may facilitate the coexistence of resident and invading *Daphnia* species with different food and temperature requirements.

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 alternative food sources 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. We found that intraguild prey and predator can only coexist in warm, nutrient-limited environments close to the metabolic meltdown threshold of the predator.

Comparing results between modules, we found that intraguild prey (regardless of body size, IGP module), larger consumers (EC module) and larger resource species (AC module) were the least likely successful invaders. This contrasts with frequent successful invasions of intraguild predators (IGP module). Overall, we predict that

successful invasions involve comparatively smaller species, i.e. smaller competitors at lower trophic levels and predators not much larger than their prey. Invaders with other traits can succeed in specific environments: for example, larger competitors at lower trophic levels and intraguild prey may only invade relatively warm and nutrient-limited environments that are not suitable for their predators. Moreover, invaders can fill vacant niches when resident species disappear. For example, the predicted poleward shift of smaller zooplankton species may benefit warming habitats (Evans et al., 2020). Invading predators may also buffer local communities against eutrophication effects at lower temperatures (as in [Hughes et al., 2013]).

These results depend on the size scaling of biological rates used in our models, which primarily derive from studies on terrestrial arthropods (Binzer et al., 2016), and how these allometric scaling influence minimum resource requirements (R^* rule) and maximum viable predation pressure (P^* rule). Further studies are needed to identify communities where our assumptions may not hold and the ‘smaller is better’ rule no longer applies.

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

Overall, our results confirm the classic diversity–stability hypothesis, which states that more diverse ecosystems are more resilient to disturbance (Elton, 2001; Rooney & McCann, 2012; Tilman & Downing, 1994). We found that successful invaders can stabilize the community by increasing local diversity or disrupt its stability and cause species extinctions. These contrasting results highlight the ambivalence of invasions for local biodiversity (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 outcome-dependent changes in system stability. Our results suggest that one-to-one species substitutions in simple communities rarely alter system stability, while invasions leading to increased diversity can both destabilize (outcome type: integration) and stabilize (occupancy and, to a lesser extent, integration) community dynamics. These changes in stability occurred primarily in nutrient-rich environments where communities are vulnerable to population fluctuations (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).

Surprisingly, our study revealed that even failed invasions can affect community diversity and stability in cold, nutrient-rich environments. Diversity could decrease due to increased population cycles by failed invasion of a smaller

consumer (EC module). Diversity could also increase due to rescue by an invading top predator (TC module) if its temporary presence dampens consumer-resource cycles and rescues the basal resource, but not the consumer, from collapse caused by the paradox of enrichment. Such feedbacks from transient top predators to resident species may also arise from cascading effects of an invading top predator on lower trophic levels in more complex food webs (Gallardo et al., 2016; Reynolds & Aldridge, 2021). However, 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 simplify the structure of larger food webs (Binzer et al., 2012), facilitating species invasions and increasing their impact on invaded systems (Sentis et al., 2021). Our findings reveal the central role of body size and trophic position in species invasions and their potential to modulate the effects of environmental stressors on local communities. Our results are based on size and temperature scaling of biological rates based primarily on terrestrial invertebrates; future studies should explore their validity across other taxa and habitat types. Overall, we predict that successful invaders will encompass smaller competitors, intraguild predators and relatively small top predators. Species invasions may thus contribute to the downsizing of food webs (Young et al. 2016). Our results imply that this trend will be especially prominent in warm, nutrient-rich habitats which are projected to become more prevalent as global change continues (Rodgers, 2021).

AUTHOR CONTRIBUTIONS

DSB, AS and SD designed the study. SD performed all numerical computations and analyses based on preliminary analyses by NAP, with additional input from AS and DSB. All authors discussed the results and their presentation. SD wrote the first draft of the manuscript and all co-authors contributed to the manuscript revision.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data and code required to replicate all results have been deposited in GitHub (https://github.com/Samuel-Dijoux/2023-Invasion_modules) and Zenodo (<https://doi.org/10.5281/zenodo.8296873>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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