Biol Invasions (2025) 27:183
https://doi.org/10.1007/s10530-025-03625-1

ELTON REVIEW 7

Revisiting invasional meltdown: mechanisms and consequences of positive non-native species interactions

Anthony Ricciardi · Daniel Simberloff

Received: 5 March 2025 / Accepted: 16 June 2025

Abstract A popular hypothesis predicts that positive interactions involving non-native species will cause ecosystems to become more easily invaded and modified, resulting in an accumulation of invaders and their impacts—a process termed *invasional meltdown*. This model contrasts with the classical theory of biotic resistance, which emphasizes increasing antagonistic interactions among species as a community grows. Invasional meltdown can be an emergent consequence of serial or concomitant facilitations and their indirect effects. However, it has often been narrowly equated with simple biotic facilitation in which the establishment, population expansion, spread, or impact of one invader is enhanced through a positive interaction with another; the hypothesis has rarely been explored beyond these single pairwise facilitations. The original model emphasized continuous self-reinforcing effects of positive interactions of non-native species in general, but here we propose that invasional meltdown can arise through other mechanisms—including an influx of coevolved species, a cluster of interactions driven by a single keystone facilitator, and indirect interactions among both native and non-native species—all of which can result in an increasing invasion rate and cumulative, potentially synergistic impacts. Furthermore, invasional meltdowns are not likely to be indefinite; for example, they may be punctuated by periods in which the invaded community temporarily resists further invasion until a biotic or abiotic phenomenon disrupts the resistance and triggers another series of facilitations. Although invasional meltdown can potentially transform entire ecosystems, its ecological consequences at the community and ecosystem levels have rarely been tested, owing to the complexity of interactions and pathways involved.

Keywords Biotic resistance · Commensalism · Facilitation · Invasion rate · Invasive species · Mutualism

Introduction

Among the fundamental questions explored by invasion science from its inception is why some communities are more vulnerable to invasion by non-native species (Anon. 1985; Pantel et al. 2017; Ricciardi et al. 2021). This question has been addressed by dozens of hypotheses with varying empirical support (Jeschke et al. 2012). One of these is the invasional meltdown hypothesis (Simberloff and Von Holle 1999)—which, despite being highly popular (the original paper has been cited 2860 times; Google Scholar,

A. Ricciardi
Bieler School of Environment and Department of Biology, McGill University, Montreal, Quebec, Canada H3A 1B1
e-mail: tony.ricciardi@mcgill.ca

D. Simberloff (✉)
Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA

May 27, 2025), has been tested only narrowly thus far. Here, we 1) present the historical context of the concept and review the limitations and controversies surrounding it; 2) distinguish potential mechanisms of invasional meltdown and organize them into testable subhypotheses; and 3) present a series of future research directions that demonstrate the fundamental and applied value of the concept to invasion science and ecology in general.

Invasional meltdown in the context of invasion science

Classical theories of community assembly assume that antagonistic (e.g., competitive) interactions between introduced species predominate. Prominent among these theories is the concept of biotic resistance, which predicts that species-rich communities are more likely to contain competitors or other antagonists that can exclude potential invaders (Elton 1958; Levine and D'Antonio 1999; Beaury et al. 2020). Mathematical models demonstrating a declining rate of establishment of new species as species richness increases (Case 1990, 1991) support the notion that successive invasions progressively limit community membership. Attention to biotic resistance was enhanced by a surge in studies of the enemy release hypothesis, which underlies the science of biological control and relates the impact of non-native species to the reduction or absence of pathogens, parasites, and predators in the invaded community (e.g., Thellung 1915; Elton 1958; Keane and Crawley 2002; Torchin and Mitchell 2004; but see Colautti et al. 2004).

By contrast, the role of facilitation was historically neglected in ecological theory (Bruno et al. 2004; Bertness et al. 2024), particularly for invasions, although it has been mentioned in the literature for decades (e.g., Crosby 1986; see below). For example, Elton (1927) highlighted the example of a facilitation in which European starlings dispersed seeds of English blackberry in New Zealand. Nevertheless, a burgeoning number of studies in the past twenty-five years demonstrates that establishment and population growth of introduced non-native species are commonly facilitated, either unidirectionally or reciprocally, by other non-native species (Simberloff and Von Holle 1999; Richardson et al. 2000; Ricciardi 2001; Traveset and Richardson 2014; Prior et al. 2015; Cavieres 2021). This can occur through various direct and indirect mechanisms involving physical and biological components of an ecosystem (Fig. 1).

It is now increasingly acknowledged that multiple introductions can, at times, produce synergistic impacts, in which the joint effect of two or more invasions exceeds the sum of their individual effects (e.g., Ricciardi 2005; Schoeman and Samways 2013; Wei et al. 2020; Brandt et al. 2023). Through facilitation, invaders and synergistic effects are predicted to accumulate over time—a phenomenon termed *invasional meltdown* by Simberloff and Von Holle (1999), who, in emphasizing the accumulation of invaders, drew a parallel to mutational meltdown (Gabriel et al. 1993). Invasional meltdown (IM) was originally defined as the process by which a group of non-native species "*facilitate one another's invasion in various ways, increasing the likelihood of survival and/or of ecological impact, and possibly the magnitude of impacts. Thus, there is an accelerating accumulation of introduced species and effects rather than deceleration as envisioned in the biotic resistance model*" (Simberloff and Von Holle 1999, p. 22). Although this definition implies that each non-native species is facilitated, the authors made clear that if one interactant was facilitated and the other unimpacted (i.e., a commensalism) the interaction would be considered an IM.

The original conception of IM was "an auto-catalytic process that would accelerate the replacement of native communities, perhaps to the point of no return" (Simberoff 2006). Such an effect was suggested by Howarth (1985), while addressing the impact of non-native terrestrial invertebrates on native plants and animals in Hawaii. He reasoned that non-native species can create new niches that may then be occupied by either native species or new non-natives, and he emphasized the ecologically disruptive power of mixed non-native species "acting in concert". IM was similarly anticipated by Crosby (1986) in his description of how groups of coevolved species of livestock, weeds, insects, and pathogens ("portmanteau biotas") accompanying European colonists have substantially replaced native biotas in the Americas, Australia, New Zealand, and the Canary Islands:

> "*One of the most important factors in the success of the portmanteau biota is so simple that it is easy to overlook. Its members did not function alone, but as a team… Sometimes the mutual*

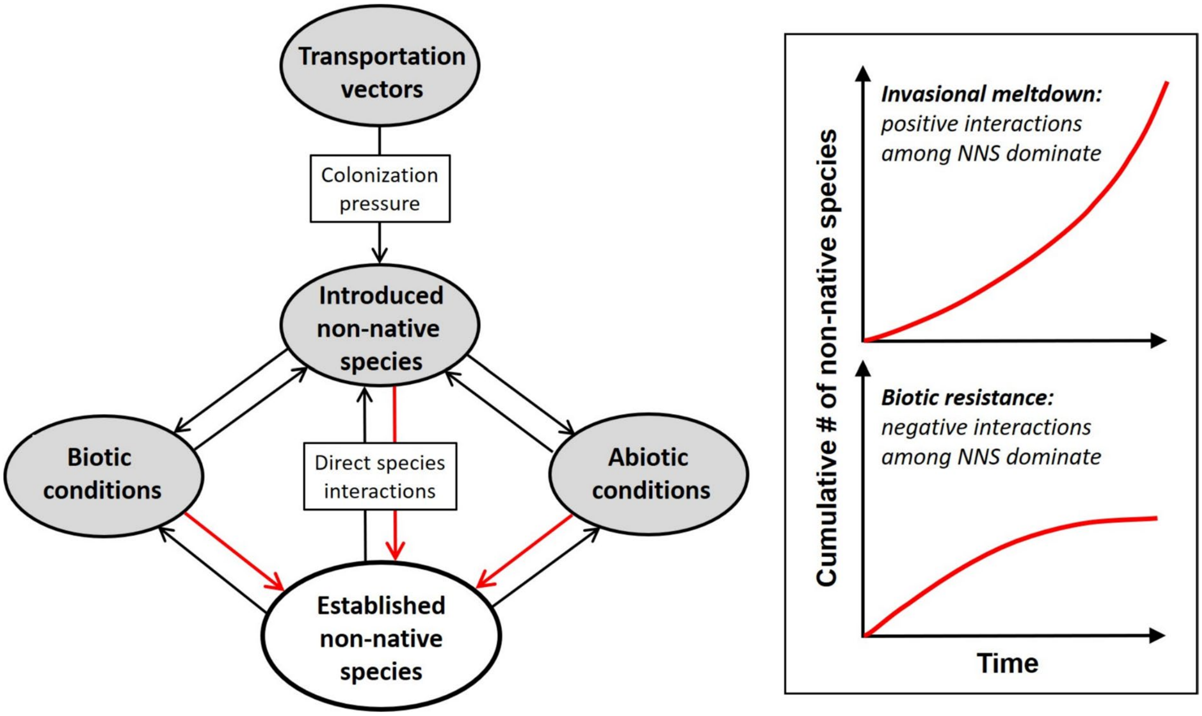

Fig. 1 Interaction pathways linking numbers of introduced non-native species (NNS) to rates of invasion. Introduced NNS can alter biotic conditions (e.g. food web structure, species dominance, native diversity) and abiotic (physical habitat) conditions to the benefit or detriment of currently established NNS and subsequent arrivals. Invasion theory predicts that the rate of invasion is exponentially increasing (invasional meltdown model) or asymptotic (biotic resistance model), depending on whether the proximate interactions (red arrows) are predominantly positive or negative, respectively

> *support is obvious, as with Europeans importing honeybees to pollinate their crops. Sometimes the connection is obscure: In the Great Plains, the whites and their hirelings killed off almost all the buffalo – encouraging the spread of venereal pathogens, some of which were certainly immigrants* (p. 287–288)… *The success of the portmanteau biota and of its dominant member, the European human, was a team effort by organisms that had evolved in conflict and cooperation over a long time. The period of that co-evolution most significant for the success overseas of this biota with sails and wheels occurred during and after the Old World Neolithic, a multispecies revolution whose aftershocks still rock the biosphere*” (p. 293).

It is now apparent that one non-native species can facilitate another, directly and indirectly, in myriad ways. For non-native plants, direct facilitation might arise by virtue of pollination or seed dispersal by a non-native animal (Richardson et al. 2000; Traveset and Richardson 2014; Aizen and Torres 2024) or by non-native mycorrhizal or bacterial symbionts aiding resource acquisition (Díez 2005). Facilitation can also be indirect, as when a non-native ant removes predators of a non-native scale insect from which it extracts honeydew (Bach 1991; Green et al. 2011). Non-native animals may further facilitate non-native plants by grazing, trampling, or otherwise disturbing the habitat in a way that is inimical to native plants and favorable to non-natives (Mack 1986, 1989).

Facilitation often arises when a non-native species invades along with a non-native mutualist from its native range (e.g., invasions of *Eucalyptus* in Spain were facilitated by ectomycorrhizal fungi introduced with them; Díez 2005), or a previously introduced non-native species is subsequently joined by a mutualist from its native range—e.g., the invasion of Florida by the fig *Ficus microcarpa* was later facilitated by the arrival of its obligate pollinating wasp, *Eupristina verticillata* (McKey and Kaufmann 1991; Nadel et al. 1992) [see *Coevolved species assembly*, below]. However, non-native species from different biogeographic regions can also facilitate one another, as in the case of the Argentine ant (*Linepithema humile*) from South America protecting the Asian red scale (*Aonidiella aurantia*) from predators, thereby increasing scale density on California citrus (DeBach et al. 1951).

Controversies and complexities

Although IM attracted enough attention that Jeschke et al. (2012) found it to be the most generally supported among six prominent hypotheses about invasions, empirical support for the concept quickly became controversial (Gurevitch 2006; Simberloff 2006) on two related grounds:

1. Did observed examples of facilitation amount to a population-level response for one or more interactants? For example, a non-native species pollinating a non-native plant is typically described as a facilitation, but it would not affect the population of the plant if that population were not limited by pollination; and determining pollination-limitation requires substantial research (Parker 1997; Richardson et al. 2000). Neither would an introduced ant attacking predators of an introduced scale insect necessarily facilitate population growth of the scale, if predation were not limiting the scale population.
2. How frequently does facilitation have a population impact on a non-native species relative to other co-occurring forces, such as biotic resistance or enemy release? In other words, how significant is IM as a community-structuring force?

These questions remain important considerations as this concept continues to be tested and expanded.

Braga et al. (2018a,b) found that 876 published studies invoking IM substantially supported it with empirical evidence, but there were perceived ambiguities owing to somewhat different phenomena being lumped under the same term. The authors called for clarification by distinguishing three situations: (i) where one non-native species facilitates another, but the facilitation is not reciprocated; (ii) where two non-native species facilitate one another; and (iii) where more than two non-native species interact directly or indirectly.

The original conception of IM highlighted positive interactions between non-native species as potentially the principal cause of an accelerated rate of invasion and increased frequency of synergistic effects and other impacts (Fig. 1; Simberloff and Von Holle 1999). Examples of direct pairwise interactions among non-native species were presented as *prima facie* evidence that facilitation among invaders was at least as frequent as antagonistic interactions (Simberloff and Von Holle 1999; Ricciardi 2001; Gallardo and Aldridge 2015; but see Jackson 2015). It was later recognized that facilitation is broader than direct pairwise mutualisms (+/+) and commensalisms (+/0). In particular, exploitative (+/−) relationships can be facilitative, because one non-native species benefits from the other's presence (Ricciardi 2001). Furthermore, this interaction can be strongly asymmetric such that a non-native predator/herbivore/parasite is facilitated at negligible cost to the non-native prey/plant/host population, because of the relatively low population density of the former or the high recruitment rate of the latter. Examples include a molluscivorous fish, the round goby (*Neogobius melanostomus*), and its natural prey, the zebra mussel (*Dreissena polymorpha*), or planktivorous fishes (e.g. alewife, *Alosa pseudoharengus*; rainbow smelt, *Osmerus mordax*) and zebra mussel larvae; such cases are effectively virtual commensalisms (+/0) (Ricciardi 2001). These relationships can span ecosystem compartments—e.g., a resource subsidy from a terrestrial plant to an aquatic animal (Cheek et al. 2024). It is also apparent that *facultative* facilitations (in which the probability of establishment and population expansion of a non-native species is enhanced but does not depend upon the presence of other non-native species) are more common than *obligate* facilitations in some ecosystems (e.g., Ricciardi 2001; Gallardo and Aldridge 2015) but can nonetheless increase the overall establishment, spread, and impact of invaders—similarly to the role of biotic resistance in dampening but not preventing invasion establishment, spread, and impact.

Indirect effects were also not emphasized in the original tallies of positive interactions, although they play major roles in the few examples of ecosystem-level impacts ascribed to IM through species interactions or habitat alteration (O'Dowd et al. 2003;

Ricciardi 2001, 2005; Simberloff 2011; Kuebbing 2020). An example of the former is an invasion facilitated by removing a biotic or abiotic constraint through activities of another non-native species—as occurred when the establishment of the American bullfrog (*Lithobates catesbeianus*) in ponds in western North America was facilitated by a coevolved non-native fish, bluegill (*Lepomis macrochirus*), that increases tadpole survival by reducing predatory dragonfly nymphs (Adams et al. 2003). Another case is the enhanced abundance of feral cats following suppression of a competitor/predator, the yellow-spotted monitor lizard, through the latter's toxic ingestion of cane toads in Australia (Doody et al. 2024). An example of facilitation through habitat alteration is increased soil nitrogen caused by European earthworms facilitating invasion of northeastern North American forests by Japanese barberry, *Berberis thunbergii* (Nuzzo et al. 2009).

Despite myriad examples of facilitation between pairs of non-native species, an IM in which multispecies facilitation has accelerated the rate of accumulation of invaders and synergistic impacts has rarely been demonstrated (Simberloff 2006; but see Collins et al. 2020). One potential case involves eleven Eurasian species in a North American terrestrial ecosystem (Heimpel et al. 2010). Among these species, European buckthorn, *Rhamnus cathartica*, whose population growth was promoted by a mutualism with the European nightcrawler (*Lumbricus terrestris*) and possibly also through seed dispersal by the European starling (*Sturnus vulgaris*), provided food resources for two crop pests: oat crown rust *Puccinea coronata* and the soybean aphid *Aphis glycines*. In this system, the soybean aphid is itself exploited by non-native predators including the lady beetle *Harmonia axyridis* and the ground beetle *Agonum muelleri*, as well as by the non-native parasitoid wasp *Aphelinus certus*, and the regional abundances of these species are assumed to have been enhanced by the aphid. Furthermore, the European nightcrawler likely facilitated the North American invasion of the Asian flatworm *Bipalium adventitium*, which preys on earthworms (Fiore et al. 2004).

The Great Lakes offer another case study in which the IM model better describes the observed patterns of invasion and impact than the classical biotic resistance model (Ricciardi 2001). However, DeVanna et al. (2011) argued that interactions between non-native species in the Great Lakes did not constitute an IM, for three reasons: (1) a single taxon (zebra and quagga mussels, *Dreissena* spp.) is responsible for the majority of reported facilitations in the Great Lakes; (2) *Dreissena* facilitates both native and non-native species at similar frequencies; and (3) facilitated species have not themselves promoted more invasions—there is no second-tier of facilitations between resident and incoming non-native species. Each of these points is disputable. First, nothing in the original definition of IM prevents a single invader from being involved in the majority of facilitations; in fact, several well known cases of multispecies facilitation involve a dominant facilitator, like the firetree *Morella faya* or the crazy ant *Anoplolepis gracilipes* (see discussion below). Second, facilitation of multiple native species by a non-native ecosystem engineer (i.e., an organism that modulates the availability of resources to other species by changing the physical environment; Jones et al. 1994) is unsurprising, nor does it disqualify a case of IM—unless the facilitated native species provide biotic resistance against the accumulation of invaders and their impacts (similarly, hindrance of further invasions posed by only one or two of a larger group of resident species cannot be disqualified as an example of biotic resistance, and even species-poor communities can offer resistance; cf. Baltz and Moyle 1993). Native species do not appear to be facilitated sufficiently to have impeded either the accelerating invasion rate in the Great Lakes or an increased frequency of impacts (Ricciardi 2001, 2005, 2006). In general, there is scant evidence of biotic resistance by natives or other non-native species in the Great Lakes (Ricciardi 2001). Third, it is true that few definitive examples of obligate facilitation of non-native species establishment exist in the Great Lakes, but ample evidence exists of post-establishment population-level facilitation (Ricciardi 2001, 2005). While multi-tiered facilitations in general are not well-documented in the Great Lakes, one example overlooked by DeVanna et al. (2011) is the invasion by the sea lamprey *Petromyzon marinus*, an ectoparasitic fish that contributed to massive declines in populations of a native top predator, lake trout *Salvelinus namaycush*, thereby indirectly facilitating establishment and population explosion of a small non-native planktivorous fish, the alewife *Alosa pseudoharengus* (Christie 1974). The rapidly growing alewife population reduced native planktivores and subsequently facilitated persistence of a non-native predator (Chinook salmon, *Oncorhynchus tshawytschka*) in Lake Michigan by acting as its principal food source (Stewart et al. 1981; Jude et al. 1987). In summary, whereas historical changes to transportation vectors explain the composition and, to a large extent, the rate of invasion in the Great Lakes over time (Ricciardi 2000, 2006; Ricciardi and MacIsaac 2022), IM plausibly contributed to the rapid spread and population expansion of many non-native species in the basin.

An excellent documented example of a multispecies IM that has accelerated the accumulation of invaders and their impacts is the rapid transformation of an island ecosystem triggered by an invasive ant-scale insect mutualism (Fig. 2). The yellow crazy ant (*Anoplolepis gracilipes*), introduced to Christmas Island (Indian Ocean) in the early 1900s, maintained low abundances for decades before developing a vast supercolony by the 1990s, when it formed a mutualistic relationship with recently introduced honeydew-secreting scale insects (e.g., *Tachardina aurantiaca*) (Abbott and Green 2007). The secretions of the scale insects promoted sooty moulds that likely caused dieback of the forest canopy. Simultaneously, the ants devastated populations of the red land crab *Gecarcoidea natalis*, a dominant native omnivore-detritivore, by swarming and spraying them with formic acid. The decline of crab populations resulted in increased leaf litter and native seedling density on the forest floor, as crab omnivory previously controlled seedling recruitment (Green et al. 1997). Crab predation also limited population density of another invader, the herbivorous giant African land snail (*Lissachatina fulica*). Both the absence of the crab and the increased abundance of food in the form of leaf litter facilitated the land snail's invasion of the island. This suite of direct and indirect interactions re-engineered the island's rainforest ecosystem (O'Dowd et al. 2003; Green et al. 2011).

The previous example illustrates a point about facultative versus obligate facilitations of "secondary invasions" (Loughlan and Green 2017; Pearson et al. 2018). Pearson et al. (2018) drew a distinction between invaders being obligatorily facilitated by a primary invader and those invaders that are not excluded from the system in the absence of the putative facilitating species. In the case of Christmas Island, the yellow crazy ants were established but remained in low abundance for several decades before being triggered to become superabundant.

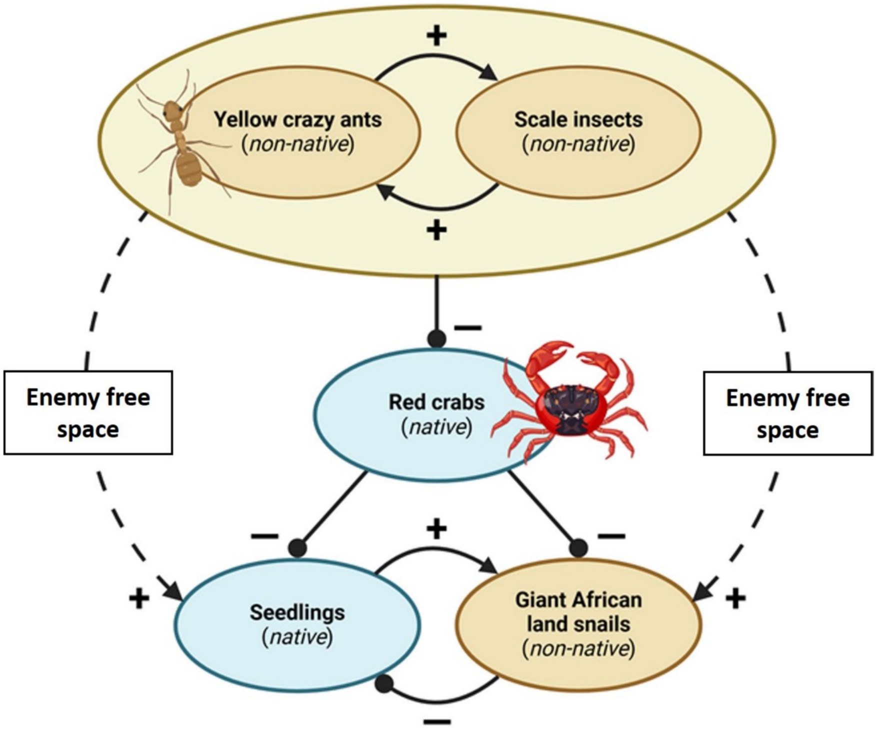

Fig. 2 Invasional meltdown on Christmas Island, as characterized by a series of direct and indirect facilitations (solid arrows and dashed arrows, respectively) between non-native invertebrates (ants, snails, scale insects). At the base of this series of interactions is the mutualism between yellow crazy ants and scale insects, which drives ant superabundance and, consequently, the decline of a native dominant omnivore-detritivore: the red crab. The loss of red crabs creates enemy-free space that promotes the recruitment of seedlings and the survival of the introduced giant African land snail. See text for detailed explanation. Figure adapted from Green et al. (2011)

The mutualism with scale insects was not an obligate facilitation of establishment, but apparently an obligate facilitation of superabundance that precipitated the IM.

An expanded concept: multiple meltdown mechanisms and scenarios

The theoretical underpinnings of IM have been slow to develop, possibly because experimental tests of the concept have been largely limited to pairwise interactions between non-native species (Simberloff 2006; Braga et al. 2018a,b). Consequently, the relationship of IM to other hypotheses and concepts in invasion science, its relevance to changing biodiversity and ecosystem function, and its implications for management have barely been explored. To help address these gaps, we present a broader view of IM as an overarching concept (similar to that of biotic resistance) that unites a cluster of related hypotheses. We propose that IM could result from a diverse set of mechanisms and scenarios that act independently or simultaneously (Table 1).

Generalized facilitation

In the generalized facilitation model proposed by Simberloff and Von Holle (1999), a group of non-native species of disparate or similar origins can facilitate one another's invasion by increasing the likelihood of establishment and further population growth. If such interactions are at least as common as antagonistic interactions, they could accelerate the accumulation of invaders and their effects in the recipient invaded system—the emergent property of IM. Indirect facilitations could result from cascading chains of non-native species interactions, whose net result can be commensal or mutually-reinforcing, thus amplifying non-native survival, spread, and/or impact (O'Dowd et al. 2003) and potentially generating synergistic effects (Ricciardi 2005). For example, during the mid-1990s in the northwestern Atlantic Ocean, the proliferation of the European bryozoan *Membranipora membranacea*, promoted by warmer ocean surface temperatures, resulted in encrusting colonies on competitively dominant native kelps (*Laminaria* spp.) along the coasts of Nova Scotia and New England, causing the kelp to become brittle and susceptible to defoliation during storms (Scheibling and Gagnon 2006). The reduction in kelp canopy cover permitted increased light penetration to the bottom sediments and thus promoted growth of a non-native competitor, the Japanese alga *Codium fragile*. *Codium* was additionally facilitated by an outbreak of *Paramoeba invadens*, a protozoan pathogen that caused mass mortality of sea urchins and thereby released *Codium* from herbivory (Lyons and Scheibling 2008). The subsequent replacement of kelp by *Codium* in the shallow subtidal zone was an unprecedented physical habitat alteration for the Northwestern Atlantic coast (Harris and Tyrrell 2001; Scheibling and Gagnon 2006).

Any introduced non-native species can affect resident native and non-native species in a community, positively or negatively, by modifying one or more key environmental factors that contribute to successful establishment, population growth, and spread of another introduced species. Invasions can promote further invasions through trophic mechanisms (e.g. Adams et al. 2003) and non-trophic effects including habitat modification (e.g. soil legacy effects; Dickie et al. 2014; Chen and van Kleunen 2022), provision of new or modified resources (e.g., Zhang et al. 2022; Sun et al. 2024), or altered disturbance regimes (Mack and D'Antonio 1998). An invader itself can act as a disturbance—defined as a discrete event that damages, kills, or removes individual organisms or living biomass (Sousa 1984; Plante et al. 2004)—by removing resident enemies of other invaders, thereby releasing non-native species from resource competition (Davis et al. 2000; Grosholz 1995; Scheibling and Gagnon 2006) or top-down control (Adams et al. 2003). These biological disturbances could thus facilitate establishment of one or more newly arrived non-native species or trigger resident non-native species to become superabundant and impactful after having persisted at low abundance for long periods ("sleeper populations" sensu Spear et al. 2021). For example, invading European green crab (*Carcinas maenas*) in California caused a tenfold reduction in abundance of native clams (*Nutricola* spp.) that became the crab's preferred prey. The decline of the native clams released another non-native species, the eastern gem clam (*Gemma gemma*), from competition and allowed it to become abundant after having been constrained to low densities for decades (Grosholz 1995). Thus, IM can be a major community

Table 1 Hypothesized mechanisms of invasional meltdown

Mechanism	Hypothesis/Explanation	Empirical support?
Generalized facilitation	A group of non-native species of disparate origins can facilitate one another's invasion success by increasing the likelihood of establishment and further population growth, thereby accelerating the accumulation of invaders and their effects in the recipient system.	Limited. Studies demonstrating pairwise facilitations between non-native species are common. However, studies showing whole-community transformations—as predicted by the IM hypothesis—are heretofore rare (but see O'Dowd et al. 2003).
Keystone facilitation	By altering one or more key resources, a single invader could trigger a series of facilitations and have cascading effects on native and non-native species, which ultimately results in an accumulation of invaders and their impacts.	Yes, as shown by several experimental studies and field surveys involving invasive ecosystem engineers (e.g., Ward and Ricciardi 2007; Potgieter et al. 2014).
Coevolved species assembly	Successive introductions that reunite coevolved species assemblages are more likely to increase the overall invasion rate, because coevolution reduces the intensity of negative interactions and thus increases the likelihood of co-existence and facilitation.	Yes. Co-introduced non-native predator–prey, plant–herbivore, parasite–host species groups have been found to mutually enhance their invasion establishment, spread, and/or impact through prey subsidies (e.g., Fritts and Rodda 1998), by differentially impacting resident natives (e.g., Tompkins et al. 2003) or through preferential facilitation (e.g., Prior et al. 2015). Non-native species assemblages with shared evolutionary history have been become established throughout the world, reflecting colonization pressure from particular source regions as well as facilitative interactions (Crosby 1986; Ricciardi and MacIsaac 2000; Ricciardi 2001, 2005; Bertelsmeier et al. 2024).
Punctuated invasional meltdown	Periods of IM are not indefinite; they can be punctuated by periods of stasis. The accumulation of non-native species can be limited by either propagule supply, environmental change, or increased biotic resistance can against further invasion. Biotic resistance can be disrupted by a physical or biotic disturbance—including another invasion that could trigger a different meltdown.	Limited. An analogous finding is that invasive species dominance can degrade over time, allowing dominance of new invaders (Yelenik and D'Antonio 2013). A modeling study has shown that a series of mutualistic interactions between a community of invaders that cause species turnover could ultimately lead to a stable novel community (Campbell et al. 2022).
Native/non-native facilitation chains	Facilitations and synergies among invaders can occur indirectly across multispecies chains whose intermediate links may include native species.	Yes. Experimental studies and field surveys have demonstrated multispecies facilitations and cascading effects involving natives (see main text).

structuring force by altering disturbance intensity and/or frequency within an ecosystem (cf. Haghkerdar et al. 2019; Santillan et al. 2019).

Keystone facilitation

By altering resource availability, physical habitat conditions, or species interactions, a single invader could precipitate a series of facilitations with cascading effects on non-native species (e.g., Heiman and Micheli 2010; Lizarralde et al. 2004; Anderson et al. 2006). We name such an invader a 'keystone facilitator', adopting the term from Stachowicz (2001) but revised to describe a species that disproportionately facilitates other non-native species by modifying biotic or abiotic conditions. This concept acknowledges that IM can be driven by a single species, as in the cases of *Dreissena* in the Great Lakes and *Morella* in Hawaii. Such species, especially non-native ecosystem engineers and foundational species, are likely to favor certain native taxa as well (e.g., Ward and Ricciardi 2010) and may even cause a facilitation cascade (sensu Altieri et al. 2007). An example from the Great Lakes is dreissenid mussels facilitating a native engineer, the filamentous attached alga, *Cladophora glomerata*, via enhanced light transparency and nutrient transfer to the benthos (Higgins et al. 2008), which in turn provides substrate for non-native epiphytes including a red alga (Sheath and Morison 1982). In addition to fundamental changes to physical habitat, some keystone facilitators promote the establishment or dominance of non-native species by altering disturbance regimes in ways that reduce resident enemies (Jauni et al. 2014; Pickard 1984).

Coevolved species assembly

It has been hypothesized that coevolved species are more likely to facilitate each other, and thus can act as mutual attractors that promote the assembly of non-native communities with a shared evolutionary history (Ricciardi 2001, 2005), based on the premise that coevolution reduces the intensity of exploitative and antagonistic interactions (cf. Case and Bolger 1991) and promotes mutualisms (Cosmo et al. 2023). If so, serial species introductions from the same donor pool could rapidly reassemble trophic and non-trophic coevolved interactions (e.g. predator–prey, parasite-host, plant-pollinator, and commensalisms) in the invaded range, leading to an IM. Indeed, coevolved non-native predator–prey and parasite–host species have been shown to enhance their colonization success mutually via, *inter alia*, prey subsidies (Fritts and Rodda 1998), differential impacts on native competitors (Tompkins et al. 2003), or preferential facilitation (e.g., Prior et al. 2015).

Crosby (1972, 1986) described successive invasions and subsequent dominance of many areas of the world by Eurasian species resulting from mutualistic interactions among the coevolved plants, animals, and pathogens moved by European colonists. In Europe, the parasitic life cycle of the Ponto-Caspian trematode *Bucephalus polymorphus* was completed through serial invasions of the zebra mussel (the trematode's first intermediate host) and the European pike-perch *Sander lucioperca* (the definitive host); these invasions facilitated the trematode's spread into inland lakes where it caused mass local mortality of cyprinid fishes that served as its second intermediate host (Combes and Le Brun 1990). A more recent example is the increasing presence of Ponto-Caspian invertebrates and fishes in the Great Lakes basin (Ricciardi and MacIsaac 2000) and western Europe (Leppäkoski et al. 2002). In the Great Lakes, the accelerated influx of Ponto-Caspian species constitutes a distinct phase in the invasion history of the basin (Ricciardi and MacIsaac 2000; Ricciardi 2006). Although the influx is explained largely by trait selection and vector traffic between donor and recipient regions (Ricciardi 2006), positive interactions among these reunited species likely facilitated their rapid expansion and dominance within the basin (Ricciardi 2001, 2005). Elsewhere, complexes of invasive species from overlapping native ranges have similarly been observed to interact facilitatively. One such example is a "synergistic trio" of North American mammals (mink, beaver, and muskrat) that have strongly affected native birds and small rodents on a Chilean island (Crego et al. 2016). With respect to terrestrial species, it has been proposed that the establishment of non-native plants is a "necessary precondition" for subsequent spread of non-native insects, owing to a long shared coevolutionary history (Bertelsmeier et al. 2024); the insects themselves may promote the establishment of coevolved specialist predators or parasitoids, such that plant invasions can generate ramifying facilitations.

A related concept is that of "nested invasions"—associated microbiota being transferred by a host species into a non-native region—as contributing factors to the successful establishment of the host and its metacommunity (Leonhardt et al. 2023). It has long been recognized that plant invasions have been fostered by deliberate or inadvertent co-introduction with microbial mutualists (Richardson et al. 2000; Nuñez and Dickie 2014). Thus, for instance, the intentional introduction of their ectomycorrhizal fungi with *Pinus* species during establishment of forestry plantations is believed to have aided many pine invasions (Richardson and Higgins 1998). Non-native legumes that do not associate with native rhizobia not only thrive when co-introduced with non-native rhizobia but may spread even further because of the propensity of rhizobia to hybridize by lateral gene transfer; hybrids between native and non-native rhizobia can invade soils that exclude the purely non-native rhizobia, thus exacerbating the spread and impacts of their associated non-native plants (Wei et al. 2009; Liu et al. 2012).

This hypothesis has implications for the survival and impact of range-shifting species spreading into the same recipient community, both of which could conceivably be enhanced through facilitation (Flickinger and Dukes 2024). As climate change further drives the spread of such species, a timely question is whether IM will increase the survival and impact of a group of native range shifters that have a shared evolutionary history; or, alternatively, whether the simultaneous range shift of multiple species with their coevolved natural enemies will limit their impacts (but see Colautti et al. 2004, for exceptions).

The coevolved assembly hypothesis has rarely been tested formally. Braga et al. (2018a) found that studies involving coevolved non-native species showed lower empirical support for IM than studies of non-native species that lacked a shared evolutionary history. Conversely, model simulations revealed that the introduction of a suite of species that have shared history elsewhere increases the slope linking invasion success to the total number of introductions, thereby accelerating the invasion rate, consistent with IM (Pantel et al. 2017). A key consideration is the extent to which coevolved relationships between non-native species are maintained in the invaded community.

Punctuated meltdowns

Feedbacks that generate IM need not (and, we expect, do not) continue indefinitely. Non-native species assembly can be interrupted by a substantive change in colonization pressure or by increasing invader-mediated biotic resistance against further invasion (e.g., Rodriguez 2001). Recent theory suggests that the influx of a community of non-native species of shared evolutionary history is likely to result in greater stability—i.e., a more static composition of species—than an equal number of random invaders (Campbell et al. 2022; Piccardi et al. 2022). However, the resistance of such communities could be disrupted by a physical or biotic disturbance (Shea and Chesson 2002; Clark and Johnson 2009), including invasion by a keystone facilitator that triggers a different IM. Therefore, IM can be ephemeral, and even serial—i.e. punctuated. Consider, for example, a series of invasions of coevolved primary producers, herbivores, and predators that facilitate each other through direct and indirect means. One can imagine that this assemblage becomes relatively stable and resists incursion from less competitive species through strong interactions (Case 1990; Campbell et al. 2022). Then, subsequently, the resistance becomes disrupted through a biotic disturbance (a new invasion) or a change in the physical environment that favors a different suite of species. Such a sequence may result in an accumulation of non-native species and/or species turnover with replacement of the dominant invader (e.g., "over-invasion", sensu Russell et al. 2014). This phenomenon contrasts with that of cases of "serial replacement" (sensu Lohrer and Whitlach 2002) in which established invaders are largely or wholly replaced by antagonistic new arrivals, and the combined effects of invaders are less than the sum of their individual impacts.

A possible example of punctuated IM involves the invasion of the Hawaiian Islands by the African grass *Melinis minutiflora*. This invasion led to the large-scale replacement of native vegetation by virtue of a drastic increase in fire size and frequency (Hughes et al. 1991; D'Antonio and Vitousek 1992). Greatly increased rates of nitrogen mineralization ensued, which favored N-limited *M. minutiflora*, thus producing a positive feedback and *Melinis* dominance (Yelenik and D'Antonio 2013). Subsequently, decline of N-mineralization rates to those before the *Melinis* invasion on the island of Hawaii ended the positive feedback and was associated with a decline in *Melinis* and rapid domination not by the original vegetation but by the invasive nitrogen-fixing tree *Morella faya* (Yelenik and D'Antonio 2013). Through provision of nitrogen-rich leaf litter, *M. faya* enhanced the abundance of non-native earthworms (Aplet 1990); the mutualistic role that earthworms may have played in the replacement of *M. minutifora* by *M. faya* has not been investigated. During senescence or dieback, *M. faya*'s legacy effect on soil nitrogen may have facilitated invasions by other non-native plants (Adler et al. 1998). Finally, *M. faya* has also enhanced the local abundance of an invasive herbivorous insect, the two-spotted leafhopper *Sophonia rufofascia* (Lenz and Taylor 2001).

The concept of punctuated IM implies that ecosystem susceptibility to invasion can vary greatly over time, owing to (1) temporal variation in colonization pressure (the number of taxa introduced to an area; sensu Lockwood et al. 2009); (2) the arrival of a keystone facilitator, and (3) environmental changes, such as altered disturbance regimes, that render the environment less hospitable to species in the current donor pool. Within the same ecosystem, facilitation and resistance can vary temporally in dominance (e.g. Beshai et al. 2023) and, as suggested by the *Melinis/Morella* case, can result in one stable community that was dominated by facilitating non-native species being replaced by another such community after a period of relative stasis. Thus, IMs can be interrupted, perhaps indefinitely, but on a lengthy time scale the overall accumulation of non-native species could still approximate a concave (e.g. exponential) curve, despite the intervening periods of stasis. Punctuated IM could be a common phenomenon but difficult to discern if these intervening periods are obscured over coarse time scales.

Native/non-native facilitation chains

Facilitations among invaders can also occur indirectly across multispecies chains whose intermediate links may include natives. Recently, the role of native species in directly facilitating non-natives has received attention (Northfield et al. 2018; Hernández-Brito et al. 2020; Cavieres 2021; Camacho-Cervantes et al. 2023). Among the most commonly documented examples are exploitative relationships (e.g., non-native predator-native prey; Grabowska et al. 2009; Monceau et al. 2013; Nurkse et al. 2016) and cases in which natives relieve environmental stress on non-native species (e.g., Wright et al. 2018; Uyà et al. 2020; Lucero et al. 2021). Some of these interactions can promote invader establishment and/or spread with substantial negative repercussions on native communities (e.g., Lucera et al. 2021). Furthermore, in some instances, an invader may be facilitated more by a resident native species than by a non-native species (e.g., Firth et al. 2021), and the positive effects of native species can enhance an invader's abundance to levels exceeding those in the invader's native range (e.g., Gribben et al. 2020).

If the natives are involved predominantly in positive links, then IM (or characteristics thereof) may be fueled by high native species richness, contrary to the classical concept of diversity-stability (Ives and Carpenter 2007). This implies that the synergistic influence of a small number of invaders could be magnified by (certain) native species. The potential complexity of such interactions suggests that we might be overlooking many of them. For instance, pollination by a native bumblebee (*Bombus dahlbomii*) facilitated the initial establishment and spread of European Scotch broom (*Cytisus scoparius*) in South America. However, pollination limitation was likely relieved by introduction of European bumblebees (*B. terrestris* and *B. ruderatus*), which also pollinated and facilitated the spread of other non-native plants (Morales and Aizen 2002; Aizen et al. 2019; Aizen and Torres 2024).

The contexts in which native diversity contributes to IM versus biotic resistance remain to be explored. We do not contend that IM is more likely than biotic resistance in the presence of diverse native species but simply that it can also result from native interactions. Several cases exist of natives serving as links in cascading interaction chains that promote non-native species. For example, dreissenid mussels (non-native engineers) promote the local abundance of native (as well as non-native) gammarid amphipods that serve as prey for non-native benthivorous fishes such as round goby *N. melanostomus* and Eurasian ruffe *Gymnocephalus cernua* in the Great Lakes (Ricciardi 2001). In southeastern Australia, the non-native alga *Caulerpa taxifolia* modified the behavior of a native ecosystem engineer, the clam *Anadara trapezia*, causing the clams to partially unbury themselves and extend nearly a third of their shell surface above the sediment, thereby providing a stable coarse substrate for colonization in an otherwise substrate-limited environment; the organisms colonizing this substrate include several native species but also an invasive alga, *Codium fragile*, which does not occur in the absence of *Caulerpa* (Gribben et al. 2009).

Native species can be part of positive or negative interaction chains that positively reinforce one or more non-native species. We demonstrate this with two plausible cases from the Great Lakes basin. An invasive planktivore, the spiny water flea *Bythotrephes longimanus*, is a visual predator whose impact is light-limited (Jokela et al. 2013). It feeds voraciously on herbivorous waterfleas, which can have similar grazing rates as the zebra mussel (Pires et al. 2005) and thus compete for limited phytoplankton resources. Therefore, alleviation of grazing competitors by *Bythotrephes* populations could have a positive feedback on zebra mussels, whereas zebra mussels can increase light transparency to the benefit of visual predators like *Bythotrephes*, creating an indirect mutualism (Fig. 3A). The second hypothetical example involves the zebra mussel and the

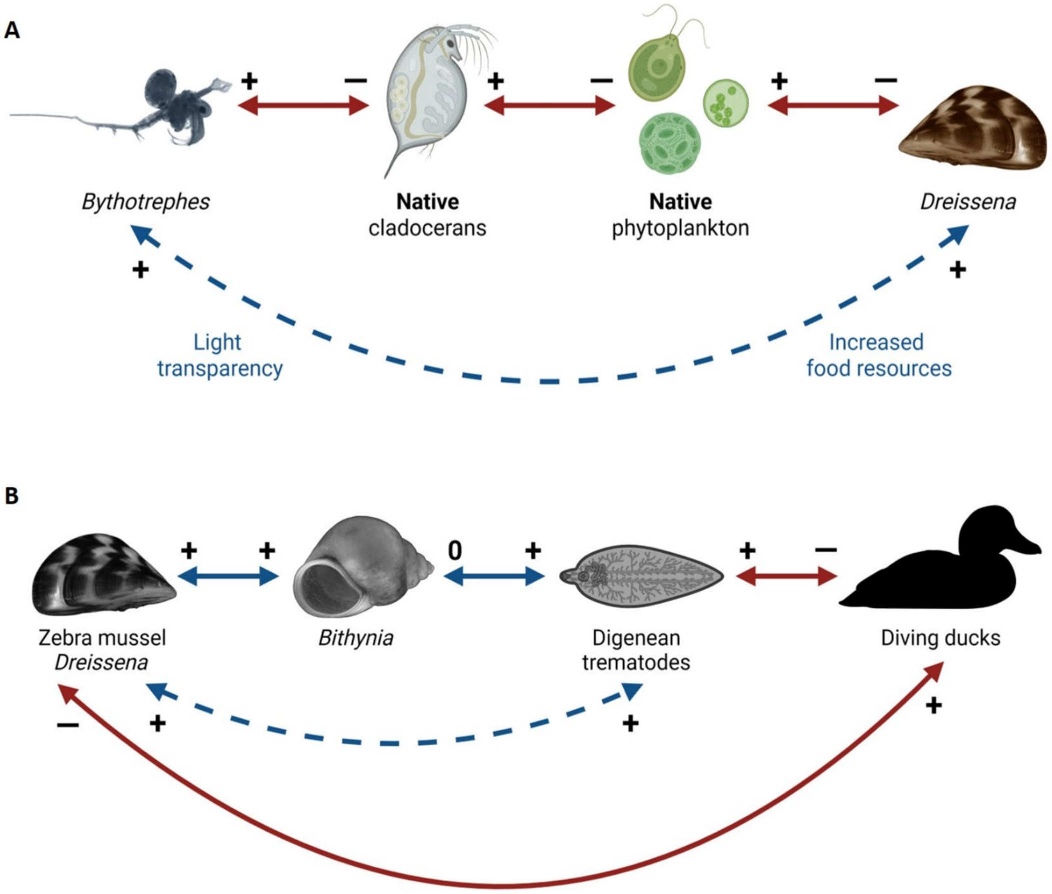

Fig. 3 Hypothetical examples of a multi-taxon facilitative interaction chain involving native and non-native species. **A** The Eurasian spiny waterflea, *Bythotrephes longimanus*, is a visual predator that feeds voraciously on herbivorous waterfleas that potentially compete with the zebra mussel for phytoplankton resources. Dreissenid mussel filtration of seston increases light transparency in the lake, enhancing the efficacy of *Bythotrephes* predation, thereby creating an indirect mutualism. **B** Zebra mussels enhance European faucet snail (*Bithynia tentaculata*) populations through provision of interstitial shelter and grazing surfaces. *Bithynia* is an intermediate host for native and non-native species of digenean trematodes (e.g., *Leyogonimus polyoon* and *Cyathocotyle bushiensis*) that cause substantial mortality in molluscivorous diving ducks, which exert significant predation pressure on zebra mussel populations. *Bythotrephes* photo by J. Leibig, NOAA GLERL. Zebra mussel photo by R. Aguilar, Smithsonian Environmental Research Center (Creative Commons Attribution 2.0)

European faucet snail, *Bithynia tentaculata*. Aggregations of zebra mussel shells provide grazing surfaces and interstitial refugia for the snail, with strong positive effects on local snail abundance (Ricciardi et al. 1997; Ricciardi 2001). *Bithynia* is an intermediate host for native and non-native species of digenean trematodes (e.g. *Leyogonimus polyoon* and *Cyathocotyle bushiensis*) that cause substantial mortality in diving ducks (Roy and St-Louis 2016). Given that diving ducks can exert significant predation on zebra mussel populations (Mitchell et al. 2000; Werner et al. 2005; van Nes et al. 2008), the facilitation of *Bithynia*—and, by extension, digenean trematodes—can release zebra mussels from predation pressure (Fig. 3B). Both these examples demonstrate how negative interactions within a chain could produce an indirect mutualistic effect on distal species, regardless of whether the intermediate chain component species are native or non-native.

Conclusions and future research directions

By describing the aforementioned scenarios, we hope to extend the dimensions and study of the IM concept beyond what has been characterized in the literature. The concept has rarely been tested at the community and ecosystem levels (Braga et al. 2018a), and there are still relatively few experimentally-proven cases in which two non-native species each enhance the probability of establishment, spread, or impact of the other (Simberloff 2006). Overall, explorations of IM have been largely constrained to simple pairwise facilitations among non-native species. To advance understanding of the concept, we propose several areas of research for consideration:

1. Multispecies interactions that accelerate the accumulation of invaders and their impacts could be as rare as the paucity of documented cases suggests; alternatively, their documented rarity might reflect the substantial technical effort required to characterize them. In attempting to test the effects of IM, ecologists should distinguish between population-level and community-level impacts, even though such impacts are linked. For example, a decline in a native plant resulting from apparent competition with a non-native plant owing to a dual interaction with a non-native herbivore would be properly described as a population-level impact. For the purpose of characterizing IM in such a case, what needs to be measured is a community-level impact resulting from this interaction (e.g., changes in diversity, foodweb topology, dominance hierarchies).
2. Three facts suggest that IM can be extensive and influential in ecosystems: 1) exploitations (+/−), including virtual commensalisms (+/0), can play a role in facilitating non-native species; 2) facilitations often arise from indirect effects, not just direct pairwise interactions; and 3) native species can facilitate non-natives, both directly and indirectly—through interaction chains. However, quantitative data on the population-level impacts of facilitations are needed to characterize interaction strengths in these various situations.
3. The strength of facilitative interactions among species is context-dependent, resulting in varied outcomes across space and time (Stachowicz 2001; Gestoso et al. 2014; Uyà et al. 2020; Lucero et al. 2021, 2022). This begs the question: What abiotic and biotic conditions affect the strength and outcome of conditional facilitations that can lead to IMs? Oduor et al. (2024) found that nutrient levels mediated whether or not co-occurring non-native plants facilitated versus competed with each other, suggesting that the IM hypothesis could be tested alongside the stress-gradient hypothesis (Bertness and Callaway 1994; Bertness et al. 2024) or the fluctuating resource availability hypothesis (Davis et al. 2000). Another question is whether *indirect* facilitations involving invaders are inherently unpredictable (cf. White et al. 2006), or can methods be developed to anticipate situations in which they are likely to occur?
4. Detailed invasion histories of ecosystems across different time scales are needed to determine whether IMs are punctuated by periods of stasis (or biotic resistance) and the conditions that cause this temporal variation. We suggest that, apart from colonization pressure—which should be considered a null model, major contributing factors to this variation include the evolutionary history of introduced species (see section on *Coevolved species assembly*), resource limitation, and disturbance dynamics. Understanding the mechanisms and conditions that enhance or

diminish facilitations and thus create periods of relative stasis could provide insight into whether management interventions can interrupt or dampen an ongoing IM.

5. Whole-ecosystem experiments (e.g. using replicated mesocosms, controlled tracts of land, or experimental islands or lakes) are needed to test the IM hypothesis and various scenarios described here. These might also involve microcosm experiments (e.g. moss-arthropod communities or microbial communities in a flask system; Robinson and Dickerson 1987; Fukami 2004). Such approaches could be used to explore whether IM is more likely to occur in certain kinds of ecosystems (e.g. islands, lakes) or biomes. In freshwater ecosystems, for example, there is little evidence that biotic resistance to establishment is prevalent, and multiple non-native species do not necessarily reduce the negative effects of each other (Ricciardi 2001; Braga et al. 2020).
6. Urban areas are focal points of invasion (Cadotte et al. 2017) but constitute a highly understudied environment for IM. Given their disturbed nature and disproportionate colonization pressure, we hypothesize that urban environments are particularly prone to IM. Urban woodlands in the midwestern United States have been invaded by non-native earthworms and shrubs that facilitate each other by altering woodland ecology (Heneghan et al. 2007), whereas some experimental evidence suggests that aquarium pet species released into urban ponds could interact facilitatively (Crone et al. 2023). Such cases have been scarcely explored to date.
7. What are the implications of the diversity-stability theory for IM, and vice versa? Future work could explore potential feedbacks of invader-induced biodiversity erosion on the rate of invasion and impact magnification. Underlying mechanisms might include, *inter alia*, changes to resource supply (Li et al. 2022; Sun et al. 2024), enemy release (Relva et al. 2010), and pathogen accumulation/spillback (Eppinga et al. 2006; Mangla 2008).

These are but a subset of potentially fruitful areas of study. Other research topics surrounding the IM concept include the influences of habitat complexity and disturbance in promoting or damping IMs; how facilitations observed at small spatial scales within an ecosystem scale-up to the entire ecosystem; and the respective roles of colonization pressure, propagule pressure, and facilitation in driving increasing invasion rates (e.g., see Colautti et al. 2006). The facilitative effects of native species in IM also merit further exploration; our scenario offers some insight into observed conflicting relationships between native and non-native species richness (the “invasion paradox”; Tomasetto et al. 2019). Finally, cases that mechanistically link facilitative interactions of non-native species to their synergistic impacts should be documented, to gain insight into when and where such phenomena may occur.

Acknowledgements Four anonymous reviewers provided valuable comments on the manuscript. We thank Wieteke Holthuijzen for assistance in designing the figures.

Author’s contribution Both authors conceived the paper. The first draft was written by AR and edited by DS. Both authors approve the final manuscript.

Funding AR gratefully acknowledges support from the Natural Sciences and Engineering Research Council of Canada (2022–03235) and the Bieler Chair in St Lawrence River Ecology. DS is supported by the Nancy Gore Hunger Endowment of the University of Tennessee.

Declarations

Conflict of interest The authors declare no conflict of interest.

References

Abbott KL, Green PT (2007) Collapse of an ant–scale mutualism in a rainforest on Christmas Island. Oikos 116:1238–1246

Adams J, Pearl C, Bury RB (2003) Indirect facilitation of anuran invasion by non-native fishes. Ecol Letters 6:343–351

Adler PB, D’Antonio CM, Tunison JT (1998) Understory succession following a dieback of *Myrica faya* in Hawai’i Volcanoes National Park. Pacific Sci 52:69–78

Aizen MA, Torres A (2024) The invasion ecology of mutualism. Ann Rev Ecol Evol Systs 55:41–63

Aizen MA, Smith-Ramírez C, Morales CL, Vieli L, Sáez A, Barahona-Segovia RM et al (2019) Coordinated species importation policies are needed to reduce serious invasions globally: the case of alien bumblebees in South America. J Appl Ecol 56:100–106

Altieri AH, Silliman BR, Bertness MD (2007) Hierarchical organization via a facilitation cascade in intertidal cordgrass bed communities. Amer Natur 169:195–206

Anderson CB, Griffith CR, Rosemond AD, Rozzi R, Dollenz O (2006) The effects of invasive North American beavers on riparian plant communities in Cape Horn, Chile: do exotic beavers engineer differently in sub-Antarctic ecosystems? Biol Conserv 128:467–474

Anonymous (1985) Ecology of biological invasions. SCOPE Newsletter 23:1–5

Aplet GH (1990) Alteration of earthworm community biomass by the alien *Myrica faya* in Hawai'i. Oecologia 82:414–416

Bach CE (1991) Direct and indirect interactions between ants, scales, and plants. Oecologia 82:233–239

Baltz DM, Moyle PB (1993) Invasion resistance to introduced species by a native assemblage of California stream fishes. Ecol Appl 3:246–255

Beaury EM, Finn JT, Corbin JD, Barr V, Bradley BA (2020) Biotic resistance to invasion is ubiquitous across ecosystems of the United States. Ecol Letters 23:476–482

Bertelsmeier C, Bonnamour A, Brockerhoff EG, Pyšek P, Skuhrovec J, Richardson DM et al (2024) Global proliferation of nonnative plants is a major driver of insect invasions. BioScience 11:770–781

Bertness MD, Callaway RM (1994) Positive interactions in communities. Trends Ecol Evol 9:187–191

Bertness MD, Cavieres LA, Lortie CJ, Callaway RM (2024) Positive interactions and interdependence in communities. Trends Ecol Evol 39:1014–1023

Beshai RA, Truong DA, Henry AK, Sorte CJB (2023) Biotic resistance or invasional meltdown? Diversity reduces invasibility but not exotic dominance in southern California epibenthic communities. Biol Inv 25:533–549

Braga RR, Gómez-Aparicio L, Heger T, Vitule JR, Jeschke JM (2018a) Structuring evidence for invasional meltdown: broad support but with biases and gaps. Biol Inv 20:923–936

Braga RR, Ribeiro VM, Padial AA, Thomaz SM, Affonso IP, Wojciechowski J et al (2020) Invasional meltdown: an experimental test and a framework to distinguish synergistic, additive, and antagonistic effects. Hydrobiologia 847:1603–1618

Braga RR, Gómez-Aparicio L, Heger T, Vitule JR, Jeschke JM (2018b) Invasional meltdown hypothesis. In: J.M. Jeschke JM, Heger T (eds), Invasion biology: Hypotheses and evidence. CAB International, Oxfordshire, UK, pp 79–91

Brandt AJ, Png GK, Jo I, McGrannachan C, Allen K, Peltzer DA et al (2023) Managing multi-species plant invasions when interactions influence their impact. Frontiers Ecol Environ 21:370–379

Bruno JF, Stachowicz JJ, Bertness MD (2004) Inclusion of facilitation into ecological theory. Trends Ecol Evol 18:119–125

Cadotte MW, Yasui SLE, Livingstone S, MacIvor S (2017) Are urban systems beneficial, detrimental, or indifferent for biological invasion? Biol Inv 19:3489–3503

Camacho-Cervantes M, Keller RP, Vilà M (2023) Could non-native species boost their chances of invasion success by socializing with natives? Phil Trans Royal Soc B 378:20220106

Campbell C, Russo L, Albert R, Buckling A, Shea K (2022) Whole community invasions and the integration of novel ecosystems. PLoS Comput Biol 18(6):e1010151

Case TJ (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. Proc Natl Acad Sci USA 87:9610–9614

Case TJ (1991) Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. Biol J Linnean Soc 42:239–266

Case TJ, Bolger DT (1991) The role of introduced species in shaping the abundance and distribution of island reptiles. Evol Ecol 5:272–290

Cavieres LA (2021) Facilitation and the invasibility of plant communities. J Ecol 109:2019–2028

Cheek CA, Peoples BK, Goforth RR (2024) Diets of invasive channel catfish are subsidized by invasive riparian trees. Ecol Freshw Fish 33:e12753

Chen D, van Kleunen M (2022) Invasional meltdown mediated by plant–soil feedbacks may depend on community diversity. New Phytol 235:1589–1598

Christie WJ (1974) Changes in the fish species composition of the Great Lakes. J Fisheries Res Board Canada 31:827–854

Clark GF, Johnson EL (2009) Propagule pressure and disturbance interact to overcome biotic resistance of marine invertebrate communities. Oikos 118:1679–1686

Colautti RI, Ricciardi A, Grigorovich IA, MacIsaac HJ (2004) Is invasion success explained by the enemy release hypothesis? Ecol Letters 7:721–733

Colautti RI, Grigorovich IA, MacIsaac HJ (2006) Propagule pressure: a null model biological invasions. Biol Inv 8:1023–1037

Collins RJ, Copenheaver CA, Barney JN, Radtke PJ (2020) Using invasional meltdown theory to understand patterns of invasive richness and abundance in forests of the northeastern USA. Natural Areas J 40:336–344

Combes C, Le Brun N (1990) Invasions by parasites in continental Europe. In: di Castri F, Hansen AJ, Debussche M (eds) Biological invasions in Europe and the Mediterranean Basin. Monographiae Biologicae, Springer, Dordrecht, pp 285–296

Cosmo LG, Sales LP, Guimarães PR Jr, Pires MM (2023) Mutualistic coevolution and community diversity favour persistence in metacommunities under environmental changes. Proc Royal Soc B 290:20221909

Crego RD, Jiménez JE, Rozzi R (2016) A synergistic trio of invasive mammals? Facilitative interactions among beavers, muskrats, and mink at the southern end of the Americas. Biol Inv 18:1923–1938

Crone ER, Sauer EL, Preston DL (2023) Non-native fish facilitate non-native snails and alter food web structure in experimental pond communities. Functional Ecol 37:947–958

Crosby AW (1986) Ecological imperialism: the biological expansion of Europe, 900–1900. Cambridge Univ Press, Cambridge, UK

Crosby AW (1972) The Columbian Exchange. Biological and cultural consequences of 1492. Greenwood Publishing Co, Westport, CT

D'Antonio CM, Vitousek PM (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu Rev Ecol Syst 23:63-87

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

DeBach P, Fleschner CA, Dietrick EJ (1951) A biological check method for evaluating the effectiveness of entomophagous insects. J Econ Entomol 44:763–766

DeVanna KM, Bodamer BL, Wellington CG, Hammer E, Mayer CM, Bossenbroek JM (2011) An alternative hypothesis to invasional meltdown in the Laurentian Great Lakes region: General facilitation by *Dreissena*. J Great Lakes Res 37:632–641

Dickie IA, St John MG, Yeates GW, Morse CW, Bonner KI, Orwin K et al (2014) Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. AoB Plants 6:plu056

Díez J (2005) Invasion biology of Australian ectomycorrhizal fungi introduced with eucalypt plantations into the Iberian Peninsula. Biol Inv 7:3–15

Doody JS, Rhind D, McHenry CM, Clulow S (2024) Invasional meltdown-under? Toads facilitate cats by removing a naïve top predator. Wildl Res 51:WR22177

Elton CS (1927) Animal ecology. MacMillan, New York

Elton CS (1958) The ecology of invasions by animals and plants. Methuen, London

Eppinga MB, Rietkerk M, Dekker SC, de Ruiter PC, van der Putten WH (2006) Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos 114:168–176

Fiore C, Tull JL, Zehner S, Ducey PK (2004) Tracking and predation on earthworms by the invasive terrestrial planarian *Bipalium adventitium* (Tricladida, Platyhelminthes). Behav Proc 67:327–334

Firth LB, Duff L, Gribben PE, Knights AM (2021) Do positive interactions between marine invaders increase likelihood of invasion into natural and artificial habitats? Oikos 130:453–463

Flickinger HD, Dukes JS (2024) A review of theory: comparing invasion ecology and climate change-induced range shifting. Global Change Ecol 30:e17612

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annu Rev Ecol Syst 29:113–140

Fukami T (2004) Assembly history interacts with ecosystem size to influence species diversity. Ecology 85:3234–3242

Gabriel W, Lynch M, Burger R (1993) Muller's Ratchet and mutational meltdowns. Evolution 47:1744–1757

Gallardo B, Aldridge DC (2015) Is Great Britain heading for a Ponto-Caspian invasional meltdown? J Appl Ecol 52:41–49

Gestoso I, Arenas F, Olabarria C (2014) Biotic resistance and facilitation of a non-indigenous mussel vary with environmental context. Mar Ecol Progr Ser 506:163–173

Grabowska J, Grabowski M, Pietraszewski D, Gmur J (2009) Non-selective predator–the versatile diet of Amur sleeper (*Perccottus glenii* Dybowski, 1877) in the Vistula River (Poland), a newly invaded ecosystem. J Appl Ichthyol 25:451–459

Green PT, O'Dowd DJ, Lake PS (1997) Control of seedling recruitment by land crabs in rain forest on a remote oceanic island. Ecology 78:2474–2486

Green PT, O'Dowd DJ, Abbott KL, Jeffery M, Retallick K, MacNally R (2011) Invasional meltdown: Invader–invader mutualism facilitates a secondary invasion. Ecology 92:1758–1768

Gribben PE, Byers JE, Clements M, McKenzie LA, Steinberg PD, Wright JT (2009) Behavioural interactions between ecosystem engineers control community species richness. Ecology Lett 12:1127–1136

Gribben PE, Poore AGB, Thomsen MS, Quesey P, Weschke E, Wright JT (2020) Habitat provided by native species facilitates higher abundances of an invader in its introduced compared to native range. Sci Rep 10:6385

Grosholz E (1995) Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proc Natl Acad Sci USA 102:1088–1091

Gurevitch J (2006) Commentary on Simberloff (2006): Meltdowns, snowballs and positive feedbacks. Ecol Letters 9:919–921

Haghkerdar JM, McLachlan JR, Ireland A, Greig HS (2019) Repeat disturbances have cumulative impacts on stream communities. Ecol Evol 9:2898–2906

Harris LG, Tyrrell MC (2001) Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. Biol Inv 3:9–21

Heiman KW, Micheli F (2010) Non-native ecosystem engineer alters estuarine communities. Integr Comp Biol 50:226–236

Heimpel GE, Frelich LE, Landis DA, Hopper KR, Hoelmer KA, Sezen Z et al (2010) European buckthorn and Asian soybean aphid as components of an extensive invasional meltdown in North America. Biol Inv 12:2913–2931

Heneghan L, Steffen J, Fagen K (2007) Interactions of an introduced shrub and introduced earthworms in an Illinois urban woodland: impact on leaf litter decomposition. Pedobiologia 50:543–551

Hernández-Brito D, Blanco G, Tella JL, Carrete M (2020) A protective nesting association with native species counteracts biotic resistance for the spread of an invasive parakeet from urban into rural habitats. Front Zool 17:13

Higgins SN, Malkin SY, Todd Howell E, Guildford SJ, Campbell L, Hiriart-Baer V, Hecky RE (2008) An ecological review of *Cladophora glomerata* (Chlorophyta) in the Laurentian Great Lakes. J Phycol 44(4):839–854

Howarth FG (1985) Impacts of alien land arthropods and molluscs on native plants and animals in Hawaii. In: Stone CP, Scott JM (eds) Hawai'i's terrestrial ecosystems: preservation and management. University of Hawaii, Honolulu, HI, pp 149–179

Hughes RF, Vitousek PM, Tunison JT (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawaii. Ecology 72:743–746

Ives AR, Carpenter SR (2007) Stability and diversity of ecosystems. Science 317:58–62

Jackson MC (2015) Interactions among multiple invasive animals. Ecology 96:2035–2041

Jauni M, Gripenberg S, Ramula S (2014) Non-native plant species benefit from disturbance: a meta-analysis. Oikos 124:122–129

Jeschke JM, Gómez Aparicio L, Haider S, Heger T, Lortie CJ, Pyšek P et al (2012) Support for major hypotheses in invasion biology is uneven and declining. Neobiota 14:1–20

Jokela A, Arnott SE, Beisner BE (2013) Influence of light on the foraging impact of an introduced predatory cladoceran, *Bythotrephes longimanus*. Freshw Biol 58:1946–1957

Jones CG, Lawton JH, Shachak M (1994) Organsisms as ecosystem engineers. Oikos 69:373–386

Jude DJ, Tesar FJ, Deboe SF, Miller TJ (1987) Diet and selection of major prey species by Lake Michigan salmonines, 1973–1982. Trans Amer Fish Soc 116:677–691

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17:164–170

Kuebbing SD (2020) How direct and indirect non-native interactions can promote plant invasions, lead to invasional meltdown and inform management decisions. In: Traveset A, Richardson DM (eds) Plant invasions: the role of biotic interactions. CAB International, Wallingford, UK, pp 1–24

Lenz L, Taylor JA (2001) The influence of an invasive tree species (*Myrica faya*) on the abundance of an alien insect (*Sophonia rufofascia*) in Hawai'i Volcanoes National Park. Biol Conserv 102:301–307

Leonhardt F, Keller A, Aveces CA, Ernst R (2023) From alien species to alien communities: host- and habitat-associated microbiomes in an alien amphibian. Microbial Ecol 86:2373–2385

Leppäkoski E, Gollasch S, Gruszka P, Ojaveer H, Olenin S, Panov V (2002) The Baltic—a sea of invaders. Can J Fisheries Aquatic Sci 59:1175–1188

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Li W, Wang Z, He S (2022) Effects of species richness and nutrient availability on the invasibility of experimental microalgal microcosms. Global Ecol Conserv 39:e02304

Liu X, Wei S, Wang F, James EK, Guo X, Zagar C et al (2012) *Burkholderia* and *Cupriavidus* spp. are the preferred symbionts of *Mimosa* spp. in southern China. FEMS Microbiol Ecol 80:417–426

Lizarralde M, Escobar J, Deferrari G (2004) Invader species in Argentina: a review about the beaver (*Castor canadensis*) population situation on Tierra del Fuego ecosystem. Interciencia 29:352–356

Lockwood JL, Cassey P, Blackburn TM (2009) The more you introduce, the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity Distrib 15:904–910

Lohrer AM, Whitlach RB (2002) Interactions among aliens: apparent replacement of one exotic species by another. Ecology 83:719–732

Loughlan LS, Green PT (2017) Secondary invasion: when invasion success is contingent on other invaders altering the properties of recipient ecosystems. Ecol Evol 7:7628–7637

Lucero JE, Callaway RM, Faist AM, Lortie CJ (2021) An unfortunate alliance: native shrubs increase the abundance, performance, and apparent impacts of *Bromus tectorum* across a regional aridity gradient. Basic Appl Ecol 57:41–53

Lucero JE, Filazzola A, Callaway RM, Braun J, Ghazian N, Haas S et al (2022) Increasing global aridity destabilizes shrub facilitation of exotic but not native plant species. Global Ecol Conserv 40:e02345

Lyons DA, Scheibling RE (2008) Context-dependant survival of the invasive seaweed *Codium fragile* ssp. *tomentosoides* in kelp bed and urchin barren habitats off Nova Scotia. Aquatic Biol 2(1):17–27

Mack RN (1986) Alien plant invasion into the intermountain West: a case history. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer, New York, pp 191–213

Mack M, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. Trends Ecol Evol 13:195–198

Mack RN (1989) Temperate grasslands vulnerable to plant invasions: characteristics and consequences. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M et al (eds) Biological invasions: A global perspective. Wiley, Chichester, UK, pp 155–179

Mangla S, Inderjit CRM (2008) Exotic invasive plant accumulates native soil pathogens which inhibit native plants. J Ecol 96:58–67

McKey DB, Kaufmann SC (1991) Naturalization of exotic *Ficus* species (Moraceae) in south Florida. In: Center TD, Doren RF, Hofstetter RL, Myers RL, Whiteaker LD (ed.), Proceedings of the symposium on exotic pest plants. Technical Report NPS/NREVER/NRTR-91/06. Washington, DC: United States Department of the Interior/National Park Service, Washington, DC, pp 221–236

Mitchell JS, Bailey RC, Knapton RW (2000) Effects of predation by fish and wintering ducks on dreissenid mussels at Nanticoke, Lake Erie. Ecoscience 7(4):398–409

Monceau K, Arca M, Leprêtre L, Mougel E, Bonnard O, Silvain JF et al (2013) Native prey and invasive predator patterns of foraging activity: the case of the yellow-legged hornet predation at European honeybee hives. PLoS ONE 8(6):e66492

Morales CL, Aizen MA (2002) Does invasion of exotic plants promote invasion of exotic flower visitors? A case study from the temperate forests of the southern Andes. Biol Inv 4:87–100

Nadel H, Frank JH, Knight RL Jr (1992) Escapees and accomplices: the naturalization of exotic *Ficus* and their associated faunas in Florida. Florida Entomol 75:29–38

Northfield TD, Laurance SGW, Mayfield MM, Paini DR, Snyder WE, Stouffer DB et al (2018) Native turncoats and indirect facilitation of species invasions. Proc Royal Soc B 285:20171936

Nuñez MA, Dickie IA (2014) Invasive belowground mutualists of woody plants. Biol Inv 16:645–661

Nurkse K, Kotta J, Orav-Kotta H, Ojaveer H (2016) A successful non-native predator, round goby, in the Baltic Sea: generalist feeding strategy, diverse diet and high prey consumption. Hydrobiologia 777:271–281

Nuzzo VA, Maerz JC, Blossey B (2009) Earthworm invasion as the driving force behind plant invasion and community change in northeastern North American forests. Conserv Biol 23:966–974

O'Dowd DJ, Green PT, Lake PS (2003) Invasional meltdown on an oceanic island. Ecol Letters 6:812–817

Oduor AMO, Yu H, Liu YJ (2024) Invasive plant species support each other's growth in low-nutrient conditions but compete when nutrients are abundant. Ecology 105:e4401

Pantel JH, Bohan DA, Calcagno V, David P, Duyck P-F, Kamenova S et al (2017) 14 Questions for invasion in ecological networks. Adv Ecol Res 56:293–340

Parker IM (1997) Pollinator limitation of a *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. Ecology 78:1457–1470

Pearson DE, Ortega YK, Runyan J, Butler JL (2018) Secondary invasion re-redefined: the distinction between invader-facilitated and invader-contingent invasions as subclasses of secondary invasion. Ecol Evol 8:5185–5187

Piccardi P, Alberti G, Alexander JM, Mitri S (2022) Microbial invasion of a toxic medium is facilitated by a resident community but inhibited as the community co-evolves. ISME J 16:2644–2652

Pickard J (1984) Exotic plants on Lord Howe Island: distribution in space and time. J Biogeog 11:181–208

Pires LMD, Ibelings BW, Grehm M, Van Donk E (2005) Comparing grazing on lake seston by *Dreissena* and *Daphnia*: lessons for biomanipulation. Microbial Ecol 50:242–252

Plante CJ, Wilde SB (2004) Biotic disturbance, recolonization, and early succession of bacterial assemblages in intertidal sediments. Microbial Ecol 48:154–166

Potgieter LJ, Wilson JRU, Strasberg D, Richardson DM (2014) Casuarina invasion alters primary succession on lava flows on La Réunion Island. Biotropica 46:268–275

Prior KM, Robinson JM, Meadley-Dunphy SA, Frederickson ME (2015) Mutualism between co-introduced species facilitates invasion and alters plant community structure. Proc Royal Soc B 282:20142846

Relva MA, Nuñez MA, Simberloff D (2010) Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. Biol Inv 12:303–311

Ricciardi A (2001) Facilitative interactions among aquatic invaders: is an 'invasional meltdown' occurring in the Great Lakes? Can J Fisheries Aquatic Sci 58:2513–2525

Ricciardi A (2005) Facilitation and synergistic interactions among introduced aquatic species. In: Mooney HA, Mack RN, McNeely J, Neville LE, Schei PJ, Waage JK (eds) Invasive alien species: a new synthesis. Island Press, Washington, DC, pp 162–178

Ricciardi A (2006) Patterns of invasion of the Laurentian Great Lakes in relation to changes in vector activity. Diversity Distrib 12:425–433

Ricciardi A, MacIsaac HJ (2000) Recent mass invasion of the North American Great Lakes by Ponto-Caspian species. Trends Ecol Evol 15:62–66

Ricciardi A, MacIsaac HJ (2022) Vector control reduces the rate of species invasion in the world's largest freshwater ecosystem. Conserv Lett 15:e12866

Ricciardi A, Whoriskey FG, Rasmussen JB (1997) The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. Can J Fisheries Aquatic Sci 54:2596–2608

Ricciardi A, Iacarella JC, Aldridge DC, Blackburn TM, Carlton JT, Catford JA, Wardle DA (2021) Four priority areas to advance invasion science in the face of rapid environmental change. Environ Rev 29:119–141

Richardson DM, Higgins SI (1998) Pines as invaders in the southern hemisphere. In: Richardson DM (ed) Ecology and biogeography of Pinus. Cambridge University Press, Cambridge, UK, pp 450–473

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmánek M (2000) Plant invasions – the role of mutualisms. Biological Rev 75:65–93

Robinson JF, Dickerson JE (1987) Does invasion sequence affect community structure? Ecology 68:587–595

Rodríguez JP (2001) Exotic species introductions into South America: an underestimated threat? Biodiv Conserv 10:1983–1996

Roy CL, St-Louis V (2016) Spatio-temporal variation in prevalence and intensity of trematodes responsible for waterfowl die-offs in faucet snail-infested waterbodies of Minnesota, USA. Int J Parasitol Parasites Wildl 6(3):162–176

Russell JC, Sataruddin NS, Heard AD (2014) Over-invasion by functionally equivalent invasive species. Ecology 95:2268–2276

Santillan E, Seshan H, Constancias F, Drautz-Moses DI, Wuertz S (2019) Frequency of disturbance alters diversity, function, and underlying assembly mechanisms of complex bacterial communities. NPJ Biofilms Microbiomes 5:8

Scheibling RE, Gagnon P (2006) Competitive interactions between the invasive green alga *Codium fragile* ssp *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Mar Ecol Progr Ser 325:1–14

Schoeman CS, Samways MJ (2013) Temporal shifts in interactions between alien trees and the alien Argentine ant on native ants. J Insect Conserv 17:911–919

Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trends Ecol Evol 17(4):170–176

Sheath RG, Morison MO (1982) Epiphytes on *Cladophora glomerata* in the Great Lakes and St. Lawrence Seaway with particular reference to the red alga *Chroodactylon ramosum* (=*Asterocytis smargdina*). J Phycol 18:385–391

Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecol Letters 9:912–919

Simberloff D (2011) How common are invasion-induced ecosystem impacts? Biol Inv 13:1255–1268

Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: Invasional meltdown? Biol Inv 1:21–32

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Spear MJ, Walsh JR, Ricciardi A, Zanden MJV (2021) The invasion ecology of sleeper populations: prevalence, persistence, and abrupt shifts. Bioscience 71(4):357–369

Stachowicz J (2001) Mutualism, facilitation, and the structure of ecological communities. BioScience 51:235–246

Stewart DJ, Kitchell JF, Crowder LB (1981) Forage fishes and their salmonid predators in Lake Michigan. Trans Amer Fisheries Soc 110:751–763

Sun Y, Ren ZK, Müller-Schärer H, Callaway RM, van Kleunen M, Huang W (2024) Increasing and fluctuating resource availability enhances invasional meltdown. Ecology 105(9):e4387

Thellung A (1915) Pflanzenwanderungen unter dem Einfluss des Menschen. Bot Jahrb Syst Pflanzengesch Pflanzengeogr 53(Beiblatt 116):37–66

Tomasetto F, Duncan RP, Hulme PE (2019) Resolving the invasion paradox: pervasive scale and study dependence in the native-alien species richness relationship. Ecol Lett 22:1038–1046

Tompkins DM, White AR, Boots M (2003) Ecological replacement of native red squirrels by invasive greys driven by disease. Ecol Lett 6:189–196

Torchin ME, Mitchell CE (2004) Parasites, pathogens, and invasions by plants and animals. Frontiers Ecol Environ 2:183–190

Traveset A, Richardson DM (2014) Mutualistic interactions and biological invasions. Annu Rev Ecol Evol Syst 45:89–113

Uyà M, Bulleri F, Wright JT, Gribben PE (2020) Facilitation of an invader by a native habitat-former increases along interacting gradients of environmental stress. Ecology 101:e02961

van Nes EH, Noordhuis R, Lammen EH, Portielje R, Reeze B, Peeters ET (2008) Modelling the effects of diving ducks on zebra mussels *Dreissena polymorpha* in lakes. Ecol Modelling 211:481–490

Ward JM, Ricciardi A (2010) Community-level effects of co-occurring native and exotic ecosystem engineers. Freshw Biol 55:1803–1817

Wei G, Chen W, Zhu W, Chen C, Young JP, Bontemps C (2009) Invasive *Robinia pseudoacacia* in China is nodulated by *Mesorhizobium* and *Sinorhizobium* species that share similar nodulation genes with native American symbionts. FEMS Microbiol Ecol 68:320–328

Wei M, Wang S, Xiao HG, Wu BD, Jiang K, Wang CY (2020) Co-invasion of daisy fleabane and Canada goldenrod pose synergistic impacts on soil bacterial richness. J Central South Univ 27:1790–1801

Werner S, Mörtl M, Bauer H-G, Rothhaupt K-O (2005) Strong impact of wintering waterbirds on zebra mussel (*Dreissena polymorpha*) populations at Lake Constance, Germany. Freshw Biol 50:1412–1426

Ward JM, Ricciardi A (2007) Impacts of *Dreissena* invasions on benthic macroinvertebrate communities: a meta-analysis. Diversity Distrib 13:155–165

White EM, Wilson JC, Clarke AR (2006) Biotic indirect effects: a neglected concept in invasion biology. Diversity Distrib 12:442–455

Wright JT, Holmes ZC, Byers JE (2018) Stronger positive association between an invasive crab and a native intertidal ecosystem engineer with increasing wave exposure. Mar Environ Res 142:124–129

Yelenik SG, D'Antonio CM (2013) Self-reinforcing impacts of plant invasions change over time. Nature 503:517–520

Zhang Z, Liu Y, Hardrath A, Jin H, van Kleunen M (2022) Increases in multiple resources promote competitive ability of naturalized non-native plants. Commun Biol 5:1150