Successful Invasions and Failed Biocontrol: The Role of Antagonistic Species Interactions

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Understanding the successes and failures of nonnative species remains challenging. In recent decades, researchers have developed the enemy release hypothesis and other antagonist hypotheses, which posit that nonnative species either fail or succeed in a novel range because of the presence or absence of antagonists. The premise of classical biological control of invasive species is that top-down control works. We identify twelve existing hypotheses that address the roles that antagonists from many trophic levels play during plant and insect invasions in natural environments. We outline a unifying framework of antagonist hypotheses to simplify the relatedness among the hypotheses, incorporate the role of top-down and bottom-up influences on nonnative species, and encourage expansion of experimental assessments of antagonist hypotheses to include belowground and fourth trophic level antagonists. A mechanistic understanding of antagonists and their impacts on nonnative species is critical in a changing world.

Keywords: antagonists, enemy release hypothesis, natural areas, trophic interactions, unifying framework

Invasive species, including the invasive terrestrial plants and insects that are the focus of this review, have been a key research topic since Elton (1958). Because of the significant ecological and economic impacts invasive plants and insects have on natural and managed systems, many invasion ecologists recognize the importance of understanding the mechanisms that facilitate or constrain invasion of nonnative species (Liu and Stiling 2006). The topics emphasized by Elton (1958) have been thoroughly explored over the last six decades, in an effort to understand why some nonnative, putatively invasive, species fail, whereas others succeed (Richardson and Pyšek 2008). As a result, invasion ecologists have proposed over 29 leading hypotheses to explain potential mechanisms that contribute to a nonnative species transforming into a burgeoning invader (Colautti et al. 2004, Catford et al. 2009).

Many hypotheses attribute invasion success to the quantity and frequency of individual introductions of the invader (propagule pressure; Simberloff 2009), characteristics of the invader and its interactions with other organisms (e.g., predators and parasitoids, competitors, and mutualists) in the introduced range (biotic), characteristics of the introduced ecosystems (abiotic), or the influence of humans (anthropogenic) on these other factors (Catford et al. 2009). Of all invasion hypotheses, the enemy release hypothesis (ERH) remains one of the more straightforward

and innately appealing explanations for the success of nonnative, invasive species (Torchin et al. 2003, Colautti et al. 2004, Prior and Hellmann 2015) and is the most well known among research professionals (Enders et al. 2018). The term *enemy* or *natural enemy* is frequently used in the literature of the invasion ecology discipline to refer to an organism, such as an herbivorous insect, parasitoid, predator, or pathogen (i.e., fungus, bacterium, virus, etc.; figure 1), that decreases the fitness or reproductive potential, reduces population density, or causes direct or indirect mortality of another organism. Broadly, the term *enemy* refers to an antagonistic relationship between two individuals or species, but it can also imply an anthropocentric bias. Therefore, we use *antagonist* rather than *enemy* when possible. The ERH specifically outlines that, on arrival in the introduced range, nonnative founders may experience a decrease in regulation by specialist antagonists from the native range (figure 1), resulting in a rapid increase in distribution and abundance in the introduced range (Keane and Crawley 2002). Traditional views of the ERH advocate that the lack of specialist antagonists in the introduced range allows nonnative species to successfully establish and invade (Keane and Crawley 2002), although, in this review, we propose that this hypothesis may also explain how biological control agents can fail to establish and successfully control target nonnative, invasive species.
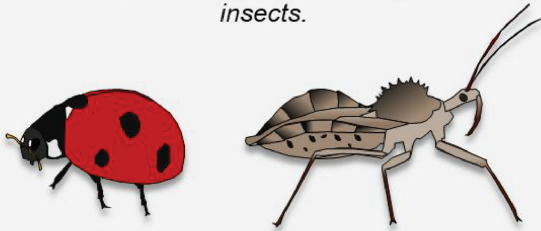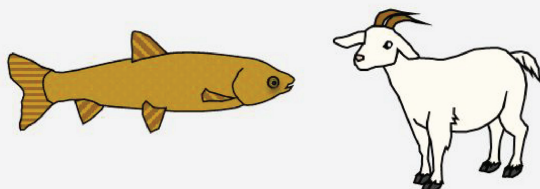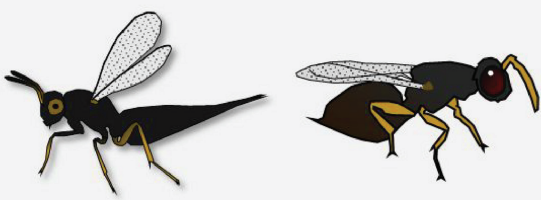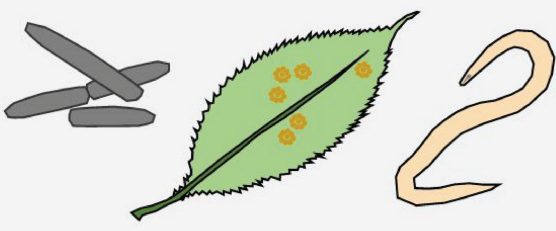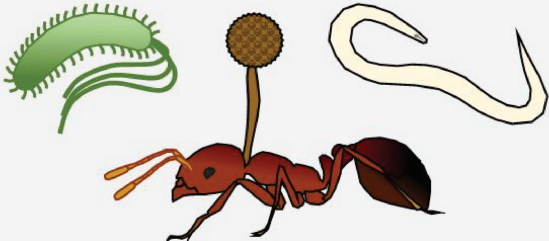
Nonnative, invasive plants	**Nonnative, invasive insects**
Phytophagous Arthropods *Phytophagous arthropods include insects and other arthropods that feed on plant material (i.e., leaves, roots, stem, seeds, flowers). They are sometimes effective biological control agents for plants.*	**Predators** *Predatory insects, such as lady beetles, kill and feed on other insects, such as herbivorous aphids. Generalist predators prey on other predacious insects.*
Herbivorous Vertebrates *Herbivorous vertebrates are animals that consume plants, often whole, rather than individual parts of the plants. They can be effective biological control agents for plants in small patches.*	**Parasitoids and Hyperparasitoids** *Parasites, or parasitoids, are organisms that live and feed in or on a host. Hyperparasitoids parasitize and sometimes kill other parasitoids.*
Pathogens *Bacteria, fungi, nematodes, and viruses are microorganisms that can infect and help reduce populations of nonnative plants.*	**Pathogens** *Bacteria, fungi, nematodes, protozoa, and viruses are microorganisms that can provide control for populations of nonnative insects.*

The left-side row label reads: **Types of Antagonists**

Figure 1. Five major types of antagonists that may affect nonnative, invasive plants and insects.

It is thought that nonnative organisms must survive and overcome obstacles to succeed (see figure 2; Catford et al. 2009, Blackburn et al. 2011, Lockwood et al. 2013). We define invader success as establishment and spread within an introduced environment, not only resulting in species colonization but also causing negative ecological, economic, or social impacts in the introduced environment (stages 4 and 5 in figure 2; Colautti et al. 2004, Gurevitch et al. 2011). A nonnative organism fails to become invasive when it does not establish a robust population or when it establishes a self-sustaining population but regulating mechanisms in the introduced range limit its population density and expansion. In both failure scenarios, the population remains small and relatively unimportant, because the nonnative organisms do not cause observable or substantial impacts on a broad scale.

In the present article, we review a subset of the many invasion hypotheses that address native and introduced antagonists and the roles they play in the success or failure
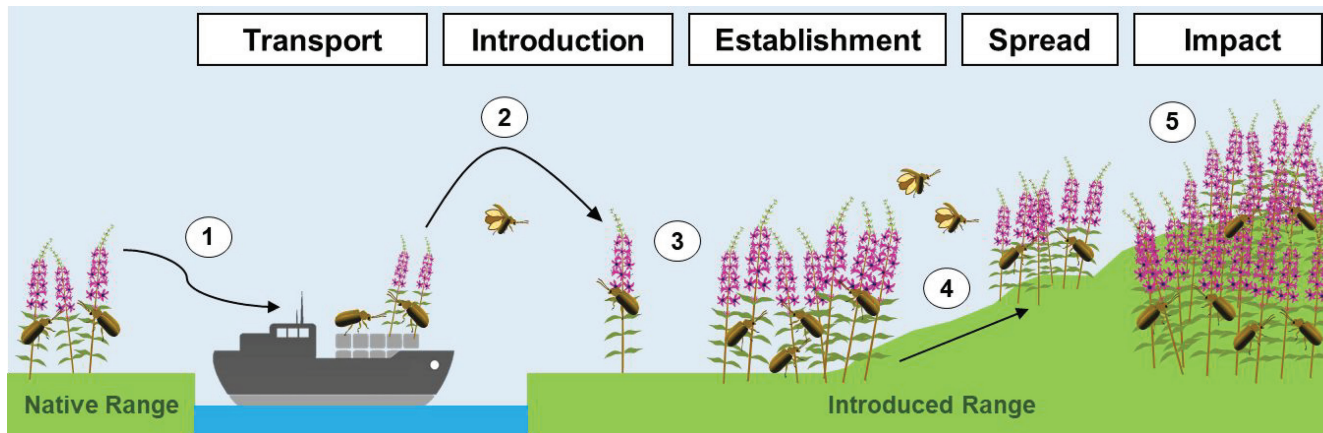
Figure 2. Five proposed stages of the invasion process in which a nonnative organism must: (1) be transported from the native range to an ecosystem outside of its native range (the introduced range); (2) survive the transportation process to become introduced into an area outside of its native range; (3) establish a reproducing population that survives any abiotic, biotic, or anthropogenic pressures present in the introduced range; and (4) spread to adjacent areas and establish new, reproducing populations. With sustained, unobstructed establishment and spread, a non-native organism can have an impact on local and/or regional ecosystems (5). The basis of this figure was derived from other papers that discuss the invasion process, including: Catford and colleagues (2009), Blackburn and colleagues (2011), Gurevitch and colleagues (2011), and Lockwood and colleagues (2013).

of nonnative species and biological control agents (antagonists that are deliberately introduced to control a nonnative, invasive species). Furthermore, we establish parallels between invasion ecology and classical biological control by illustrating how collaborative management approaches, with an understanding and sharing of both biological invasion and biological control research, may be particularly effective for study in natural systems.

What is known: Antagonist hypotheses. Through a review of the literature, we first identified twelve hypotheses that implicate antagonist effects as the major contributing factor to invasion success or failure (table 1). Ten of the selected twelve hypotheses are focused on how a lack of or a tolerance to antagonists or antagonists of biological control agents may help facilitate invasion. The ERH, also known as the herbivore escape, predator escape, and ecological release hypotheses, suggests that a nonnative species is facilitated by a complete release from their native-range specialist antagonists (Keane and Crawley 2002, Torchin et al. 2003). Release from antagonists may occur if a small subset of the native host population is introduced and that subset is not affected by antagonists, affected individuals perish during the transportation or introduction phases of species invasion, or Allee effects extinguish specialist antagonists when hosts are low in density during the initial stages of invasion (Torchin and Mitchell 2004, Yang et al. 2010, Roy et al. 2011). Some antagonists, such as insects and pathogens, may also rely on specific environmental conditions or multiple hosts to complete their life cycle. As a result, antagonist survivability is dependent on the abiotic and biotic conditions of the introduced range, where climate (abiotic) or

alternative host-species availability (biotic) can directly contribute to the success or failure of nascent migrants (Torchin and Mitchell 2004, Catford et al. 2009, Roy et al. 2011). In addition to release from antagonists from the native range, invaders may also escape detection or repel antagonists in the introduced range via novel weapons (Callaway and Ridenour 2004), which may facilitate their invasion in the introduced region (Suttle and Hoddle 2006, Roy et al. 2011). For enemy release to be the main contributing factor for invader success, specialist antagonists must limit a species in its native range (Keane and Crawley 2002, Prior and Hellmann 2013, Prior and Hellmann 2015). If antagonists are an important mechanism of control in the native range and antagonists in the introduced range have limited or no impact on the invader compared with the antagonists in the native range, then release from antagonists can be considered a facilitative effect that increases the success of the invader (Colautti et al. 2004, Prior and Hellmann 2015).

In this article, we present the ERH as our main, overarching hypothesis. The ERH has historically been the most cited hypothesis and explicitly implicates the role of antagonists and their interactions contributing to invasion success. We categorize the other related antagonist hypotheses into more specific subhypotheses of the ERH, which will shed light on the lesser known—but more realistic—antagonist hypotheses (Heger and Jeschke 2014; table 1). Ten of the subhypotheses in this framework we have developed focus on enemy release. Of these subhypotheses, the enemy reduction hypothesis is perhaps the most similar to the ERH (Enders et al. 2018). The enemy reduction hypothesis suggests that some nonnative, invasive species are more successful in their introduced range because they have benefited from a partial

Table 1. Hypotheses in invasion biology that relate to effects of antagonists.

Hypothesis	Description	Effect*	Example	Key references
Biotic interference	Biotic resistance against biological control agents, which benefits the invasive species	+	The cinnabar moth (*Tyria jacobaeae*) was introduced to control tansy ragwort (*Senecio jacobaea*), but failed due to predation by a variety of antagonists	Goeden and Louda 1976, Heimpel and Mills 2017
Biotic resistance	Antagonists in the introduced range impede invasion	–	Native crayfish fed on exotic plants more than native plants	Levine et al. 2004, Parker and Hay 2005
Enemy escape	Rapid population growth after strong reduction in enemy regulation following natural range expansion, host phenological changes, or defensive innovation	+	Monophagous antagonists (e.g., parasites, pathogens, insects) may not be able to expand their range as fast as or faster than their hosts, so they may lag behind	Mlynarek et al. 2017
Enemy inversion	Antagonists are also introduced into the new range, but are less effective in the new biotic and abiotic conditions	+	The cointroduced parasite, *Clausenia purpurea*, was able to control introduced Comstock mealybug (*Pseudococcus comstocki*) populations except in populations with native hyperparasitoids	Colautti et al. 2004
Enemy of my enemy or accumulation of local pathogens	Antagonists (e.g., generalist pathogens) limit native species more than invasive species	+	Invasive *Ammophila arenaria* accrues local pathogens, which limits its abundance but also results in the exclusion of native plant species	Colautti et al. 2004, Eppinga et al. 2006
Enemy reduction or loss	Invaders benefit from a partial, but not complete, release from antagonists	+	The total number of parasite species of *Solenopsis invicta* is lower in introduced areas	Colautti et al. 2004, Yang et al. 2010, Prior and Hellmann 2013
Enemy release	The invader is completely released from the antagonists that limit its population in its native range	+	*Silene latifolia* escaped a suite of antagonists in its native range, such as aphids, fruit predators, and smut fungus	Keane and Crawley 2002, Blair and Wolfe 2004
Enemy resistance or novel weapons†	Invaders are more likely to possess traits (e.g., secondary compounds) that are not found in native congeners and reduce the preference or performance of antagonists	+	*Mamestra brassicae* herbivores that fed on exotic *Solidago* had significantly lower relative growth than herbivores that fed on native *Solidago*, because the exotic *Solidago* have more unique metabolites and defenses than native *Solidago*	Cappuccino and Arnason 2006, Macel et al. 2014
Enemy tolerance	Invaders cannot escape all antagonists, so they maintain reproductive fitness by becoming tolerant of damage from antagonists	+	Invasive vines are not escaping herbivory in their introduced range, but tolerate herbivory by having higher growth rates, and shifts in root-shoot allocation	Ashton and Lerdau 2008
Evolution of increased competitive ability	Release or reduction of antagonists that limit the invader in its home range enables the invader to allocate more energy to growth and reproduction	+	*Acacia longifolia* (native to Australia, introduced to South Africa) produces more seeds in South Africa than Australia	Blossey and Nötzold 1995
New associations	Invaders do not have the appropriate defense mechanisms to defend against noncoevolved antagonists	+/–	*Opuntia inermis* and *Opuntia stricta* were successfully controlled by *Cactoblastis cactorum*	Pimentel 1963
Resource-enemy release†	Fast-growing species adapted to high resource availability experience stronger enemy release than slow-growing species adapted to low resource availability	+	Invaders in mesic and nitrogen-rich environments were released from more pathogen species than invaders in xeric and nitrogen-deficient environments	Blumenthal 2006

*Effects of antagonists that facilitate (+) or inhibit (–) invasion. Hypotheses denoted with † represent bottom-up pressures, while all other hypotheses represent top-down pressures. *Source:* Adapted from Catford and colleagues (2009).

release from antagonists (e.g., Yang et al. 2010), whereas the ERH suggests that the invader benefits from an absence (or seeming complete release) of antagonists. Some researchers have argued that having these as two distinct hypotheses is pedantic, whereas other researchers (e.g., Catford et al. 2009, Enders et al. 2018) acknowledge the difference and seem to perceive the difference to be substantial enough to distinguish between the two hypotheses in the literature.

Building on the enemy reduction hypothesis is the enemy tolerance hypothesis, which proposes that, when some nonnative species cannot escape their antagonists, they become

tolerant to the damage or negative impact inflicted by antagonists (Ashton and Lerdau 2008). In some cases, nonnative species will even use their tolerance to accrue antagonists (the enemy of my enemy hypothesis), especially pathogens, which helps them reduce populations of competing native species (e.g., Eppinga et al. 2006). If a nonnative species is not able to simply tolerate its antagonists, the enemy resistance hypothesis suggests that some nonnative species have been documented to possess or develop defensive traits, such as secondary chemical compounds or mechanical defenses, that help them defend against or reduce the preference or

performance of potential antagonists (e.g., Cappuccino and Arnason 2006, Macel et al. 2014). Along these same lines, the enemy escape hypothesis proposes that after some species evolve to develop new defenses, change their phenology, or expand their range to follow their hosts or damage new hosts, the species may benefit from a reduction in antagonists (e.g., Mlynarek et al. 2017). In other words, new defenses help the species actively repel antagonists, whereas a change in phenology or range expansion will help the species temporally or spatially evade antagonists.

In some cases, nonnative species may benefit from more than just enemy release. The resource-enemy release hypothesis specifically indicates that nonnative species that are fast growing (*r*-selected) and accustomed to high resource availability may benefit more from enemy release than slow-growing (*K*-selected) species that are adapted to low resource availability (Blumenthal 2006). In other words, if the nonnative species is released from antagonists, its success increases with the availability of resources in the environment. Similarly, the evolution of increased competitive ability hypothesis proposes that release from antagonists allows nonnative species to allocate more resources to gains in fitness, such as growth and reproduction, which improves their competitive ability against native congeners (Blossey and Nötzold 1995).

In other systems, the nonnative species may be introduced with some of the antagonists from their native range, but the antagonists are less effective because of differences in abiotic (e.g., climate) and biotic (e.g., intraguild competitors, increased antagonists) conditions compared with the native range (Colautti et al. 2004). This is often referred to as the enemy inversion hypothesis (Colautti et al. 2004). More specifically, the biotic interference hypothesis indicates that some antagonists that are introduced as biological control agents are less effective because higher trophic level antagonists in the introduced range attack the biological control agent, which prevents it from establishing and becoming a self-sustaining population and, therefore, fails as an effective method of control (Goeden and Louda 1976).

The last two hypotheses included in our framework explain invasion inhibition and, as a result, seem to be the least similar to the ERH. The biotic resistance hypothesis, which is similar to the biotic interference hypothesis, suggests that the presence of competitors and antagonists in the introduced range are demonstrable obstacles to successful invasion (e.g., Levine et al. 2004, Parker and Hay 2005, Hogg et al. 2014), whereas the new associations hypothesis submits that nonnative species do not possess adequate defense mechanisms to defend against antagonists that were either introduced from another region other than their native or introduced range or are native in the region to which the nonnative species has been introduced (Pimentel 1963; table 1). Both hypotheses are discussed in more detail in subsequent sections.

In classical biological control (also known as importation or traditional biological control), nonnative species are reunited with former antagonists. These former antagonists are collected from the native ranges of both the nonnative species and biological control agents (e.g., Toland et al. 2018). The premise for this selection is that antagonists from the native range of the nonnative, invasive host species have likely coevolved with the host pest, so they would be effective at searching for, finding, and attacking the host pest (Eilenberg et al. 2001). Although the field of biological control has largely been based on classical biological control, other approaches of control have been developed, including inoculation biological control, inundation biological control, and conservation biological control (Eilenberg et al. 2001, Heimpel and Mills 2017). One lesser known approach to biological control was proposed by the new associations hypothesis, which suggests that parasitoids and predators in the native range can coevolve with their prey in such a way that they become less effective biological control agents over time (Pimentel 1963). The new associations approach to biological control involves two types of antagonists: antagonists native to the introduced range of the nonnative, invasive species (e.g., Duan et al. 2015) and antagonists collected from regions separate from the native and introduced ranges of the nonnative species (e.g., Liu 2019). The premise of this approach is that antagonists from other host or prey associations may be more successful and may maintain control for longer periods of time (Hokkanen and Pimentel 1984). The new associations hypothesis also suggests that invasion can be facilitated if the invading species forms a relationship with a coexisting native species in the introduced range or if the native species are unable to compete with the invader, thereby enhancing invasion success (Colautti et al. 2004). The new associations hypothesis is similar in concept to the defense-free space (Gandhi and Herms 2010) and host naïveté (Woodard et al. 2012) hypotheses. These hypotheses address the lack of a coevolutionary history between a nonnative species and its host in the introduced range, which leaves the host defenseless or with a low level of resistance to the nonnative species (Gandhi and Herms 2010). As a result, the nonnative species is then more able to devastate populations of the host and successfully invade widely in the introduced range.

Another hypothesis in which the role of antagonists in biological invasions is considered includes the sampling hypothesis, in which invasion success depends on an invader being a better exploiter of resources or a better avoider of antagonists than the native species (Crawley et al. 1999). The sampling hypothesis is consistent with the competitive exclusion principle (Hardin 1960) and the resource competition theory (Tilman 1982). Finally, the specialist–generalist hypothesis suggests that invasion success is maximized when antagonists in the introduced range are specialists and, therefore, unable to prey on introduced species, and native mutualists are generalists and help further facilitate invasion (Callaway et al. 2004). In the present article, we review these 12 hypotheses and the respective roles antagonists play from multiple trophic levels. We propose a more streamlined,

unifying framework to improve insights into the numerous antagonist hypotheses. Finally, we explain how each subhypothesis contributes to an improved understanding of biological invasions and appropriate selection, introduction, and expectations of biological control.

The significant players: The role of antagonists in invasion. The process of invasion involves many mechanisms that affect the failure or success of nonnative species, including but not limited to niche opportunities, propagule pressure, biotic interactions, and abiotic conditions (Prior and Hellmann 2015). Prior to the green world hypothesis, which brought attention to the role of top-down pressures on regulating community composition (Hairston et al. 1960), the prevailing idea was that communities were controlled from the bottom up. In other words, populations of organisms, such as phytoplankton and plants (primary producers), are largely regulated by nutrient availability (McQueen et al. 1989), affecting productivity at higher trophic levels. After development of the green world hypothesis (Hairston et al. 1960), as well as the many invasion hypotheses that have been developed to explain top-down pressures (table 1), we now know that top-down pressures also influence the success or failure of nonnative species, both undesirable invaders and desirable biological control agents. It is now understood that both bottom-up and top-down pressures are important to consider simultaneously (Walker and Jones 2001). If a nonnative species can overcome the pressures and obstacles it encounters along the way to establishment and spread, then it will become successful; if not, it fails.

Past research on antagonists focused predominantly on the lack of specialist antagonists in the introduced range contributing to the success of an invasive species (Keane and Crawley 2002, Prior and Hellmann 2015). Support for the ERH can be found in many plant and insect studies (e.g., Colautti et al. 2004 [lists studies in support of ERH], Agrawal et al. 2005, Meijer et al. 2016). For example, Agrawal and colleagues (2005) studied a variety of nonnative plant species and their native conspecifics and were able to show that, on average, the nonnative plants experienced less insect herbivory and were subject to half the negative soil microbial feedback when compared with native plants in their home ranges. Furthermore, the native plants were more vulnerable to attack by fungal and viral pathogens or benefit less from beneficial microbes when compared with the nonnative plants (Agrawal et al. 2005).

It has been argued that many of these studies do not rigorously test the ERH, but accept enemy release as the driving force for invader success based solely on the lack of antagonists in the introduced range (Prior et al. 2015). For enemy release to truly facilitate success, the invader must be suppressed by antagonists in its native range, and the antagonists must have a lesser effect on an invaders' fitness in the introduced range than in the native range (Prior and Hellman 2015). Experimental testing of the ERH should include parallel experiments in the native and introduced ranges of the nonnative species in question to more clearly support enemy release as the major contributing driver (Williams et al. 2010, Prior and Hellmann 2013, Colautti et al. 2014). In Williams and colleagues (2010), the researchers experimentally manipulated phytophagous insect pressure and created small-scale disturbances in three introduced populations of houndstongue (*Cynoglossum officinale*) in Montana and three native populations of houndstongue in Germany to determine how herbivorous insects affected the performance of houndstongue (Williams et al. 2010). They found that the herbivorous insects in the native range reduced houndstongue size and fecundity but had little effect on plant fitness in the introduced range (Williams et al. 2010). By testing antagonist impact in the native and introduced ranges simultaneously, the researchers were able to conclude that enemy release does have a role in facilitating invasion in this study.

The ERH is not only limited to studies that focus on nonnative species, but has also been applied to native species with expanding ranges (Prior and Hellmann 2013, Mlynarek 2015, Mlynarek et al. 2017). The oak gall forming wasp (*Neuroterus saltatorius*) was discovered in both natural and experimental settings to have greater fitness and fewer parasitoids in its new, expanded range on its host, *Quercus garryana* (Prior and Hellmann 2013). It is interesting to note that their results supported enemy reduction—not enemy release—because observational surveys indicated that the overall parasitoid attack rates were lower in the expanded range, even though the parasitoids did not limit populations of the oak gall forming wasp in its native range (Prior and Hellmann 2013). Prior and Hellmann (2013) also found that reduction in antagonistic species was not the only factor driving success of the gall wasps; environmental conditions likely contributed to demographic success and possibly host ecotype naïveté, because the gall wasps were not previously known to the host individuals in the expanded range. Some researchers, such as Mlynarek (2015), have erroneously interpreted the results from Prior and Hellmann (2013) as full experimental support for the ERH. Many authors demonstrate a reduction of antagonistic species without actually demonstrating a complete release from antagonists in the native range but consider these situations consistent with full enemy release. Other research suggests that, in addition to or instead of enemy reduction, some invading species have a resistance to or tolerance of antagonists in the introduced range (Ashton and Lerdau 2008). More recently, this disruption in antagonist regulation due to natural range expansion, host phenological changes, and defensive innovation has been referred to as enemy escape (Mlynarek et al. 2017).

Although the ERH is widely cited as the main explanation for the success of introduced species, naturalization at low abundance or failure of an introduced species has been attributed to biodiversity at the site of introduction or density of congeneric species (Heimpel and Mills 2017). In invasion ecology, this concept is known as the biotic resistance hypothesis, but it has also been referred to as the
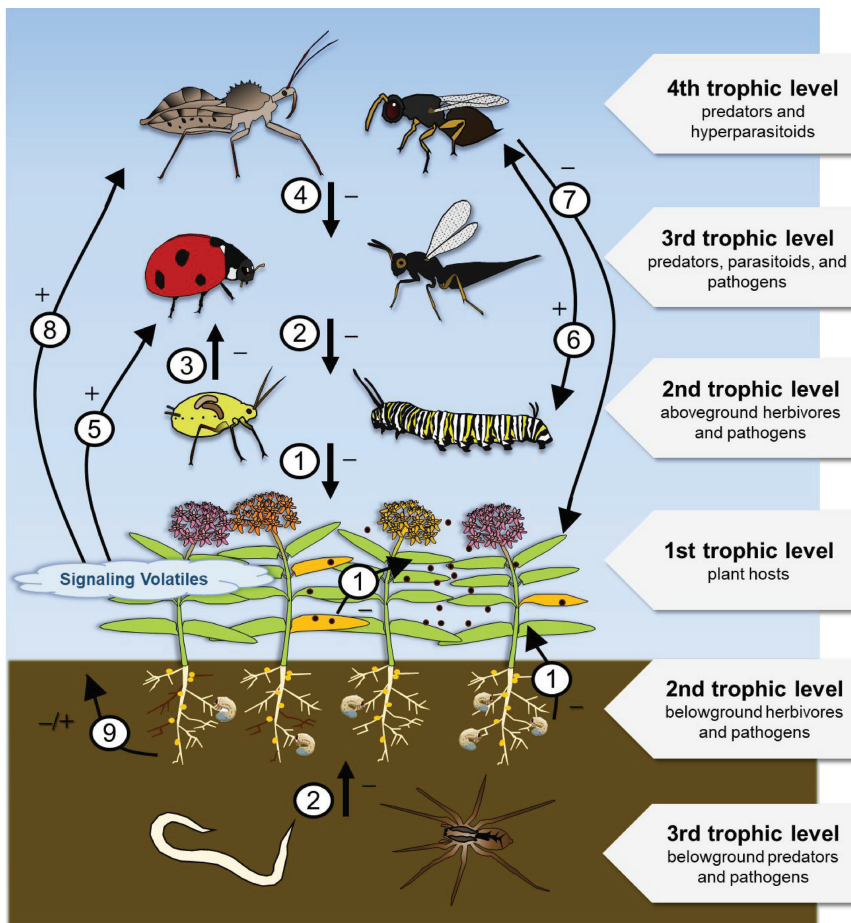
Figure 3. Four trophic levels are involved in the success or failure of a nonnative species or biological control agent. Herbivores and pathogens in the aboveground (e.g., aphids and fungi) and belowground (e.g., beetle larvae and plant-pathogenic nematodes) second trophic levels feed on plants in the first trophic level (1). Phytophagous insects can be parasitized or preyed on by the aboveground and belowground (e.g., entomopathogenic nematodes and spiders) third trophic levels (2). Some phytophagous insects contain endosymbionts that help them defend against predators and parasitoids in the third trophic level (3). Fourth level hyperparasitoids and generalist predators find their primary parasitoid and predator hosts in the third trophic level (4). Herbivory induced volatiles produced by some plants, signal presence of specific prey to predators or parasitoids, benefiting the plant (5; Dicke and Baldwin 2010). Similarly, some herbivores can produce stress pheromones that attract hyperparasitoids to parasitize primary parasitoids, benefiting the herbivore (6; Poelman et al. 2012). By assisting the herbivore, the hyperparasitoid can indirectly negatively affect the plant (7). Hyperparasitoids may also notice changes in plant volatile emissions as an indicator of their hosts' presence (8), which would benefit the hyperparasitoids and herbivores, and negatively affect the parasitoids and plants. Plant populations may also be controlled by nutrient and mycorrhizal deficiencies that have a bottom-up effect (9). Beneficial soil organisms, such as nonpest insects and nonpathogenic fungi and bacteria, can also benefit plants by improving soil health (9).

diversity resistance hypothesis (Kennedy et al. 2002) and as the diversity–invasibility hypothesis (Tilman 1999), and it is similar to the fluctuating resource theory of invasibility proposed by Davis and colleagues (2000). The biotic

resistance hypothesis suggests that failure occurs because strong biotic interactions with native or other nonnative species (through fortuitous biological control) hinder the establishment and spread of the introduced species (Maron and Vilà 2001). Kennedy and colleagues (2002) found that species diversity helped increase invasion resistance by increasing species density and richness, whereas Funderburk and colleagues (2016) found that native predators, along with other competing insects, limited the invasiveness of western flower thrips (*Frankliniella occidentalis*) in Florida. It has been argued that biotic interactions with native organisms rarely make communities completely resistant to invasion; instead, the biotic interactions only limit the abundance of invasive species once they have successfully established (Levine et al. 2004). In short, the biotic resistance hypothesis is the counterpoint to the ERH, because biotic resistance helps explain how invasions fail, whereas the ERH helps explain how invasions succeed (see Heimpel and Mills 2017 for more on the relationship between biotic resistance and the ERH).

Why does biological control fail? The role of antagonists in biological control. The entire field of classical biological control is built on the premise that antagonists can control populations of the next lowest trophic level. For example, phytophagous insects and plant pathogens in the aboveground and belowground second trophic level may be considered for use in the control of nonnative, invasive plants in the first trophic level, whereas predators, pathogens, and parasitoids in the aboveground and belowground third trophic level may be considered for control of phytophagous insects (figure 3). These belowground second and third trophic levels are important considerations for control of some nonnative, invasive species (e.g., Marianelli et al. 2017), but they are sometimes overlooked (Harvey et al. 2010). A fourth trophic level includes more predators, as well as hyperparasitoids, which are a type of secondary antagonist that attacks the larvae and pupae of primary parasitoids (figure 3; Sullivan and Völkl 1999). If biological control agents never successfully controlled a target nonnative

species, we could easily dismiss the ERH and other hypotheses involving antagonistic interactions. However, because biological control agents have been reported to control some nonnative species, we know that these antagonists must be crucial, at least in the control of some invasions.

In the previous section, we focused on the research that has been conducted on nonnative species and the role that antagonists have had in the success or failure of invaders (figure 1). When it comes to biological control agents, research on the role of antagonists (native and introduced) in biological control agent success or failure in natural ecosystems appears to be less abundant or perhaps less published because of less funding than research concerning the role of antagonists in the success or failure of nonnative, invasive species in natural ecosystems. In cases in which biological control agents have had great success (see Stiling and Cornelissen 2005), the biological control agent effectively controls the population density of its host (nonnative, invasive species), ideally without causing any nontarget effects. If the host was effectively controlled by antagonists in its native range but was released of its specialist antagonists on arrival in the introduced range, the success of the biological control agent in controlling the host indicates that enemy release or enemy reduction is a likely, contributing factor influencing the success of the nonnative, invasive host species. Perhaps a less obvious contributor to biological control agent success is that threats to the intentionally introduced biological control agents from native or accidentally introduced antagonists may have been low (i.e., the biological control agents were released from their antagonists; Heimpel and Mills 2017). In these cases, the biological control agents flourished, possibly because of a lack of top-down pressure from antagonists or a lack of bottom-up pressure from hosts that have well-developed defenses (Heimpel and Mills 2017). It has also been hypothesized that, in the absence of enemy release, some biological control agents may benefit from a release from competitors (Denoth et al. 2002). Without competition or the simultaneous threat from their own antagonists, the biological control agents can establish high population densities and successfully control their respective hosts without demonstration of the ERH (Heimpel and Mills 2017). Finally, in the case of phytophagous biological control agents, success may be partially attributed to the abundance and high density of their nonnative plant hosts. The resource concentration hypothesis, developed by Root (1973), indicates that herbivores are more likely to successfully find and remain on hosts in dense stands. Because many nonnative plant species tend to form monocultures or nearly pure stands (e.g., purple loosestrife, *Lythrum salicaria*; Lavoie 2010), phytophagous biological control agents may have a better chance of successfully controlling their hosts than entomophagous biological control agents with moving prey.

A 1990s survey of biological control agent failures showed that recipient-range climate and a lack of alternative hosts, as well as predation or parasitism by native fauna (biotic interference; Goeden and Louda 1976, Heimpel and Mills 2017),

accounted for approximately 50% of biological control agent failure (Stiling 1993). Of these failures, predation and parasitism by generalist native fauna accounted for approximately 20% of failed biological control introductions (Stiling 1993), demonstrating that native generalist antagonists do play an important role in the success or failure of introduced biological control agents. In addition to potential predation and parasitism, biological control agents may fail because of competition or disruptive mutualisms between their host organism and another species in the introduced range. For example, some pests in Hemiptera (e.g., aphids) produce honeydew, which attracts ants that feed on the honeydew in exchange for protection from antagonists (Stadler and Dixon 2005). Plants have also been found to produce food for ants in exchange for protection from phytophagous insects and larger herbivores (e.g., elephants that browse on *Acacia* plants; Mayer et al. 2014). Biological control agents may also be controlled from the bottom-up in cases in which a host species has defensive endosymbiotic bacteria or fungi to protect them from potential antagonists. Many aphids contain heritable endosymbiotic bacteria, such as *Hamiltonella defensa*, to protect them from parasitoids (Rothacher et al. 2016), whereas some grasses contain endophytic fungi that produce alkaloid compounds (Clay 2014) or endophytic bacteria that produce cyanogenic compounds (Sorokan et al. 2017), which are a deterrent to herbivores. Although competitors and host mutualists may not be immediately detectable in the system in which the biological control agent is going to be released, they can deter an agent's success in controlling the target nonnative host species, so it is important to consider these complex associations when planning and executing a biological control program.

Biological control agent failure may also occur after a period of success if the host species evolves resistance to the controlling agent. Heimpel and Mills (2017) discussed evolved resistance to biological control agents, such as pathogens and parasitoids, in the context of entomopathogenic fungi–insect and insect–insect control systems. In some cases, the host being controlled will acquire an endosymbiont to help resist a biological control agent after years of successful control (e.g., Scarborough et al. 2005). Insect pests have been documented to develop genetically based resistance or change their behavior to avoid detection by other insect antagonists (e.g., Pascoal et al. 2014). Another study documented the larch sawfly (*Pristiphora erichsonii*), encapsulating the eggs and pupae of its parasitoid, *Mesoleius tenthredinis*, which then reduced the effectiveness of the parasitoid biological control agent (Muldrew 1953).

To promote the success of biological control agents, biological control practitioners seek to ensure that the introduced biological control agent is free from any of its own specialist antagonists prior to introduction into the introduced range (figure 2; Keane and Crawley 2002, Goldson et al. 2014). In rare cases, secondary antagonists (e.g., hitchhiking parasitoids, hyperparasitoids, predators, or pathogens) can be accidentally released with the biological

control agent host and cryptically inhibit its control success (e.g., Goldson et al. 2014). Secondary antagonists may also be accidentally introduced to the region after the biological control agents are released. For example, if a hyperparasitoid species successfully invades a new region along with or after its primary parasitoid prey (the presumed biological control agent), it could negatively affect the biological control agent and impede success of the release program. One example is in populations of *Eucalyptus* in New Zealand, in which the parasitoid, *Enoggera nassaui*, was deliberately introduced to control *Paropsis charybdis*, an herbivorous pest of *Eucalyptus nitens* (Murray and Mansfield 2015). The parasitoid controlled populations of *P. charybdis* for a few years until *Baeoanusia albifunicle*, an obligate egg hyperparasitoid, was self-introduced into New Zealand, likely wind dispersed from Australia (Murray and Mansfield 2015). After *B. albifunicle* and *Neopolycystus insectifurax*—an obligate egg parasitoid that directly competes with *E. nassaui*—were self-introduced, *E. nassaui* was found to be heavily parasitized, likely leading to disruption in *P. charybdis* control (Murray and Mansfield 2015). In all, there are few records of intentional or accidental secondary antagonist introductions, so these scenarios may be infrequent or cryptic. Given the high frequency of other accidentally introduced organisms becoming invaders, it is probable that secondary antagonist introductions occur more frequently than is readily recognized or reported (Murray and Mansfield 2015).

Introduced parasitoids (third trophic level; figure 3) and hyperparasitoids (fourth trophic level; figure 3) are not the only potential antagonists of nonnative species and biological control agents. Other examples of parasitism involve native parasitoids that affect the introduced biological control agents. In western Montana, thirteen species of phytophagous biological control agents that were released to control the invasive aster, *Centaurea stoebe*, were documented to be parasitized by nine different species of native parasitoids, with parasitism rates reaching as high as 100% (Herron-Sweet et al. 2015). In the northeastern United States, *Cyzenis albicans* was introduced as a biological control agent of winter moth (*Operophtera brumata*), but populations of the control agent were relatively slow to establish. Researchers detected a variety of predators and three genera of ichneumonid hyperparasitoids that preyed on and parasitized the released biological control agent, which reduced its overall success in controlling the undesirable winter moth (Broadley et al. 2018). These examples demonstrate that some introduced biological control agents face threats from native organisms at higher trophic levels, as well as those that occupy the same trophic level via intraguild and interguild predation and parasitism in both predator (Vance-Chalcraft et al. 2007) and parasitoid species (Cusumano et al. 2016).

The effects of introduced hyperparasitoids on biological control agents are mixed. There is some argument that parasitoids and hyperparasitoids disrupt the performance and effectiveness of predator and parasitoid biological control agents, respectively (Berry and Mansfield 2006). Declines

in herbivore parasitism have been quantitatively related to hyperparasitoid density, potentially because of primary parasitoids vacating those areas with high hyperparasitoid densities or suffering mortality from being parasitized by these hyperparasitoids (Höller et al. 1993). The contrasting argument is that hyperparasitoids can stabilize both coevolved and naive primary parasitoid populations by applying regulatory pressure on the primary parasitoids (Tougeron and Tena 2019). As a result, one might argue that it may be beneficial to have a hyperparasitoid introduced along with the nonnative parasitoid to maintain a balanced population density. Such an approach may help prevent the introduced parasitoids from having nontarget effects; however, a great deal of effort, time, and money are expended to seek and establish effective and appropriate biological control agents that must also not create nontarget impacts. Therefore, it may better serve the biological control release and establishment effort to leave the secondary antagonists behind, if and when possible, through sanitation.

Several of the examples above support the biotic interference and enemy inversion hypotheses, which are two key antagonist hypotheses that address the vulnerability of biological control agents to antagonists from their native or introduced ranges. This vulnerability of biological control agents to parasitism and predation by native, cointroduced, and subsequently introduced parasitoids and hyperparasitoids should be a concern for biological control researchers, especially if the nonnative biological control agents have been established for decades (Herron-Sweet et al. 2015). Hyperparasitoids have been reported to cue into plant-produced volatiles to find their primary parasitoid hosts (Poelman et al. 2012). If the hyperparasitoids are able to track and parasitize much of the primary parasitoid population or if the population leaves the region to escape hyperparasitoids (Höller et al. 1993), herbivore populations would then be released, thereby increasing the amount of damage to native plants (table 1). To accurately make predictions about the effects of antagonists on biological control agents and invasive species, it is essential to assess impacts within a multitrophic framework (Harvey et al. 2010), including belowground second and third (i.e., contained in the pedosphere; Agrawal et al. 2005) and aboveground fourth trophic levels (i.e., predators and hyperparasitoids; Gagic et al. 2011).

A proposed unifying framework for antagonist hypotheses. In the field of ecology, hypotheses are rarely expressed in absolute terms and are usually not immediately discarded when inconsistent data or conflicting observations emerge. These conservative techniques allow researchers to test many organisms in several situations, after which assessment of the overall usefulness and generalizability of the hypothesis can be made (Heger and Jeschke 2014). After more than six decades of research on enemy release, it is still difficult to determine whether the ERH is a useful hypothesis, because of the large amount of disagreement over its accuracy as the
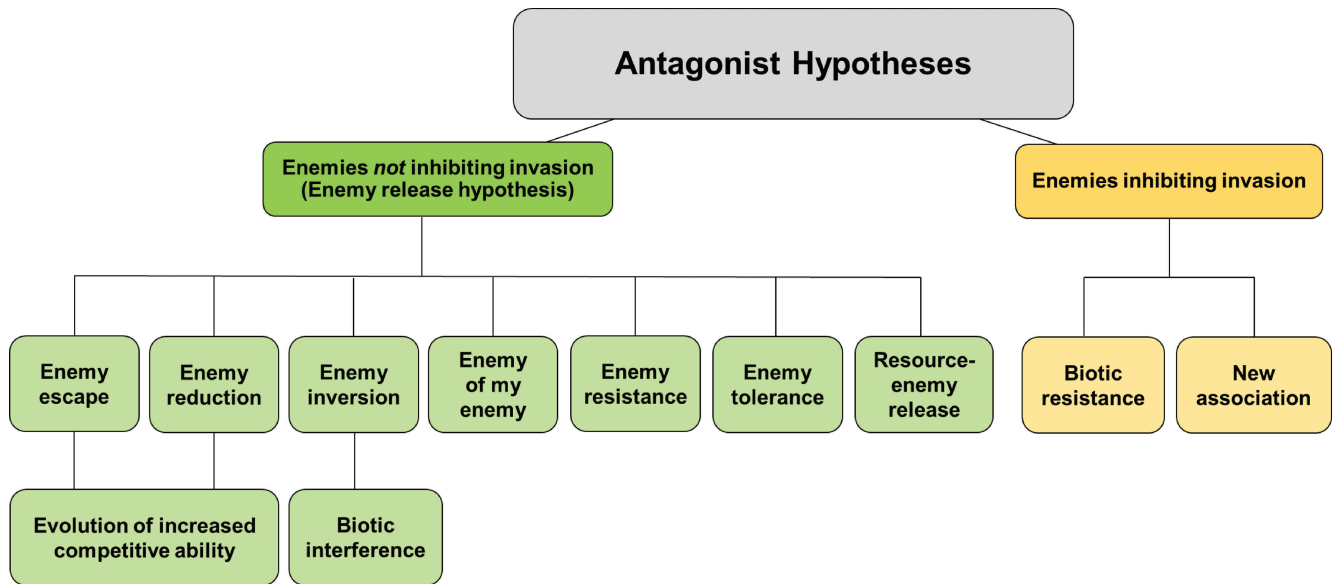
Figure 4. Framework of major antagonist hypotheses.

mechanistic explanation for nonnative species success or failure. Some researchers have shifted away from the ERH alone to evaluating more nuanced approaches and less absolute hypotheses, such as the enemy reduction hypothesis, which suggests that invaders succeed through reductions in antagonist populations rather than complete enemy release (Colautti et al. 2004). These nuanced and less absolute hypotheses are still derived from the ERH in some capacity. Meanwhile, because of the plethora of invasion hypotheses, some researchers refer to the enemy reduction hypothesis and other related hypotheses as the ERH (e.g., Yang et al. 2010), which lends support to place it as the overarching hypothesis that branches into other, more specific, and perhaps more useful, enemy subhypotheses (Heger and Jeschke 2014).

Following our review of the literature, we propose a unifying framework that includes many of the most commonly cited antagonist hypotheses (table 1, figure 4) and could be updated as researchers develop new or discard existing hypotheses regarding the specific roles that antagonists play in the success or failure of biological invasions and biological control agents. Our simplified framework includes subhypotheses that fall under two categories: hypotheses concerning antagonists not inhibiting invasion and hypotheses concerning antagonists inhibiting invasion (figure 4). We emphasize the importance of this framework not only for nonnative species but also for biological control agents. Similar frameworks have been proposed by Heger and Jeschke (2014; a hierarchy of antagonist hypotheses) and Heimpel and Mills (2017; a biotic resistance-ERH framework).

Antagonists, or a lack thereof, can influence the success or failure of nonnative species and biological control agents, because they are both introduced and subject to the same pressures and requirements to establish and develop self-sustaining populations. Therefore, if our end goal is to aid in the failure of nonnative species and the success of biological control agents, we should take antagonists at various trophic levels into consideration. To this end, we have combined the concepts from figure 3 and figure 4 to map the antagonist hypotheses that are most relevant to each of the four trophic levels discussed in this review (figure 5). Many of these hypotheses, such as biotic resistance, enemy escape, enemy reduction, enemy release, evolution of increased competitive ability, and new associations, can be applied to studies of plant hosts, as well as herbivores, predators, parasitoids, and hyperparasitoids. Other hypotheses are more specific and are only relevant to some of the trophic levels. For example, the enemy of my enemy, enemy tolerance, and resource-enemy release hypotheses are most relevant to nonnative plants, whereas the biotic interference and enemy inversion hypotheses are only relevant to biological control agents. Since plants are rarely used as biological control agents, these hypotheses are unlikely to apply. Finally, the enemy resistance hypothesis is most often documented in and relevant to nonnative plants (e.g., production of secondary compounds for defense) and herbivores (e.g., symbiotic relationship with endosymbiotic bacteria that help repel antagonists). This categorization of hypotheses by trophic level is intended to aid researchers in determining which antagonist hypotheses are relevant to the trophic levels of interest for their respective research systems.

We anticipate that our framework will help researchers of multiple disciplines better understand the vast ideological diversity that has formed around the role of antagonists in biological invasions and biological
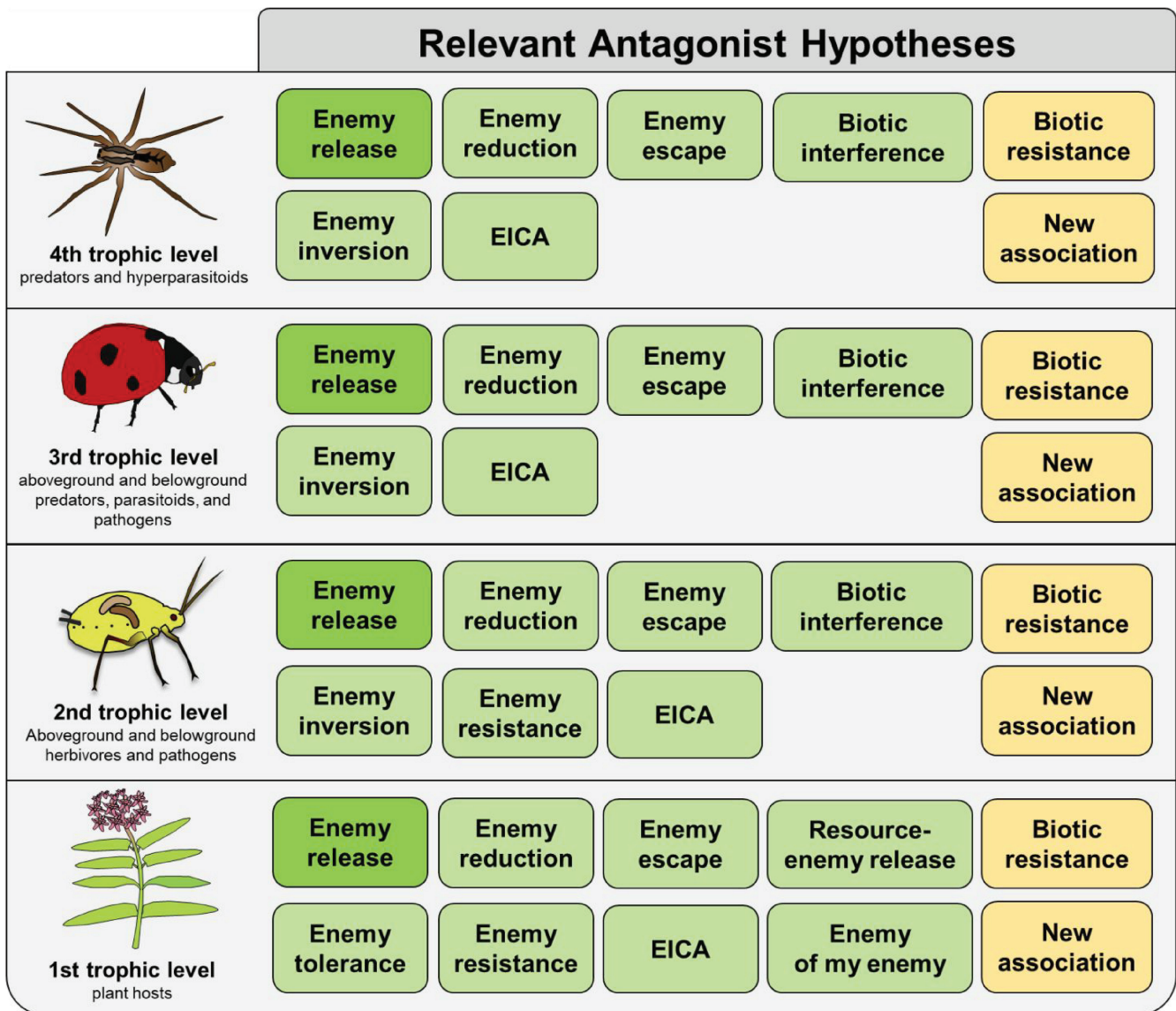
Figure 5. Antagonist hypotheses that are relevant to each of the four trophic levels included in this review. Abbreviation: EICA, evolution of increased competitive ability.

control. Although the ERH has long been the most referenced hypothesis concerning antagonists and invasion success, it is often not the best explanatory hypothesis because of its absolute nature. However, because of the wide recognition and absolute nature of the ERH, it may serve as a gateway to the many sub-hypotheses involving the role of antagonists in a more nuanced and complex manner, which is the nature of the systems we study. A unified summary of antagonist hypotheses will allow scientists to more easily reference and research more specific and suitable hypotheses, which will help researchers better pinpoint the specific mechanisms contributing to invasion success or failure. Future studies should be focused on testing multiple mechanisms of invasion to provide a clearer picture of invader success.

Conclusions

Many developed nations (e.g., New Zealand, the United States, and those of the European Union) have implemented policies and programs to detect and intercept potential invaders at airports and other ports of entry. Beyond prevention and early detection, rapid response requires the effort to control nonnative species when they become established but before they expand (Early et al. 2016). Without defined actions and approaches for each stage of the invasion process, there is the threat that founding nonnative species populations can then become so expansive as to prevent eradication (Lockwood et al. 2013). Invasive species, and their present-day global interchange, will continue to threaten our ecosystems, affecting people and our economic resources. Researchers continue searching for ways to improve strategies to strengthen

defenses against, as well as provide innovative insights and approaches to our detection and management of, invasive species. To do so, we must consider the complexity of species invasions, the multiple mechanisms of invasion, and many other potential contributors to invader success (Catford et al. 2009, Gurevitch et al. 2011, Lau and Schultheis 2015, Prior et al. 2015). In general, most experimental studies only assess one mechanism and frequently, only one focal invader, in evaluating invasion success. In some cases, mechanisms of invasion act synergistically (Lau and Schultheis 2015). For example, a direct, synergistic link can be found in invasions that follow the structure of the resource-enemy release hypothesis (Blumenthal 2006), but there are also cases in which there may be more obscure but important links among hypotheses, such as the enemy release or the evolution of increased competitive ability hypotheses (Blossey and Nötzold 1995, Uesugi and Kessler 2013). The mechanisms at work in each of these hypotheses may be operating at different trophic levels but still interact with one another. We contend that future studies should not only evaluate the role of antagonists in the success and failure of invasive species, but also the success and failure of biological control agents. Both fields of study should consider the similar hypotheses, top-down and bottom-up biotic influences, and multiple trophic levels (Harvey et al. 2010) that are involved. Classical biological control programs provide the opportunity for a planned invasion, which can allow researchers to experimentally manipulate biological control agents to test various invasion hypotheses, such as propagule pressure, defense-free space, and enemy release. Such interdisciplinary research between both fields of invasion ecology and biological control will enhance shared understanding of the mechanisms associated with species introduction and invasion (Marsico et al. 2010). Unification of scientific fields with overlapping interests allows researchers to make better decisions and design better experiments to evaluate the role of antagonists in the success or failure of nonnative species that we want to manage and the biological control agents that we spend time and resources to select and introduce for the control and management of invaders.

Acknowledgments

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