8 How Direct and Indirect Non-native Interactions Can Promote Plant Invasions, Lead to Invasional Meltdown and Inform Management Decisions

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Abstract

In 1999, Daniel Simberloff and Betsy Von Holle introduced the term 'invasional meltdown'. The term and the concept have been embraced and critiqued but have taken a firm hold within the invasion biology cannon. The original formulation of the concept argued two key points: first, biologists rarely study how non-natives interact with one another. Second, nearly all the conceptual models about the success and impact of invasive species are predicated on the importance of competitive interactions and an implicit assumption that non-natives should interfere with establishment, spread and impact of other non-natives. In response, Simberloff and Von Holle called for more research on invader interactions and proposed an alternative consequence of non-native species interactions – invasional meltdown – where facilitative interactions among non-natives could increase the invasion rate or ecological impacts in invaded systems.

This chapter outlines the primary pathways in which direct and indirect interactions among non-natives could lead to invasional meltdown. It provides examples of how different types of interactions among non-natives could lead to net positive effects on the invasion success of non-native plants or the impact of non-native plants on invaded ecosystems. Direct effects are by far the most commonly explored form of non-native–non-native interaction, primarily focusing on plant mutualisms with pollinators, seed dispersers or soil microbial mutualists. There are, however, also examples of non-native plants that benefit from commensal and even herbivorous interactions with other non-natives. Indirect interactions among non-natives are very infrequently studied. Although examples are scarce, non-natives may indirectly benefit other non-native plants through trophic cascades, apparent competition and indirect mutualisms. It remains unclear whether indirect effects are important pathways to invasional meltdown. More work is needed on studying ecosystems that are invaded by multiple non-native species and we need to consider the full range of interactions among non-natives that could either stymie or promote their spread, population growth and impact. Only then can we address how common facilitative interactions are relative to competitive interactions among non-natives or provide robust suggestions on how to manage ecosystems.

8.1 Introduction

There are few hypotheses in invasion biology that consider interactions among non-native species. The most prominent is the Invasional Meltdown Hypothesis (Catford *et al.*, 2009; see also Chapter 7, this volume; Fig. 8.1). During an invasional meltdown, non-natives facilitate the probability of establishment, spread or increase in abundance of other non-natives, potentially

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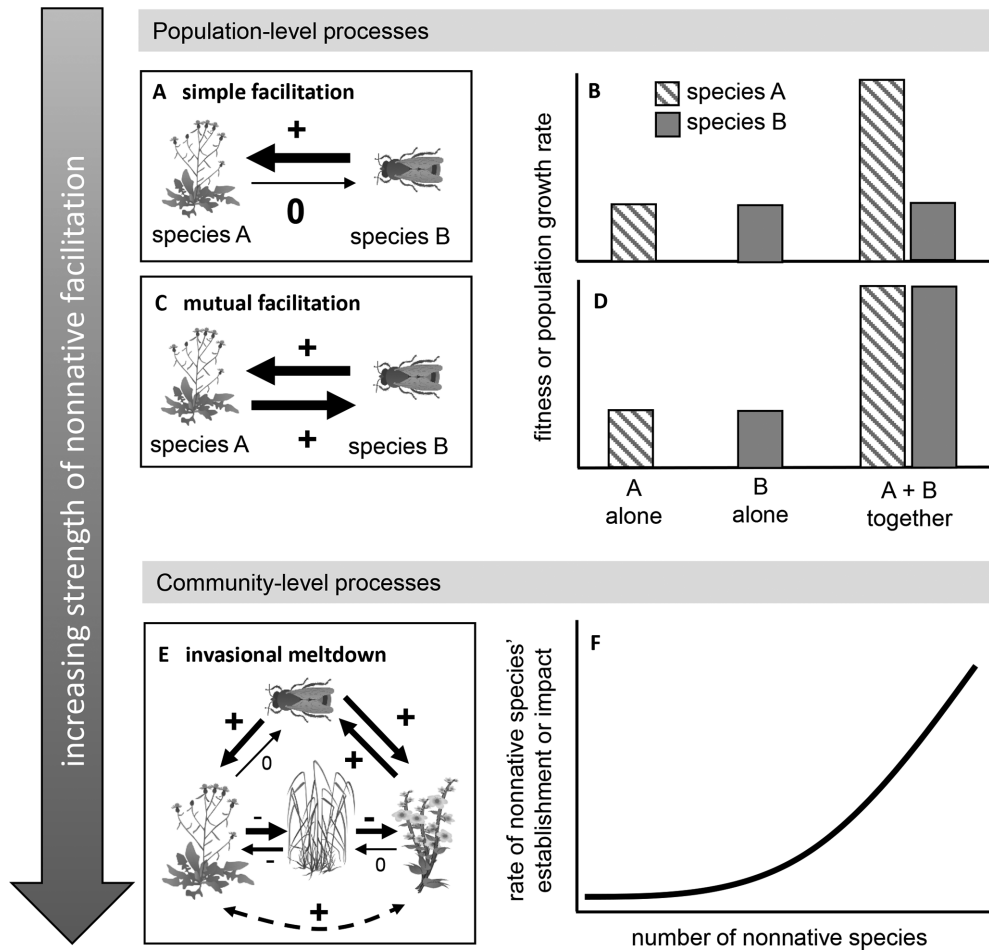
Fig. 8.1. The term 'invasional meltdown' is sometimes broadly defined as any form of facilitation among non-native species (a, c, e). The original definition of the term by Simberloff and Von Holle (1999), however, narrowly defined invasional meltdown as a community-level phenomenon (e) that may arise from facilitative population-level processes (a, c). Different types of ecological data on population size or fitness (b, d) or community invasion rates or impacts (f) are required for distinguishing between population- and community-level processes. Symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols).

causing synergistic increases in the impact of non-natives (Simberloff and Von Holle, 1999; Simberloff, 2006). In the original framing of the concept, a range of faciliatory interactions were considered potential pathways to invasional meltdown (Simberloff and Von Holle, 1999; Simberloff, 2006). The weakest interaction to promote a meltdown is 'simple facilitation' or a one-way positive interaction among non-natives that only benefits one of the two interacting non-natives (Fig. 8.1a). A stronger interaction that could promote a meltdown is 'mutual facilitation' where both non-natives benefit from the other (Fig. 8.1c). These interactions are population-level processes that are supported by an increase in a non-native's population growth rate or fitness in the presence of another non-native relative to when the non-native is found alone (Fig. 8.1b,d). By themselves, these types of positive interactions among non-natives do not constitute a meltdown, although they could aid in the process.

An invasional meltdown scenario constitutes a community-level process where facilitation among non-natives could lead to a runaway 'auto-catalytic process that would accelerate the replacement of native communities, perhaps to the point of no return' (Simberloff, 2006; Fig. 8.1e). In a full meltdown, the net effect of all interactions among non-natives leads to an increasing rate of establishment, spread or impact of more non-native species (Fig. 8.1f). In other words, as the number of non-natives increases in a community, the probability that more non-natives will establish or have greater impacts will increase exponentially. The vast majority of invasional meltdown studies focus on how non-native interactions facilitate the establishment, spread or population growth of non-natives while only a handful of studies have attempted to understand whether co-occurring non-natives generate additive or non-additive impacts (Kuebbing *et al.*, 2014, 2016; Pearson *et al.*, 2016a; Tekiela and Barney, 2017).

Since the introduction of the concept, some biologists advocate that discussions of meltdowns focus only on instances that meet the 'full' invasional meltdown criteria (Gurevitch, 2006) because these are the most consequential (and potentially interesting) outcomes of invasion in ecological communities. For this chapter, I discuss the full range of interactions – from weak to strong – that could lead to invasional meltdowns (Fig. 8.1). I do so in part to identify the multiple pathways that could lead to meltdowns and highlight the range of interactions that may occur among two or more non-native species. I also do so because in many cases gathering the necessary community-level data to support invasional meltdowns may be unethical if it requires experimentally introducing new non-native species (Simberloff, 2006; Fig. 8.1c) or data may be impossible to collect. For example, in Mauritius, the non-native common bulbul bird (*Pycnonotus jocosus*) preferentially feeds on fleshy fruits of non-native shrubs. Although spread of many non-native plants coincided with the bird's introduction, this occurred over a century ago and no one collected bird or plant population data so we cannot confirm a meltdown occurred (Linnebjerg *et al.*, 2010). Perhaps in this instance, hindsight of these 'historic' meltdowns provides a strong caution to carefully monitor new introductions of 'meltdown-prone' systems. The bulbul was recently introduced to La Réunion Island where it is spreading the same fleshy-fruited non-native shrubs into primary successional forests. For these early-successional ecosystems, only time and continued monitoring will tell whether these bird-plant facilitative interactions lead to invasional meltdowns (Potgieter *et al.*, 2014). While few of the examples included in this chapter are evidence of 'full' invasional meltdown (Fig. 8.1c), they are valuable to consider for laying a foundation for the many types of interactions that could be involved in an invasional meltdown.

Recent studies have quantitatively reviewed empirical support for the Invasional Meltdown Hypothesis (Braga *et al.*, 2018a,b) and the alternative hypothesis to invasional meltdown – the Biotic Resistance Hypothesis – is reviewed in detail in Chapter 9 (this volume). Thus, I intentionally focus on providing examples of how different types of interactions among non-natives could lead to net positive effects on the invasion success of non-native plants or the impact of non-native plants on invaded ecosystems. I do not attempt to quantify or assess whether these potential pathways to invasional meltdown are more frequent or more important than competitive or negative interactions for a few reasons. First, although it has been two decades since the introduction of the invasional meltdown concept, the study of interactions among non-native species and the resulting impacts of co-occurring invaders is still infrequent and subordinate in the literature relative to the study of interactions between native and non-native species or the impact of single invasive species (Kuebbing *et al.*, 2013; Jackson, 2015; Kuebbing and Nuñez, 2016). Second, studies on non-native interactions typically focus on direct, pairwise interactions among non-native species (White *et al.*, 2006; Chapter 17, this volume) and we have limited empirical data on how indirect interactions affect patterns of invasion in communities comprised of multiple native and non-native species. Because of these two limitations, it is still premature to answer one of the key questions posed by Simberloff and Von Holle (1999): 'Are faciliatory interactions more frequent or more important than hindering ones?' (Simberloff, 2006).

8.2 Direct Interactions Among Non-native Species

One of the easiest invasional meltdown mechanisms to detect occurs when a non-native plant is directly facilitated by another non-native species. Here, I define direct interaction as an interaction between two species that is not mediated through a third species (Strauss, 1991). Non-native species can facilitate non-native plants through mutualistic, commensalistic or herbivorous interactions (Fig. 8.2). Non-native plants engage in mutualisms – where both non-natives facilitate the other – with their pollinators, seed dispersers and soil microbial symbionts (Richardson *et al.*, 2000; Traveset and Richardson, 2014; Fig. 8.2a). In commensalisms, a plant's fitness is enhanced while the other non-native is neither benefited nor harmed. Nearly all the examples of commensalisms among non-natives involve non-native ecosystem engineers that modify the environment to the benefit of a non-native plant (Fig. 8.2b). Interactions between non-native plants and herbivores are rarely considered in discussions of invasional meltdown because herbivory is not typically thought to be beneficial to a plant. However, for some non-natives, herbivory can facilitate the spread or growth of the non-native plant (Fig. 8.2c).
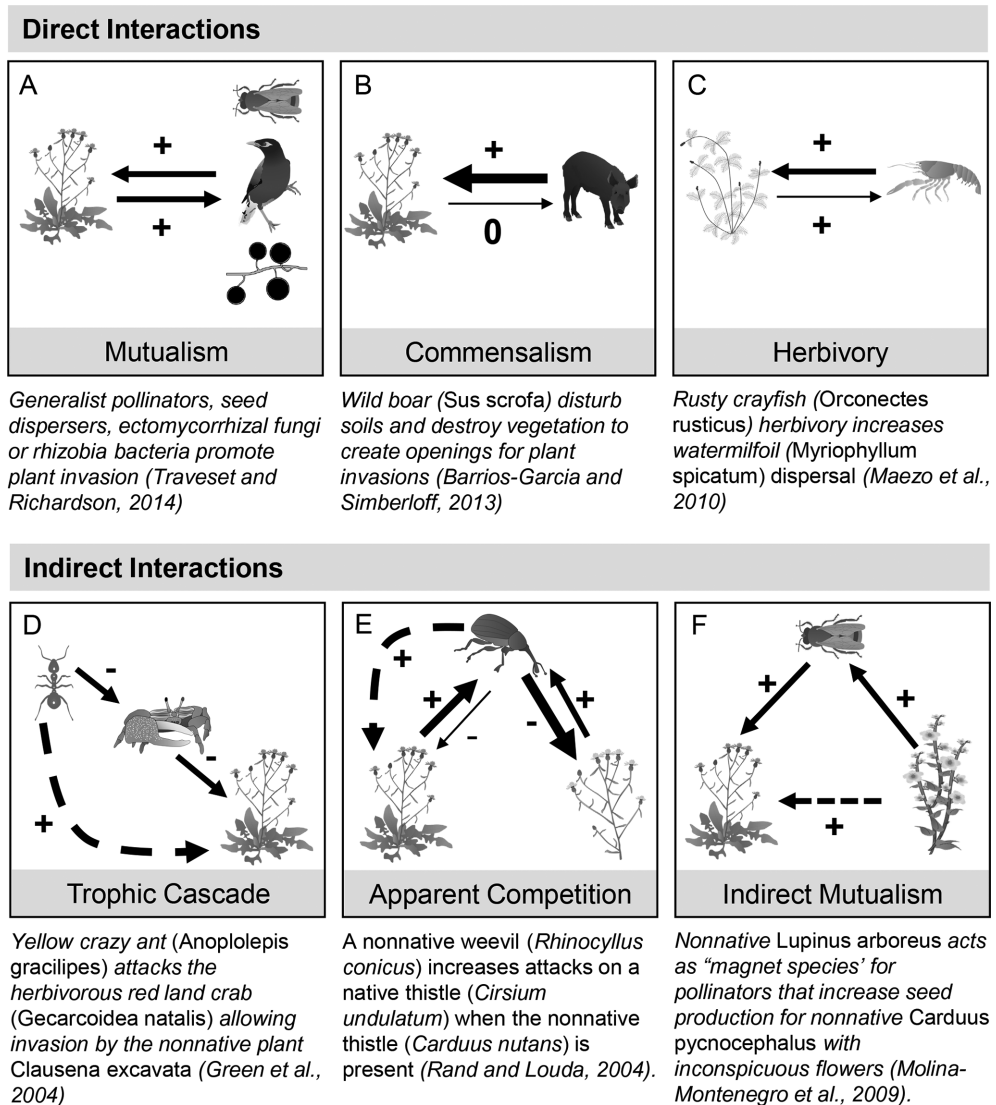
8.3 Mutualisms and Invasional Meltdown

One of the most obvious patterns in plant invasional meltdown studies is that mutualistic interactions are more likely to occur between plants and species in other trophic levels (Simberloff and Von Holle, 1999; Richardson *et al.*, 2000; Simberloff, 2006; Chapter 7, this volume). Early examples of facilitation focused on interactions occurring aboveground, between non-native plants, pollinators and seed dispersers (Fig. 8.2a). Today, we are accumulating examples of belowground interactions that facilitate invasions, and more examples are likely to be unearthed in the coming years (Nuñez and Dickie, 2014; Traveset and Richardson, 2014).

8.4 Non-native Plants and Pollinators

There is ample evidence that non-native plants routinely benefit from non-native pollinators (Richardson *et al.*, 2000; Goulson, 2003; Traveset and Richardson, 2014) but limited evidence that non-native pollinators are receiving large population-level benefits. Early writing foreshadowed that widely introduced super-generalist pollinators, like the European honeybee (*Apis mellifera*) and European bumblebee (*Bombus terrestris*), may facilitate the establishment of many non-native plants (Richardson *et al.*, 2000). Because these non-native pollinators are domestic species introduced for crop pollination (Goulson, 2003) they likely receive less benefits than the non-native plants they pollinate, forming simple facilitative interactions (Fig. 8.1a). Many non-native plants receive a large proportion of their pollination services – sometimes their only pollination services – from one or both of these two pollinators. Supergeneralist non-native pollinators are frequently integral components in non-native plant—pollinator community networks and facilitate non-native plants relative to native plants in these complex interaction webs (Richardson *et al.*, 2000; Morales and Aizen, 2006; Aizen *et al.*, 2008; Bartomeus *et al.*, 2008; Padrón *et al.*, 2009; Abe *et al.*, 2011; Morales *et al.*, 2017). Interestingly, these *generalist* pollinators can also facilitate the spread of non-native plants with *specialist* pollination syndromes. Hummingbirds pollinate the banana passionfruit vine (*Passiflora tripartita* var. *mollissima*) in its native range in the South American Andes. Surprisingly, it is one of the most invasive vines in New Zealand (Beavon and Kelly, 2012, 2015) even though hummingbirds do not occur on the island. Instead, non-native bees act as surrogate pollinators for the vine; preventing bee access to flowers reduced the vine's fruit set by nearly 70% (Beavon and Kelly, 2012).

This is likely an incomplete list of examples of non-native plant–pollinator pairs because the pollination biology of non-native plants and bees is infrequently studied (Goulson, 2003; Russo, 2016) and bees are not the only possible pollinators of non-native plants. The global establishment rate of non-native invertebrates has

Direct Interactions

A

+ **+**

Mutualism

Generalist pollinators, seed dispersers, ectomycorrhizal fungi or rhizobia bacteria promote plant invasion (Traveset and Richardson, 2014)

B

+ **0**

Commensalism

*Wild boar (*Sus scrofa*) disturb soils and destroy vegetation to create openings for plant invasions (Barrios-Garcia and Simberloff, 2013)*

C

+ **+**

Herbivory

*Rusty crayfish (*Orconectes rusticus*) herbivory increases watermilfoil (*Myriophyllum spicatum*) dispersal (Maezo et al., 2010)*

Indirect Interactions

D

- **-** **+**

Trophic Cascade

*Yellow crazy ant (*Anoplolepis gracilipes*) attacks the herbivorous red land crab (*Gecarcoidea natalis*) allowing invasion by the nonnative plant* Clausena excavata *(Green et al., 2004)*

E

- **+** **+** **-** **-** **+**

Apparent Competition

*A nonnative weevil (*Rhinocyllus conicus*) increases attacks on a native thistle (*Cirsium undulatum*) when the nonnative thistle (*Carduus nutans*) is present (Rand and Louda, 2004).*

F

+ **+** **+**

Indirect Mutualism

Nonnative Lupinus arboreus *acts as "magnet species' for pollinators that increase seed production for nonnative* Carduus pycnocephalus *with inconspicuous flowers (Molina-Montenegro et al., 2009).*

Fig. 8.2. An invasional meltdown is a community-level phenomenon where the *net effect* of all interactions is positive and leads to an increasing rate of establishment or accelerating impact of non-native species (Simberloff and Von Holle, 1999; Simberloff, 2006). There are many possible types of direct (bold lines) and indirect interactions (dashed lines) between non-native species that could lead to an invasional meltdown. Line width indicates the relative strength of the interaction. Symbols for diagrams courtesy of the Integration and Application Network (ian.umces.edu/symbols) and PhyloPic (www.phylopic.org).

more than doubled in the past quarter-century (Hulme, 2009). Some proportion of these invertebrates will be generalist pollinators, which creates a formidable palate of potentially facilitative non-native plant—pollinator interactions for ecologists to explore.

There are limited examples of specialized non-native plant–pollinator mutualisms, which

are more likely to lead to 'full' invasional melt-downs (Fig. 8.1e). To my knowledge, the only example of a 'full' plant–pollinator meltdown is the tightly coevolved plant—insect pairing of *Ficus* trees and their host-specific wasps in Florida, USA (Ramírez and Montero, 1988; McKey and Kaufmann, 1991). This may be because plants with specialized pollination syndromes should be far less likely to become invasive relative to plants with generalist pollination syndromes (Baker, 1965, 1974; Richardson *et al.*, 2000). This does not mean 'full' plant—pollinator melt-downs do not occur, it just means they may be infrequent.

An innovative approach to identify potential plant—pollinator invasional meltdowns is studying non-natives *early* in the invasion process. Many non-native plants are cultivated (van Kleunen *et al.*, 2018) but have not invaded outside of cultivation, potentially owing to a lack of pollinators (Bufford and Daehler, 2014; Moodley *et al.*, 2016). This was the case in Hawaii, USA, where cultivated milkweed (*Calotropis gigantea*) only fruited when it was hand pollinated, suggesting a missing mutualist is limiting its spread (Bufford and Daehler, 2014). Although tracking failed invasions is difficult (Zenni and Nuñez, 2013), it may provide a promising avenue for detecting future meltdowns (Bufford and Daehler, 2014).

8.5   Non-native Plants and Seed Dispersers

There are many documented examples of non-native animals dispersing non-native plant seeds (Richardson *et al.*, 2000; Traveset and Richardson, 2014; Martin-Albarracin *et al.*, 2015). As with non-native pollinators, non-native animals with wide diet breadths are more likely to successfully invade a new range (Martin-Albarracin *et al.*, 2015) and most non-native seed dispersers include generalist birds (Bartuszevige and Gorchov, 2006; Foster and Robinson, 2007; Kawakami *et al.*, 2009; Spotswood *et al.*, 2012; Martin-Albarracin *et al.*, 2015) and mammals (Davis *et al.*, 2010; Calvino-Cancela, 2011; Beavon and Kelly, 2015; Bobadilla *et al.*, 2016; Calvino-Cancela, 2011). Of those examples of non-native animals

that disperse seeds of non-native plants, there is limited evidence that the plants are dispersal-limited or that the animals are food-limited. While a few studies show that seed germination rates increased after passage through non-native dispersers' guts (Bartuszevige and Gorchov, 2006; Beavon and Kelly, 2015; Bobadilla *et al.*, 2016), it was not tested whether native seed dispersers provided the same service or if increased germination rates led to increased population growth rates of non-native plants. This suggests that while non-native plants and animals may frequently facilitate one another, many of these interactions do not constitute 'full' invasional meltdowns.

There are a few circumstances, however, where generalist seed dispersers could promote an invasional meltdown. Plant–disperser meltdowns may be more likely to occur when the fruiting phenology of non-native plants differs from native plants. In this scenario, non-native plants may boost the population size and spread the rate of a non-native seed disperser. For example, in the Mascarene Islands in the Indian Ocean, the non-native red-whiskered bulbul (*P. jocosus*) invaded the island much more rapidly than during prior introduction events in other regions (Clergeau and Mandon-Dalger, 2001). One hypothesis for the bird's rapid spread is that the island's large population of non-native plants that produce year-round fruit increased the bird's population growth and spread (Mandon-Dalger *et al.*, 2004). Indeed, the bulbul's population size is larger in sites that contain fleshy-fruited non-natives with year-round fruit relative to sites dominated by native plants with seasonal fruit (Mandon-Dalger *et al.*, 2004). Seeds of the most invasive non-native plants are prevalent in bulbul faecal samples and the seed germination rates of some non-natives increase significantly after passage through the bulbul gut (Mandon-Dalger *et al.*, 2004; Linnebjerg *et al.*, 2010). Similarly, in Mediterranean dunes the non-native succulent hottentot fig (*Carpobrotus edulis*) produces a water and energy-rich food source during the dry season when natives are not producing fruit. The fig is eaten by many non-native mammals including the European rabbit (*Oryctolagus cuniculus*), the Norway rat (*Rattus rattus*) and the wood mouse (*Apodemus*

sylvaticus), which disperse seeds and enhance seed germination relative to uneaten fruit (Bourgeois *et al.*, 2004, 2005).

Another form of plant–disperser meltdown may occur through positive feedback loops that arise when a non-native seed disperser has strong preferences for non-native fruit relative to native fruit (Martin-Albarracin *et al.*, 2015; Traveset and Richardson, 2014). If a seed disperser prefers non-native fruit, they will spread more non-native seed and increase the non-native plant's abundance. As the plant becomes more abundant, it becomes the dominant food source and perpetuates the feedback. A bevy of studies demonstrate non-native dispersers prefer non-native plant fruit (Foster and Robinson, 2007; Lafleur *et al.*, 2007; Rowles *et al.*, 2009; Chimera and Drake, 2010; Spotswood *et al.*, 2012; Prior *et al.*, 2015; MacFarlane *et al.*, 2016) and that non-native plants comprise a large proportion of all seeds found in faecal samples of non-native dispersers (Kawakami *et al.*, 2009; Chimera and Drake, 2010; Linnebjerg *et al.*, 2010; Spotswood *et al.*, 2012). These positive feedback loops could be when non-native animals act as both seed predators and seed dispersers. For example, in the Hawaiian Islands, non-native rats (*Rattus* spp.) may act as seeds dispersers for the most widespread non-native plants, but seed predators for many native plants (Shiels and Drake, 2011; Shiels, 2011).

Seed-dispersing non-native ants demonstrate this same pattern of disperser-preference-driven feedback loops. The invasive Argentine ant (*Linepithema humile*) is one of the most aggressive and globally widespread invasive insects and is a poor seed disperser for native plants (Rodriguez-Cabal *et al.*, 2009). In coastal scrublands in south-eastern Australia, the Argentine ant accounts for 92% of all ant—seed interactions and disperses significant fewer seeds of the native tree *Acacia retinodes* and significantly more seeds of the invasive South African shrub, *Polygala myrtifolia*, relative to native ant dispersal patterns at uninvaded sites (Rowles *et al.*, 2009). Similarly, in north-eastern US deciduous forests, the non-native ant *Myrmica rubra* preferred seeds of the non-native herb, *Chelidonium majus,* relative to three other common native plants (Prior *et al.*, 2015). When the non-native ant was present, the non-native plant had eight times more seedlings and produced almost two times more flowers than when a native seed-dispersing ant was present (Prior *et al.*, 2015).

The majority of examples of non-native plants benefiting from seed dispersal services focus on consumptive dispersal of non-native plant seed (endozoochory). However, animals can also disperse seeds though non-consumptive means (exozoochory), although this dispersal mechanism is infrequently studied (van Leeuwen, 2018). It has been suggested that non-native livestock or other wide-ranging mammals may promote long-distance spread of non-natives (Simberloff and Von Holle, 1999), but the only demonstrated example of this is from Santa Catalina Island, California, USA, where non-native bison (*Bison bison*) carry viable seeds of the non-native forbs *Marrubium vulgare* and *Xanthium strumarium* (Constible *et al.*, 2005).

8.6   Non-native Plants and Soil Microbial Mutualists

Some of the most exciting, and potentially devastating, interactions among non-natives may be occurring belowground. For some non-native plant taxa – primarily those that affiliate with nitrogen-fixing bacteria or ectomycorrhizal fungi – there is now clear evidence that the absence or presence of soil mutualists can prevent or promote plant invasions (Richardson *et al.*, 2000; Nuñez *et al.*, 2009) or facilitate the invasion of plants and microbes (Nuñez *et al.*, 2009; Dickie *et al.*, 2010; Rodríguez-Echeverría, 2010; Hayward *et al.*, 2015a). Many barriers to detecting microbial symbionts have disappeared with the advent of new molecular tools that can identify soil microbial taxa (Widder *et al.*, 2016). There are now clear patterns in non-native plant–soil mutualisms. First, humans are frequently and successfully co-introducing non-native plants with their soil microbial mutualists (Richardson *et al.*, 2000; Nuñez and Dickie, 2014); second, plant–microbe co-introduction events are facilitating the spread of both plants and microbes; and third, there are likely synergistic impacts on native soil microbes and native plant—microbe interactions that could fundamentally alter the composition of soil microbial communities, plant communities and perhaps even above-ground plant–pollinator

or plant–disperser mutualisms (Rodríguez-Echeverría and Traveset, 2015).

It is likely that we will see an increase in examples of invasional meltdown – both historic and contemporary – as we continue exploring interactions between non-native soil microbes and plants. Co-introduction of non-native plants and their soil mutualist partners may be much more common than co-introductions of plants and pollinators or seed dispersers because many non-native plants with obligate belowground mutualisms were intentionally introduced as economic commodities (Richardson *et al.*, 2000; Richardson and Rejmánek, 2011; Ambrosini *et al.*, 2016). For example, non-native *Pinus* are over-represented relative to their global taxonomic diversity (Richardson and Rejmánek, 2011). This is likely because humans intentionally co-introduce *Pinus* and their ectomycorrhizal fungi mutualists in forestry plantations, which has enabled *Pinus* species to overcome barriers to invasion (Richardson and Higgins, 1998). Humans have transported at least 200 ectomycorrhizal fungal species around the globe and the majority of these recorded introductions were intentional with forestry plantations of *Pinus* or *Eucalyptus* species (Vellinga *et al.*, 2009). Additionally, even if soil microbe mutualists are not intentionally introduced, they are incredibly robust to a range of environmental conditions and survive transport through a variety of pathways including free-living in soils, on the roots of live plants or even on the exterior of dried plant seeds (Perez-Ramirez *et al.*, 1998; Stępkowski *et al.*, 2005; Pringle *et al.*, 2009; Litchman, 2010).

While co-introduction of plants and their mutualists does not necessarily lead to co-invasion and a full invasional meltdown, it sets the stage for one. Many intentionally introduced ectomycorrhizal fungi fail to establish in soils outside of the original forestry plantation (Nuñez *et al.*, 2009). In some instances, however, a single 'pioneer' ectomycorrhizal fungus can initiate a plant invasion (Hayward *et al.*, 2015b). For example, the fungal genus *Suillus* associates with tree roots on the leading edge of *Pinus* invasions in Patagonia (Hayward *et al.*, 2015b; Ureclay *et al.*, 2017), New Zealand (Dickie *et al.*, 2010) and Hawaii (Hynson *et al.*, 2013). *Suillus* spp. are good 'pioneer' fungi because they produce many fruiting bodies that are ingested and dispersed by large mammals and their spores are hardy and persist in the soil until a suitable host plant establishes (Hayward *et al.*, 2015b). Wind-dispersed *Pinus* seeds that land on *Suillus*-inhabited soils can establish and then provide a suitable soil habitat for later-successional non-native ectomycorrhizal fungi (Hayward *et al.*, 2015a). In some cases, the spread of non-native ectomycorrhizal fungi from plantations can facilitate plant invasions to environments in which they are not typically found, such as high-elevation mountains that typically experience lower levels of invasion (Ureclay *et al.*, 2017). Lower fungal diversity in the soils around invading *Pinus* species relative to native ectomycorrhizal trees (Dickie *et al.*, 2010) or *Pinus* in their native range (Hynson *et al.*, 2013) supports the idea that this 'leapfrog' invasion pattern may be common in *Pinus* invasions.

The potential for invasional meltdown does not end with tree–fungal mutualisms. Non-native mammals can facilitate invasion by dispersing fungal spores to new locations. Non-native wild boar (*Sus scrofa*) and fallow deer (*Dama dama*) in Patagonia, non-native brushtail possum (*Trichosurus vulpecula*) in New Zealand and red deer (*Cervus elaphus*) in both regions, disperse a wide range of non-native, but not native, ectomycorrhizal fungal spores (Nuñez *et al.*, 2013; Wood *et al.*, 2015). In both regions, these non-native mammals are functionally unique because there are no native large mammals to disperse fungal spores (Nuñez *et al.*, 2013; Wood *et al.*, 2015).

Plant—microbe invasional meltdowns also seem common among leguminous plants that form mutualistic relationships with symbiotic nitrogen-fixing bacteria, or rhizobia. One of the first recorded plant—rhizobia co-invasions was in the Hawaiian Islands, USA, where the non-native shrub *Morella faya* and *Frankia* rhizobia invaded early successional and nutrient-poor soils (Turner and Vitousek, 1987). There are now many more examples of plant—rhizobia co-invasion. South and Central American mimosa trees (*Mimosa* spp.) predominantly affiliate with American lineages of *Cupriavidus* and *Burkholderia* rhizobia in their non-native range in the Philippines (Andrus *et al.*, 2012), Taiwan (Chen *et al.*, 2005) and Yunnan Province in southern China (Liu *et al.*, 2012). Partnerships between European legumes and *Bradyrhizobium*

bacteria have been found in Scotch broom (*Cytisus scoparius*) populations in north-western USA (Horn *et al.*, 2014), seven non-native clover species (*Trifolium* spp.) in New Zealand (McGinn *et al.*, 2016), and invasive lupines (*Lupinus albus, L. angustifolius, L. cosentinii* and *L. luteus*) and serradella (*Ornithopus* spp.) in Australia and South Africa (Stępkowski *et al.*, 2005). Finally, nitrogen-fixing *Acacia* species that evolved in Australia are some of the most widely introduced woody plants (Richardson and Rejmánek, 2011) and are nearly always found with Australian *Bradyrhizobium* that were likely co-introduced with the *Acacia* (Rodríguez-Echeverría *et al.*, 2011). Thus far, non-native *Bradyrhizobium* have been detected in non-native *Acacia* tree roots and soil in western Australia (Birnbaum *et al.*, 2012, Birnbaum *et al.*, 2014, 2016), Portugal (Crisóstomo *et al.*, 2013; Rodríguez-Echeverría, 2010; Rodríguez-Echeverría *et al.*, 2012), and South Africa (Ndlovu *et al.*, 2013).

Many of these non-native legumes do not affiliate with native rhizobia (Weir *et al.*, 2004; La Pierre *et al.*, 2017), suggesting that without the co-introduction of the non-native rhizobia, plant invasion would not occur. For example, there was nearly no overlap in *Bradyrhizobium* genotypes between three invasive European legumes (*Genista monspessulana*, *Spartium junceum* and *Ulex europaeus*) and six native legumes (*Acmispon glaber, A. heermannii, A. micranthus, A. strigosus, Lupinus arboreus* and *L. bicolor*) in California, USA (La Pierre *et al.*, 2017). This was also the case for a suite of non-native legumes in New Zealand (Weir *et al.*, 2004).

Co-invasion of non-native legumes and rhizobial mutualists may also have large population impacts on co-occurring native plants. Native legumes do interact with non-native rhizobia, which may potentially disrupt co-evolved native plant—rhizobial mutualisms (Rodríguez-Echeverría, 2010). More concerning, new evidence suggests that native and non-native rhizobia can readily hybridize. Rhizobia can evolve rapidly through lateral gene transfer that may foster invasional meltdowns. In some regions invaded by non-native legumes, rhizobial strains in the soils combine genetic elements of native and non-native bacterial genomes. The 'core' native bacterial genome contains basic housekeeping genes for the species with evolved tolerance to unique soil conditions, while the 'accessory' non-native bacterial genomes include the specific signalling genes that stimulate a plant to produce nodules for the bacteria (Remigi *et al.*, 2016; Andrews *et al.*, 2018). These novel, hybrid rhizobia can invade soils that a non-native rhizobial lineage could not (Wei *et al.*, 2009; Liu *et al.*, 2012), increase soil rhizobial diversity for plants in their non-native relative to their native range (Ndlovu *et al.*, 2013; Horn *et al.*, 2014) and potentially disrupt native legume–rhizobia symbioses (Rodríguez-Echeverría, 2010; Le Roux *et al.*, 2017).

8.6.1 Commensalisms and invasional meltdowns

Non-native animals and plants can directly facilitate other non-native plants by modifying the environment (Simberloff and Von Holle, 1999; Fig. 8.2b). Non-native species can impact nutrient and carbon cycling, fire and hydrological regimes or the physical structure of an ecosystem (Liao *et al.*, 2008; Ehrenfeld, 2010; Simberloff, 2011) earning some non-natives the label 'ecosystem engineer' (Jones *et al.*, 1994). Ecosystem engineers are broadly defined as species that modulate the availability of resources to other species by modification of the biotic or abiotic environment. Non-native species can facilitate plant invasions as allogenic engineers – by transforming materials from one physical state to another – or as autogenic engineers – by changing the environment through their own physical structure (Jones *et al.*, 1994). While ecologists disagree whether interactions mediated through environmental modification constitute direct or indirect interactions (Strauss, 1991; Wootton, 1994), for this chapter, I consider these commensalisms to be direct interactions because they are not mediated by the presence of a third species. Regardless of whether these habitat-modifying non-natives are directly or indirectly affecting non-native plants, they represent a viable pathway to invasional meltdown. Nearly all of these examples constitute 'weak' facilitative interactions among non-natives (Fig. 8.1a) because there is typically no evidence that the non-native plant facilitates the ecosystem-modifying invader.

8.7 Allogenic Ecosystem Engineers and Invasional Meltdown

Some of the first examples of non-natives modifying ecosystems were of nitrogen-fixing non-native plants that invaded nutrient-poor soils, increased plant-available soil nitrogen and facilitated the establishment of other non-native plants (Simberloff and Von Holle, 1999). This same scenario has now been documented a few more times. The annual herbaceous legume, partridge pea (*Chamaecrista nictitans*), facilitates invasion of non-native fountain grass (*Pennisetum setaceum*) into native dry Hawaiian grasslands (Carino and Daehler, 2002). Nutrient-poor oak (*Quercus* spp.) forests that are invaded by black locust (*Robinia pseudoacacia*) in north-eastern USA (Vilà and Weiner, 2004) or *Acacia dealbata* in north-western Spain (González-Muñoz *et al.*, 2012) had higher plant-available soil nitrogen levels and percentage of non-native plants relative to oak-dominated forest soils.

Invasive invertebrate pests and microbial pathogens cause dramatic alterations to ecosystems by eliminating entire species from forests (Lovett *et al.*, 2016; Kenis *et al.*, 2017). The loss of foundational canopy trees increases light availability to the forest floor, alters carbon and nutrient cycles and affects the abundance of other non-plant species (Ellison *et al.*, 2005). Approximately 63% of the USA's forests (334 million hectares) are at risk of substantial tree mortality by non-native forest pests (Lovett *et al.*, 2016). There is a growing list of non-native species that invade and persist in closed-canopy forests (Martin *et al.*, 2008) and may be primed to spread more rapidly with large-scale tree canopy losses. For example, the invasion of the non-native insect Emerald ash borer (*Agrilus planipennis*) in midwestern USA forests leads to complete ash tree (*Fraxinus* spp.) mortality in less than five years. Loss of the ash, a once dominant canopy tree, creates canopy gaps that are quickly colonized by a variety of non-native shrubs that increase in abundance much more rapidly than native shrubs (Klooster *et al.*, 2018).

Non-native animals can also modify ecosystems thorough trampling or destroying vegetation or digging and disrupting soils. The wild boar (*S. scrofa*) is globally one of the most widespread invasive mammals. Boar are omnivorous with feeding habits that include destructive soil rooting practices that eliminate vegetation and disturb soils (Barrios-Garcia and Ballari, 2012). In Patagonia, Argentina, non-native plants had twice the rate of establishment and biomass in boar-rooting patches relative to undisturbed sites and boar-dispersed non-native plants into their rooting patches through their droppings (Barrios-Garcia and Simberloff, 2013). Similarly, in Texas, USA, the non-native tallow tree (*Sapium sebiferum*) was more than twice as abundant in areas with boar than areas without boar (Siemann *et al.*, 2009).

Similar to wild boar disruption of soils, the introduction of non-native earthworms in northern North America has led to rapid and dramatic impacts on soil structure, litter decomposition rates and nutrient cycling, and plant community composition (Hendrix and Bohlen, 2002; Cameron *et al.*, 2016; Craven *et al.*, 2017). One of the most conspicuous patterns is that non-native earthworm abundance tends to be positively related to non-native plant abundance and negatively related to native plant abundance (Kourtev *et al.*, 1999; Heneghan *et al.*, 2007; Nuzzo *et al.*, 2009; Clause *et al.*, 2015; Dávalos *et al.*, 2015; Craven *et al.*, 2017; Mueller *et al.*, 2018; Lloyd *et al.*, 2019). Proposed mechanisms for these patterns include earthworm disruption of important native plant–mycorrhizal mutualisms (Lawrence *et al.*, 2003; Paudel *et al.*, 2016), increase of soil nutrient cycling rates or changes in soil pH that preferentially promote non-native plant growth (Belote and Jones, 2009; Lloyd *et al.*, 2019) and the ingestion and deposition of non-native seeds into nutrient-rich earthworm burrows that enhances non-native germination and establishment (Quackenbush *et al.*, 2012; Clause *et al.*, 2015 but see Roth *et al.*, 2015). The majority of studies on non-native plant—earthworm interactions are observational, probably because removing earthworms is challenging and introducing earthworms is unethical. However, non-native plant removal experiments provide evidence that non-native plants facilitate non-native earthworms. Removal of the non-native shrub Chinese privet (*Ligustrum sinense*) in south-eastern US forests led to decreased soil pH and a significance decrease in non-native and a fourfold increase in native earthworm abundance (Lobe *et al.*,

2014). Similarly, the removal of the non-native woody shrubs buckthorn (*Rhamnus cathartica*) and bush honeysuckle (*Lonicera* x *bella*) in northern USA forests reduced nutrient-rich leaf litter inputs and non-native earthworm biomass by 50% (Madritch and Lindroth, 2009).

While it is premature to conclude that non-native earthworms and plants are benefiting from each other and not a symptom of other ecosystem disturbances (Dávalos *et al.*, 2015), these are notable patterns worth exploring. Promising avenues of study include experimental manipulations of non-native plant abundance or establishing observational plots along the front lines of earthworm invasions to capture ecosystem and plant community properties before and after invasion. Additionally, it is likely that the impact of non-native earthworms is not restricted to North America. Humans have introduced invasive earthworms to many other regions of the globe that have yet to be studied (James and Hendrix, 2004).

8.8 Autogenic Ecosystem Engineers and Invasional Meltdown

Non-native plants generally have higher net primary productivity and produce more shoot biomass that native species (Liao *et al.*, 2008; Vilà *et al.*, 2011), which increases the likelihood that they can alter an ecosystem's structure through increasing total plant biomass (Simberloff, 2011). Non-native plants can protect other non-natives from predation, ameliorate harsh environmental conditions or provide physical structures that enhance the growth of other non-native plants. For example, emergent non-native cattails (*Typha* spp.) in Michigan, USA, wetlands provide structural protection for a free-floating non-native plant, European frogbit (*Hydrocharis morsus-ranae*). Cattail removal led to a fivefold decrease in frogbit cover because no other plants protected frogbit in otherwise open-water lakes (Monks *et al.*, 2019). The non-native floating water hyacinth (*Eichhornia crassipes*) in coastal wetlands in Texas, USA, also increased in abundance when the emergent invasive herb alligator weed (*Alternanthera philoxeroides*) was present (Wundrow *et al.*, 2012). In the coastal foredunes of the north-western USA,

non-native invasive dune grasses (*Ammophila* spp.) alter the physical shape of sand dunes through differences in shoot and root growth relative to dominant native grasses (Zarnetske *et al.*, 2012). The biophysical alteration of sand dunes changes competitive relationships among native and non-native dune grasses and leads to competitive exclusion of native dune grasses and co-dominance of non-native dune grasses (Zarnetske *et al.*, 2013).

Finally, when non-native woody plants invade ecosystems primarily dominated by low-stature vegetation, such as trees invading early-successional habitats, they provide perching, nesting and protective structures for a variety of wildlife species. The non-native tree *Casuarina equisetifolia* is an aggressive invader of recent lava flows in La Réunion Island in the Indian Ocean (Potgieter *et al.*, 2014). Birds are attracted to *C. equisetifolia* branches as perch sites and deposit many seeds of other non-native plants underneath *C. equisetifolia*'s canopy (Potgieter *et al.*, 2014). Interestingly, one of the primary seed dispersers is the invasive red-whiskered bulbul (*P. jocosus*; see 'Non-native Plants and Seed Dispersers'), which has been implicated in invasional meltdown in the nearby island of Mauritius. Similarly, the non-native tree *Pyracantha angustifolia* in central Argentine shrublands harboured eight-times higher densities of other bird-dispersed non-native species than under a co-occurring native shrub or in areas without a shrub. The authors suggested this occurred because the fruiting phenology of non-native plants in these ecosystems were synchronous (Tecco *et al.*, 2006).

The accumulation of senesced plant litter can also change ecosystem structure. In California, USA grasslands, two herbaceous non-natives, medusa-head (*Elymus caput-medusae*) and wild oat (*Avena* spp.), form dense thatch layers. While native plant seed production and growth was negatively affected by deep thatch, wild oat growth and medusa-head fitness increased with thatch depth, promoting the persistence of both non-natives (Mariotte *et al.*, 2017). Finally, increasing amounts of senesced litter can increase the frequency or intensity of fires (Brooks *et al.*, 2004; Gaertner *et al.*, 2014). Non-native pine plantations increase fuel loads and the number of fires that spread from plantations into native vegetation. In New Caledonia

in the south-west Pacific, more fires promote the fire-tolerant non-native fern *Pteridium aquilinum* in and around pine plantations, which then replaces native species and increases fire frequency (Simberloff *et al.*, 2010).

8.9   Herbivory and Invasional Meltdown

Interactions between non-native herbivores and plants could lead to a net positive effect for a plant if it responds positively to browsing, or if herbivory promotes dispersal (Fig. 8.2c). Non-native geese (*Branta canadensis*) in the Gulf Islands of British Columbia, Canada, predominantly browsed non-native grasses. Goose browse decreased grass height, increased tiller production and reduced accumulation of senesced grass litter, ultimately increasing non-native grass fitness relative to native forbs. The authors attributed this unexpected outcome as evidence for evolved tolerance to intense browsing of non-native grasses in their European native ranges (Best and Arcese, 2009). Herbivory may also promote the spread of non-native plants. The non-native rusty crayfish (*Orconectes rusticus*) feeds on the non-native submerged aquatic plant, Eurasian watermilfoil (*Myriophyllum spicatum*). At moderate densities, crayfish browse does not impact milfoil biomass but does increase milfoil dispersal rates by creating reproductive vegetative fragments that disperse through the water (Maezo *et al.*, 2010).

8.10   Indirect Interactions Among Non-native Species

Positive interactions may be the most conspicuous when considering direct interactions between pairs of non-natives. However, invasional meltdown is any instance where the *net effect* of all interactions is positive (Simberloff and Von Holle, 1999; Ricciardi, 2001; Simberloff, 2006; Fig. 8.1e). Thus, positive direct pairwise interactions are not the only pathway to meltdown. In communities comprising many interacting native and non-native species, the net effect of a non-native on another non-native will be the sum of all direct and indirect interactions (Miller, 1994;

Ricciardi, 2001). Detecting indirect interactions in multispecies communities is difficult, controversial and frequently ignored (Strauss, 1991; Miller, 1994; Levine *et al.*, 2017; Wright *et al.*, 2017), including in invasion biology (White *et al.*, 2006; Godoy, 2019). In communities containing more than two species, indirect interactions may be highly influential (Miller, 1994; Ricciardi, 2001) but the paucity of studies that consider indirect effects in invasion limits our ability to fully assess the relative importance of indirect vs direct effects (see Chapter 17, this volume).

Below, I review a handful of case studies where indirect effects of multiple non-native species has promoted plant invasions. Many of these examples are interaction chains where non-native animals promote the growth or fitness of non-native plants by reducing herbivory on plants in a trophic cascade (Fig. 8.2d) or increasing herbivory on native competitors in apparent competition (Fig. 8.2e). Similarly, non-native plants may affect the fitness or growth of other non-native plants through indirect mutualisms mediated by shared mutualists or competitors (Fig. 8.2f).

8.11   Trophic Cascades

Non-native plants may indirectly benefit from non-native predators when the predator reduces the effects of herbivores on the non-native. Although I only found one example of non-native plants benefiting from trophic cascades, we may expect to find more examples in island ecosystems that tend to be invaded by multiple invasive species in a range of trophic positions (Russel and Kaiser-Bunbury, 2019). For example, on Christmas Island in the Indian Ocean, invasion by the non-native yellow crazy ant (*Anoplolepis gracilipes*) attacks and reduces the population of the red land crab (*Gecarcoidea natalis*), which consumes non-native plant seeds and seedlings (Green *et al.*, 2004, 2011). Thus, ants indirectly facilitate plant invasion by reducing crab herbivory and allowing non-native plants to establish in the island's forest interior (Green *et al.*, 2004, 2011).

8.12   Apparent Competition

Invasional meltdowns via apparent competition can occur when a non-native plant benefits

relative to a native plant competitor through an asymmetrical relationship with a shared non-native herbivore, pest or pathogen (Fig. 8.2e; Chapter 17, this volume). In some cases, the non-native plant increases the population size of an herbivore, pest or pathogen that then reduces the population of a native plant competitor. The introduction of non-native biocontrol organisms is one avenue to apparent competition-mediated meltdowns (Pearson and Callaway, 2005, 2008). For example, in the midwestern USA, the non-native biocontrol weevil (*Rhinocyllus conicus*) had a three to five-fold increase in its attack rate on a native thistle (*Cirsium undulatum*) when the native thistle grew near the biocontrol's target non-native thistle (*Carduus nutans*; Rand and Louda, 2004). Non-native biocontrol gallflies (*Urophora* spp.) were introduced to control the invasive spotted knapweed (*Centaurea maculosa*) in western US grasslands. Populations of native deer mice (*Peromyscus maniculatus*) increased in abundance in knapweed patches because gallflies became a favoured food. Larger deer mouse populations increased predation rates on native plant seeds and decreased germination rates. This 'second order' apparent competition may indirectly benefit knapweed populations by reducing native forb competition (Pearson and Callaway, 2008).

Non-native plants may also harbour non-native pathogens that can 'spill over' to a native plant competitor (Strauss *et al.*, 2012; Flory and Clay, 2013), which may allow other non-native plants to invade. The invasive wild oat (*Avena fatua*) in western US grasslands is a reservoir of the non-native barley yellow dwarf virus and wild oat populations increase viral prevalence. Native grassland plants have reduced growth and fitness near virus-infected oat populations while other non-native species, like cheatgrass (*Bromus tectorum*), are unaffected by the virus (Power and Mitchell, 2004).

Apparent competition can also manifest when non-native herbivores preferentially browse native plants over co-occurring non-native plants (Parker *et al.*, 2006; de Villalobos *et al.*, 2011; Nuñez *et al.*, 2008; Relva *et al.*, 2010). Non-native herbivore-mediated apparent competition may be common between non-native and native plants; a meta-analysis of 63 published studies of 100 non-native plant species found that the presence of non-native

herbivores enhanced the relative abundance of non-native plants by 65% while reducing the absolute abundance of native plants (Parker *et al.*, 2006). More specifically, in Patagonia, Argentina, a variety of large mammalian herbivores are altering the composition and abundance of native grassland and forest plant communities (Von Holle *et al.*, 2006; Relva *et al.*, 2010; de Villalobos *et al.*, 2011). In Patagonian grasslands where non-native feral horses preferentially grazed native plants, native plant cover and biomass decreased and non-native, unbrowsed *Pinus halepensis* seedlings were taller and had higher shoot mass relative to ungrazed locations (de Villalobos *et al.*, 2011). In Patagonian forests, non-native deer browse significantly reduced the growth of the native trees *Austrocedrus chilensis* and *Nothofagus dombeyi* but not the non-native trees *Pseudotsuga menziesii* and *Pinus ponderosa* (Nuñez *et al.*, 2008; Relva *et al.*, 2010). Non-native gypsy moth (*Lymantria dispar*) feeding preferences in eastern North America could indirectly promote the persistence of particular shrub species, including the non-native shrubs bush honeysuckle (*Lonicera maackii*) and Chinese privet (*L. sinense*) after large gypsy moth outbreaks (McEwan *et al.*, 2009). Similarly, the non-native snail *Pomacea maculata* intensively grazed native wetland plants in Texas, USA, which allowed the invasive herb alligatorweed *A. philoxeroides* to increase its abundance in the wetland (Meza-Lopes and Siemann, 2015).

Detecting apparent competition between native and non-native plants mediated through shared generalist herbivores may be empirically challenging. Ecologists typically use animal exclusion experiments to test the effects of herbivory, either using fences to exclude mammals or insecticides to exclude invertebrates. These coarse experimental treatments will exclude all native and non-native herbivores, making it difficult to distinguish the differences in the impacts of native vs non-native herbivores. This is likely why the few examples of these indirect interactions are either in areas where the predominant herbivores are all non-native – such as large mammals in Patagonia – or when the generalist non-native herbivore is the focus of the experimental study.

8.13   Indirect Mutualisms

Indirect mutualisms are defined as indirect positive effects of one species on another (Wootton, 1994; Fig. 8.2a). In the context of invasional meltdowns, two non-native plants may indirectly facilitate one another through a shared mutualist, herbivore or competitor. For example, non-native plants with large, showy floral displays may enhance pollination services of other non-native plants if they attract pollinators to their neighbour's flowers. This occurred in Chile for the pollen-limited *Carduus pycnocephalus* that has small, inconspicuous flowers. *Carduus* plants that grew near the large-flowered non-native *L. arboreus* had enhanced pollinator visitation and seed production relative when growing alone (Molina-Montenegro *et al.*, 2008). Non-native plants may also physically protect other non-native plants from herbivores. The invasive South African grass *Ehrharta calycina* escapes herbivory from a native herbivore, the black-tailed jackrabbit (*Lepus californicus*), in coastal foredunes in northern California, USA. When *E. calycina* is found near other non-native dune plants, *Ammophila arenaria* and *C. edulis*, it has lower herbivory, higher biomass and higher numbers of reproductive spikelets than in open areas of the dune (Cushman *et al.*, 2011).

Indirect mutualisms among non-native plants can also arise within competitive plant community networks if there is asymmetry in the strength of direct pairwise interactions (Stone and Roberts, 1991; Miller, 1994; White *et al.*, 2006; Levine *et al.*, 2017). Thus, non-native plants may indirectly facilitate one another if competitive interactions between native and non-native plants are stronger than competitive interactions between two or more non-native plants (Kuebbing and Nuñez, 2016). For example, the non-native herb garlic mustard (*Alliaria petiolata*) had higher biomass and more reproductive siliques in experimental plots with the non-native annual grass Japanese stiltgrass (*Microstegium vimineum*) relative to grass-free areas. The non-native grass indirectly facilitated the non-native herb by reducing native competitors within the plots (Flory and Bauer, 2014). In a mesocosm study of non-native plants common to the midwestern US tallgrass prairie, pairwise interactions among non-native plants were always competitive. However, the direct competitive effects of non-natives on one another were sometimes reduced when natives were present (Oschrin and Reynolds, 2019). Like many of these indirect mutualisms, it is impossible to assess how common or important asymmetric competition among co-occurring native and non-native plants is for promoting plant invasions. It would be premature to say that this mechanism is common or causing invasional meltdowns in plant communities, but it is rarely studied and warrants further research.

Importantly, indirect mutualisms among two or more non-native plants can lead to positive net effects even in the presence of *direct negative interactions* among non-native plants (Kuebbing and Nuñez, 2016). In other words, pairwise interactions among non-natives may be negative, but if the presence of native species alters those direct negative effects then the sum of all interactions in the community may be net positive and lead to non-native accumulation (Fig. 8.1e, Fig. 8.2d-f). Thus, just because studies of pairwise interactions among invaders find evidence of negative interactions (Kuebbing and Nuñez, 2015), these direct pairwise negative interactions may not manifest as non-native biotic resistance when those same two species are also interacting with other species (Ricciardi, 2001; Kuebbing and Nuñez, 2016). Ignoring the larger interaction web of co-occurring native and non-native species may inadvertently deemphasize the importance of indirect interactions and may potentially mask 'invasional meltdowns' occurring through positive indirect effects among non-natives. Thus, to truly assess the invasional meltdown paradigm, we need to consider how direct and indirect interactions in ecological communities comprised of many interacting non-native and native species shape invasion patterns and ecological impacts of non-native species.

8.14   Conclusions and Management Implications

The Invasional Meltdown Hypothesis was originally introduced as an alternative paradigm to a biotic resistance model of invasion (Simberloff and Von Holle, 1999). In a biotic resistance scenario, the probability of invasion by a non-native
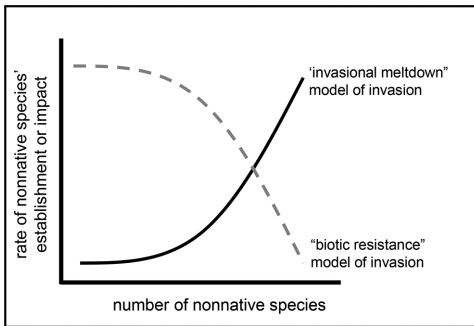
Fig. 8.3. The concept of invasional meltdown was originally proposed as an alternative to a biotic resistance model of invasion. As communities accumulate non-native species, resident non-native species could either facilitate or inhibit the establishment, population growth or spread of newly invading non-native species. In a biotic resistance invasion model, antagonistic interactions among non-natives would decrease the rate or probability of invasion by a new non-native (dashed line). In an invasional meltdown model, facilitative interactions among non-natives would increase the rate or probability of invasion by a new non-native (solid line).

species should become progressively *less* likely with an increasing number of non-native species in a community (Fig. 8.3). In an invasional meltdown scenario, the probability of invasion by a non-native species should become progressively *more* likely with an increasing number of invasive species in a community (Fig. 8.3). Differentiating between biotic resistance and invasional meltdown models is imperative for informing management decisions. For example, if non-native species are likely to repel other invaders, a manager may decide to allow a current non-native species to persist to decrease the likelihood of invasion by a potentially more damaging species. However, if non-natives are likely to promote the invasion of other non-natives, the removal of non-natives from the ecosystem may become a high priority for preventing a rapid accumulation of more non-natives.

Interestingly, current management of non-native plant species may provide evidence for determining whether plant invasions are hindered or facilitated by other non-natives. Frequently, the removal of a dominant non-native plant is followed by the invasion of another non-native plant

and not the recovery of native plants (Kettenring and Adams, 2011; Pearson *et al.*, 2016a). This phenomenon has been termed a 'secondary invasion' (Pearson *et al.*, 2016b) or 'invasion treadmill' (Thomas and Reid, 2007) and suggests that non-native plants are suppressing or competitively excluding other non-native plants from that community. At face value, this supports the biotic resistance paradigm. However, there is abundant evidence that native plants are *also* competitively suppressed by non-native plants (Vilà and Weiner, 2004; Kuebbing and Nuñez, 2016), yet native plants typically do not increase in abundance after removal of dominant natives (Kettenring and Adams, 2011; Pearson *et al.*, 2016a). Native plants may be limited by the size of their soil seed banks, dispersal ability or other disturbances that exclude them from the ecosystem. Another plausible hypothesis is that dominant non-native invasive plants are competitively suppressing resident native and non-native plants, but the strength of this competitive suppression differs between non-natives and natives (Kuebbing and Nuñez, 2016). In other words, native plants may be indirectly facilitating the co-occurrence of multiple non-natives by mediating competitive interactions between non-natives (Stone and Roberts, 1991; Miller, 1994; Flory and Bauer, 2014; Northfield *et al.*, 2018). Under this scenario, you would still see the same pattern of secondary invasions and limited response of natives, but the net community effect would be promotion of multiple invasive plant species.

Preventing invasional meltdowns should be a top management priority. Yet, extracting management recommendations from this collection of examples is challenging because of the wide variety of ways non-native species may interact with one another. However, a few trends emerged from these examples that may reduce the likelihood of plant invasional meltdown:

- *Prevent the introduction of plant soil microbial mutualists:* a major pathway of plant microbes is the live-plant trade, which can introduce plants with their mutualist soil organisms that could facilitate their invasion or soil pathogens that could 'spill over' to infect native species (Liebhold *et al.*, 2012). It seems prudent to reduce, cautiously monitor or prohibit live-plant imports that vector soil microbes.

- *Prioritize prevention, early detection and control of 'repeat offenders':* there are some non-native taxa that are implicated in facilitative plant interactions in many different ecosystems around the globe. Some of the most frequently cited species in plant invasional meltdowns include the generalist pollinators European honeybee (*A. mellifera*) and bumblebee (*Bombus* spp.), ecosystem-modifying non-native earthworms and wild boar (*S. scrofa*), the widespread seed-dispersing songbirds the Japanese white-eye (*Zosterops japonicus*) and common bulbul bird (*P. jocosus*), as well as 'indirect mutualists' like the Argentine ant (*L. humile*).
- *Prioritize early detection of non-native plants that cannot spread because they lack their mutualists:* the vast majority of the global naturalized non-native flora are grown in domestic and botanical gardens (van Kleunen *et al.*, 2018). These cultivated plants provide an opportunity to test the likelihood a species may spread beyond their cultivated boundaries. If non-native plants are severely pollen-limited – suggesting they lack the necessary native pollinator mutualism – these plants could be prioritized for removal before a non-native pollinator is introduced (Bufford and Daehler, 2014; Moodley *et al.*, 2016).
- *Disrupt mutualisms to improve management efficacy:* there are many non-native plant mutualists, like introduced honeybees and bumblebees, that facilitate plant invasion. While complete eradication of these agriculturally important pollinators may be unrealistic, a reduction in their population sizes could facilitate non-native plant management. For example, in New Zealand, the efficacy of a seed-feeding biocontrol beetle (*Bruchidius villosus*) on the non-native Scotch broom (*C. scoparius*) increased when beehives were removed

from fields near Scotch broom populations (Paynter *et al.*, 2010). Together, reduced mutualism and increased seed predation more effectively managed broom populations.

- *Manage more than one species at a time:* there is growing evidence that the removal of one non-native allows other non-natives to invade or increase in abundance (Courchamp *et al.*, 2011; Ballari *et al.*, 2016; Pearson *et al.*, 2016b). Unless interactions among multiple non-native species within a community are well-known, managers should be prepared for 'surprise effects', 'secondary invasions' or 'invasion treadmills' after management. When possible, managing multiple non-native species could reduce the likelihood of these adverse management outcomes.
- *Combine management and research more effectively:* removal experiments of non-native plants may be a potentially powerful means to test direct and indirect interactions within invaded communities. Removal experiments are used to understand species interactions in natural communities (Schmitz, 1997; Vázquez *et al.*, 2015; Kumschick *et al.*, 2015; Novak *et al.*, 2016) and may be particularly useful for invasion biology for a few of reasons. First, ethical issues surrounding introducing or manipulating non-native populations in natural communities is a limitation in invasion biology research. Removal experiments are the natural foil to introduction experiments and provide an ethical alternative to this problem. Second, non-natives are frequently removed by land managers concerned about non-native species in their conservation areas. Invasion biologists could capitalize on these removals by partnering with land managers to design experiments that both reduce the non-native abundance and teach us about non-native interactions.

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