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Invasive Species Response to Natural and Anthropogenic Disturbance

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5.1 Introduction

Much of the literature dealing with the biology and management of invasive species has focused on the damaging ecological and economic consequences of invasions (see Chaps. 2, 3, and 14 of this volume for review). In this chapter, we shift the focus to the causes of invasion, with the goal of proactively limiting or preventing invasions rather than reacting to them once they have occurred. Preventing the introduction of invasive species is one key element in this proactive approach (Chap. 6, this volume). Here, we specifically focus on ecosystem attributes that affect whether or not an ecosystem is vulnerable to invasion, that is, the features that affect its invasibility (Lonsdale 1999), with particular emphasis on the role of natural and anthropogenic disturbance.

The question of what makes an ecosystem susceptible to invasion has been the subject of intense scientific investigation for several decades, and the literature on this topic is very extensive. Unfortunately, scrutiny of the many thousands of studies on invasion has not resulted in the emergence of a clear paradigm that can explain the invasion process. Several research groups have attempted to use this large body of knowledge to create a conceptual framework or synthesis for invasion biology that can at least provide a basis for the design of studies that can fill knowledge gaps and critically address long-held assumptions based on limited information (Catford et al. 2009; Davis et al. 2000; Funk et al. 2008; Sher and Hyatt 1999; Theoharides and Dukes 2007). These syntheses often have the specific intent of describing the concepts of invasion biology under the more general rubric of ecology, with the idea that the underlying processes regulating community assembly in native ecosystems should be the same as those that mediate invasions (Davis et al. 2005; Facon et al. 2006; Gurevitch et al. 2011; MacDougall et al. 2009; Moles et al. 2012; Shea and Chesson 2002). More recently, there has been recognition of the complexity of the invasion process and the low likelihood that broad generalizations applicable across classes of organisms (e.g., plants, pathogens, insects, earthworms, vertebrates) will emerge (Catford et al. 2012a; Heger et al. 2013; Jeschke et al. 2012; Jeschke 2014; Kueffer et al. 2013). Nonetheless, these syntheses provide a good starting point for discussing the factors that predispose an ecosystem to invasion. A principal tool of more recent syntheses is meta-analysis, where the results of numerous published studies are analyzed together to look for underlying patterns.

Historically, the concepts of ecosystem invasibility and species invasiveness have been considered largely separately. Many have attempted to define what attributes make an ecosystem prone to invasion (e.g., Catford et al. 2012a; Davis et al. 2000; Fridley et al. 2007; Lonsdale 1999) and also what attributes make a species a potentially serious invader (e.g., Colautti et al. 2014a; Dick et al. 2014; Hayes and Barry 2008; Moles et al. 2008; Rejmanek and Richardson 1996; Shea et al. 2004). In practice, however, invasibility is not a static property of an ecosystem but instead results from an interplay between current ecosystem condition and ecological properties of the potential invader. The probability of a significant invasion is a result of the interaction of these two sets of factors, along with factors involved with the current population status of the

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potential invader, particularly as it affects local propagule pressure, that is, the number of invader individuals in proximity to an uninvaded area of interest (Simberloff 2009; Strayer et al. 2006).

5.2 Natural Versus Anthropogenic Disturbance

Disturbance regime is a key ecosystem attribute that can play a major role in mediating invasibility. Ecosystem response to disturbance depends on ecological resilience, that is, the capacity to return to a relatively undisturbed condition following disturbance (Gunderson 2000; Holling 1973). A resilient ecosystem can rebound from disturbance rather than shifting to a different structural and functional condition that is likely to represent a permanent change, that is, a transition to an alternative stable state (Briske et al. 2008). Disturbance regimes that are within the historic range of variation, within the bounds that existed prior to the initiation of human influence, have persisted through long periods of time. This implies that the ecosystem has generally been resilient to this range of disturbance variation and can return to its previous condition following a disturbance event (Landres et al. 1999).

Anthropogenic (human-caused) disturbance, on the other hand, can quickly take an ecosystem outside the bounds of the natural range of disturbance variation and potentially into another stable state. Ecological resilience is not a constant property of an ecosystem, but is itself subject to change. Processes that erode ecological resilience increase the chances of apparently catastrophic changes in state that are often interpreted by managers as “ecological crises” (Gunderson 2000). A decrease in resilience may result from narrowly focused management for a single goal such as timber harvest or livestock production, which can itself impose severe disturbance or chronic stress. For example, reduced resilience, largely as a consequence of the chronic stress of livestock grazing, resulted in a transition from savanna to wooded thickets as an alternative stable state in parts of the American Southwest (Gunderson 2000).

Ecological resilience to disturbance is directly tied to resistance to invasion and therefore to invasibility. This is because disturbance usually decreases resistance to invasion, particularly for invasive plants (Davis et al. 2000; Hobbs and Huenneke 1992). When an invasive species enters the scene after ecosystem resilience and resistance to invasion have been reduced, its arrival represents a disturbance event that can lead to expanding invader monocultures that replace native vegetation as an alternative stable state (e.g., Chambers et al. 2014).

We define natural disturbance very broadly to include episodic events such as earth movement (e.g., landslides), fire, flooding, weather-related events such as wind throw and ice-storm breakage, and biological phenomena such as native insect and disease outbreaks. Land-use changes for agricultural and urban development are examples of drastic anthropogenic disturbance, but road construction, mining, energy development, hunting, recreational use, and harvest of timber, firewood, and other natural products are also important sources of anthropogenic disturbance. We also include chronic disturbance or stressors such as livestock grazing, nutrient pollution, changes in hydrologic regime, and prolonged drought. Many sources of chronic stress are anthropogenic in origin.

We also recognize that disturbance occurs on many temporal and spatial scales and that there is a continuum between processes, such as the activities of native herbivores, that may not disturb the system in the short run, but which, when they occur at abnormally high levels, can qualify as sources of disturbance (e.g., Kalisz et al. 2014). Other examples of this continuum of disturbance include the effects of endemic versus epidemic levels of native insects and pathogens (e.g., bark beetles (*Ips* spp.; Raffa et al. 2008)).

5.3 Resistance to Invasion

The invasion process can be considered in three stages: introduction, establishment, and spread. The introduction stage is considered in detail in Chap. 6 of this volume. Here we consider factors that affect the likelihood of establishment and spread. Much of the discussion in this section pertains to plant invasions. The broader concepts of invasibility and resistance to invasion can meaningfully be applied to consumer invasions, however, as discussed later in this chapter.

5.3.1 Abiotic Resistance

In order to succeed, a potential invader must first establish locally, a process that is regulated largely by the “match” of its ecological tolerance to climatic and other environmental conditions in the ecosystem potentially invaded. If the match is poor, the potential invader has arrived in an environment that is outside its range of environmental tolerance. This means that the invasion will not take place regardless of the potential invasibility of the ecosystem. This type of resistance to invasion is called abiotic resistance and is probably the most common reason that invaders fail to establish. Abiotic resistance to invasion by a newly arrived species is a direct consequence of the species’ lack of ecological match to the environment. An ecosystem could have high abiotic resistance to one invader, yet present low abiotic resistance to another invader with contrasting ecological tolerance that is a better match.

If the potential invader is only marginally adapted to the abiotic environment but able to establish a founder population, it may undergo microevolution in situ, either through selection on standing genetic variation present in the founder population or through selection on novel forms that arise by chance, thereby increasing its degree of adaptation to the abiotic environment. This microevolutionary process has been documented for several invasive plants and is thought to be one explanation for the commonly observed "lag phase" of plant invasion (Aikio et al. 2010; Crooks 2005). It is important to realize that invader populations are not necessarily static in terms of genetic composition, and that such evolution can take place over short time scales and play an important part in increasing the magnitude and severity of particular invasions (Bossdorf et al. 2005; Lee 2002). Another explanation for the "lag phase" is the trend for exponential increase, that is, even for a well-adapted invader, propagule pressure takes time to build to levels that permit large-scale invasion (Crooks 2005).

5.3.2 Biotic Resistance

Another form of resistance to invasion that is presented by natural ecosystems is termed biotic resistance. Biotic resistance can be defined as the sum of all negative ecological impacts that the native organisms (and any other organisms) in an ecosystem can have on a particular invasive species and that can reduce or prevent its success (Levine et al. 2004). For plant invaders, these impacts can include competition, herbivory, impacts from pathogens and parasites, and negative soil microbial effects. In a meta-analysis of the sources of biotic resistance to plant invasion, Levine et al. (2004) found that both competition from resident native plants and herbivory from resident native herbivores had a large negative effect on invasibility, while the few studies that examined the effects of the soil microbial community produced contradictory evidence. They found that these sources of biotic resistance could not prevent initial colonization but instead operated to slow the rate of population increase and spread. However, biotic resistance may only constrain the extent of an invasion when propagule pressure is low (Kerns and Day 2017).

Biotic resistance to population increase and spread is probably another reason why most non-native species do not become invasive even in ecosystems where they are adapted to the abiotic regime. Most remain minor players in the ecosystems they colonize, and only a few become problematic as major invaders. The distinction between "weak" and "strong" invaders is an important one (Ortega and Pearson 2005). Weak invaders may behave much like native species in the regional species pool, able to establish and persist under conditions of moderate disturbance but not likely to experience major population growth. Although they are non-native, they do not meet the definition of an invasive species. This may be due to intrinsic features of life history that make the introduced species unable to experience explosive growth even under favorable conditions, or it may be due to a poor ecological fit with a particular ecosystem. The distinction between weak and strong invaders can therefore sometimes be ecosystem-dependent.

Disturbance and Resource Availability

On a community level, processes that increase resource availability (e.g., water, light, nutrients) have been found to make a community more open to invasion by both natives in the regional species pool and non-native species, while processes that reduce resource availability make it less open to invasion. Resource availability can be increased through physical disturbance or other processes that reduce plant biomass and therefore resource demand, or through resource pulses, which temporarily flood the system with resources that the resident community cannot efficiently use (Davis et al. 2000). The unpredictability of invasion hinges on the necessity of propagule arrival that coincides temporally with such a period of increased resource availability, which itself fluctuates unpredictably through time.

Disturbance can occur on multiple spatial scales, and the scale of disturbance has a major effect on both resource availability and on the likelihood that newly arriving invader propagules will "find" a resource-rich disturbance. Wildfire probably represents the broadest scale natural disturbance in many ecosystems, and its effects on invasibility for disturbance-responsive invaders are well documented (Zouhar et al. 2008). Kerns and Day (2017) found that at fine scales, cheatgrass (*Bromus tectorum*) establishment in areas with cheatgrass in the vicinity was correlated with burn extent even for low-intensity prescribed burning in forested stands. But even the most stable ecosystems have fine-scale disturbances that can provide an initial toe-hold for invaders, for example, rodent mounds, new soil deposition from localized flooding events, or gaps formed by the death of individual trees.

The distinction between invasibility and invadedness is crucial in the interpretation of correlative studies of factors such as disturbance that mediate species invasions. Level of invadedness results from the interaction of ecosystem invasibility with the invader species pool and the ecological attributes of both invaders and recipient ecosystems, as well as with propagule pressure and the timeline of invasion (Guo et al. 2015; Simberloff 2009; Strayer et al. 2006). Post hoc level of invadedness is therefore not a reliable indicator of ecosystem invasibility. For example, Moles et al. (2012) found in a meta-analysis that current and past disturbance regimes per se had low ability to predict the degree of plant invasion, accounting for <10% of the variation in invadedness. They used a correlative approach to relate the degree of invadedness in a large number of different ecosystems to reported levels of disturbance in those ecosystems. This approach conflates invasibility with observed levels of invadedness, which casts doubt on its conclusion that disturbance is a relatively unimportant factor in invasibility.

It has been pointed out that most studies of invasion deal with species that are disturbance-responsive even in their native range, and this may have led to an overemphasis on disturbance as a mediator of invasion (Martin et al. 2009). The first serious plant invaders to arrive in North America were likely inadvertently introduced by people, often in the context of agriculture or animal husbandry. They originated in human-disturbed landscapes and were likely favored by such disturbance in both the native and introduced ranges. More recently, however, the majority of new invaders have been introduced deliberately, often as horticultural selections, and species attractive to horticulturalists can originate from any ecosystem in any condition of disturbance (Reichard and White 2001). Undisturbed forests have been thought to be relatively resistant to invasion, but this could have been an artifact of the poor match of most of these early invaders to the deep shade environment of mature forests. The list of invasive plant species that have succeeded in mature forests is becoming longer through time, and virtually all of these invaders are horticultural introductions (Martin et al. 2009). This emphasizes the importance of the ecological match of the new invader to the ecosystem and implies that protecting an ecosystem from disturbance is no guarantee that it will remain uninvaded, particularly by this new invader class, which presents a much wider array of ecological tolerances than invaders introduced as accidents of agriculture.

Species Composition

Another community-level factor that has been found in many small plot studies to reduce invasibility on a local scale is biodiversity or species richness. Ecological niche theory predicts that the more species included in a community, the more completely the niche space will be filled, and therefore the more completely resources will be utilized (Shea and Chesson 2002). Experimental studies of community assembly almost always yield this negative effect of species richness on probability of subsequent successful invasion by novel species (e.g., Fargione and Tilman 2005; Kennedy et al. 2002; Maron and Marler 2007). Theoretical work has also supported this hypothesis (Case 1990).

Sometimes the negative effect of increased diversity on invasibility can be credited to the increased presence of species that are functionally similar to a newly invading species or in some other way better able to fill its niche (Fargione and Tilman 2005). Evidence for the importance of the presence of functionally similar species in biotic resistance to plant invasion is equivocal, however. For example, Price and Partel (2013) showed in a meta-analysis that functionally similar species could limit herbaceous dicot invasion but not grass invasion. Similarly, in a manipulative removal study, Pokorney et al. (2005) showed that removal of a functionally similar group (herbaceous dicots) increased invasion of spotted knapweed (*Centaurea stoebe*) more than removal of dominant grasses. Even uncommon species can add to the overall biotic resistance of a plant community to a potential invader (Lyons and Swartz 2001). Experimental changes in biodiversity through random removal of species may not reflect the real impact of species loss on invasibility (Zavaleta and Hulvey 2007). Selments et al. (2012) showed in experiments in serpentine grassland that realistic species removal, i.e., removal of species most likely to be lost during extended drought, increased invasibility more than random species removal.

Biodiversity studies at regional scales have often yielded results that seem to contradict the results of local-scale studies, in that native biodiversity is commonly positively associated with non-native biodiversity (e.g., Stohlgren et al. 1999; Stohlgren et al. 2003). This alarming result seems to suggest that native biodiversity “hot spots” are more prone to invasion by non-native species than less diverse ecosystems. The reasons for this “invasion paradox” appear to be complex (Fridley et al. 2007). One possibility is that, on a regional scale, high environmental heterogeneity creates a multiplicity of niches that can potentially be filled by any species from the regional species pool, whether native or introduced. As mentioned earlier, high non-native biodiversity can result from colonization of weak invaders from the regional species pool and may not indicate imminent invasion by a strong invader. This regional-scale relationship does not negate the finding that high native biodiversity at a local scale can decrease community invasibility.

Recent work by Iannone et al. (2016) on the relationship between non-native species richness and community attributes in eastern hardwood forests showed that native and introduced species richness were positively correlated at the landscape scale as in earlier large-scale studies. However, a measure of native diversity that incorporated degree of phylogenetic relatedness (“evolutionary diversity”) was negatively correlated with introduced species diversity, indicating that species richness per se may not be the best measure for predicting biotic resistance. Their study would predict, for example, that a forest dominated by multiple species of oak (*Quercus* spp.) would be more easily invaded than a forest dominated by the same number of tree species that are not so closely related and perhaps better able to fill the available niche space.

Natural Enemies

One of the principal hypotheses explaining why a species that is not invasive in its native range becomes invasive in the introduced range is the idea of escape from natural enemies that keep it in check, particularly host-specific natural enemies that are unlikely to have homologues in the introduced range (Heger and Jeschke 2014; Keane and Crawley 2002). This hypothesis is the basis of classical biocontrol, which seeks to reunite invasive species with their specialist natural enemies from the native range (Clewley et al. 2012; see Chap. 7 this volume). Generalist natural enemies, on the other hand, are often represented by similar species in the introduced range, and these can contribute substantially to biotic resistance to invasion if they feed on the invasive species. Native generalist herbivores often increase resistance to invasion by introduced plant species (Parker et al. 2006), though there are exceptions (Maron and Vila 2001; Vavra et al. 2007). For example, excessive native deer (*Odocoileus virginianus* Boddaert) herbivory on native vegetation caused by overstocking has been shown to facilitate plant invasion (Eschtruth and Battles 2008; Kalisz et al. 2014).

Facilitation of plant invasion by non-native herbivores is a much more common pattern than facilitation by native herbivores. It represents the type of synergistic interaction among invaders that has been termed "invasional meltdown" (Simberloff and Von Holle 1999). An example of this involves the facilitation of plant invasion by invasive defoliating insects that open the forest canopy and increase light levels in the understory (Eschtruth and Battles 2009). Sometimes a single defoliation event can set a long-term trajectory of plant invasion in motion so that years later, it would not be possible to detect the cause of the population increase that initiated the successful plant invasion (Eschtruth and Battles 2014).

In a meta-analysis of generalist herbivore effects on plant invasion, Parker et al. (2006) found that native generalist herbivores often added to biotic resistance to invasion, whereas introduced generalist herbivores, including domestic ungulates, facilitated non-native plant invasion in an "invasional meltdown" effect. They suggested that removal of introduced generalist herbivores, e.g., domestic livestock, might be as effective as introduction of specialist herbivores in control of invasive plants, and that this would not involve the perceived risks associated with introducing non-native specialist herbivores. This idea has never been explicitly tested, however.

5.4 Stress and Invasibility

Ecosystems vary widely in their general level of abiotic stress, but this stress level is part of the natural regime to which resident species are already adapted. Many ecologists believe that invasibility is negatively correlated with abiotic stress, largely because stressful abiotic environments often impose severe resource restrictions that limit productivity and niche space, whereas less stressful, more productive environments are usually less resource-limited and therefore more likely to present unused resources and niche space (Albert et al. 2000). Some of the least-invaded ecosystems, including alpine tundra and more arid deserts, are also among the most abiotically stressful, whereas highly productive ecosystems such as grasslands are often highly invaded. On the other hand, productive ecosystems with high standing biomass, such as closed forests, are also often relatively uninvaded, for reasons that are discussed later in this chapter.

In contrast to episodic disturbance such as fire, geomorphic movement, or insect or disease outbreaks, chronic stress as defined here represents disturbance that operates over a longer time scale and generally at a lower grade (Albert et al. 2000). Chronic stress may not open a system to invasion immediately, but it tends to erode ecological resilience, so that resistance to invasion and to other forms of irreversible change is decreased over the long term. Many sources of chronic stress that can eventually push the disturbance regime beyond the natural range of variation are anthropogenic, but some, such as decadal drought, are of natural origin.

One good example of a chronic anthropogenic stressor is nutrient pollution. Many natural ecosystems have evolved with very low levels of plant macronutrients, particularly nitrogen and phosphorus. The influx of high levels of one of these nutrients into such an oligotrophic (nutrient-limited) system over time can have a strong destabilizing effect. One of the best-documented cases involves phosphorus pollution from agriculture and its impacts on the oligotrophic wetland system of the Everglades (Childers et al. 2003). Excess phosphorus strongly favored the increase of cattails (*Typha domingensis* Pers.), which rapidly became dominant in the system, causing loss of the structure of sawgrass (*Cladium jamaicense* Crantz) wetland and tree hummocks that had been the long-term ecosystem configuration. Eutrophication is also implicated in the spread of many aquatic invaders, e.g., water hyacinth (*Eichornia crassipes*; Coetzee and Hill 2012). Invasive plants that are nitrogen fixers can also be agents of nutrient enrichment, dramatically increasing nitrogen availability in naturally nitrogen-poor ecosystems, thereby increasing resource availability that facilitates invasion by additional species (e.g., fire tree (*Myrica faya*) in Hawai'i; Vitousek and Walker 1989).

In another example of nutrient pollution, the serpentine grasslands of California represent an oligotrophic plant community high in endemism and biodiversity. Experimental work showed that low nitrogen was a main factor preventing the invasion and domination of this plant community by introduced annual grasses from surrounding areas with higher soil fertility (Huenneke et al. 1990). Subsequently, it was shown that nitrogen deposition originating from automobile catalytic converters was causing the breakdown of this invasion barrier, so that serpentine grasslands are now readily invaded by these nitrogen-loving annual grasses, which have the capacity to outcompete the endemic species and potentially cause the extinction of a rare butterfly that depends on them (Weiss 1999).

5.5 Propagule Pressure and Dispersal Corridors

The importance of propagule pressure in mediating invasion has recently received more emphasis (Simberloff 2009), and experimental studies have shown that propagule pressure can frequently overwhelm biotic resistance (Von Holle and Simberloff 2005). Several methods are now available to measure plant propagule pressure independently (e.g., Eschtruth and Battles 2011; Miller et al. 2014). In one study, it was found that the higher levels of invadedness of riparian versus upland forest sites were due, not to higher invasibility as had been thought, but to a higher rate of arrival of invader propagules, that is, higher propagule pressure (Eschtruth and Battles 2011). Mechanistic studies that tease apart the factors responsible for a given level of invadedness across invasion stages (establishment, spread, and impact) are essential for understanding the invasion process.

Another reason that plant invasions are often associated with disturbance at least initially is that the dispersal corridors that introduce propagules into natural ecosystems are almost always associated with humans and therefore with anthropogenic disturbances such as roads, trails, and pipeline and powerline corridors (Gelbard and Belnap 2003; Wilson et al. 2009).

5.6 Modeling Invasibility and Invadedness

Guo et al. (2015) recently proposed a methodology for quantifying invasibility and degree of invadedness independently. Their conceptual model captures the idea that the degree of invasion is ultimately constrained by community invasibility, but that at a given level of invasibility, extrinsic factors determine invasion success. These factors could include ecological match, invader ecological attributes (e.g., weak or strong invader), propagule pressure, and invasion timeline (Fig. 5.1a). Their scheme for quantifying invasibility accounts for the effects of both disturbance (expressed in terms of biomass as a proportion of maximum, i.e., biomass in the undisturbed condition) and species richness (expressed as a proportion of maximum species richness) on invasibility (Fig. 5.1b). They used a very large long-term data set generated as part of the Forest Inventory and Analysis program for three eastern deciduous forest types to demonstrate the usefulness of this approach.

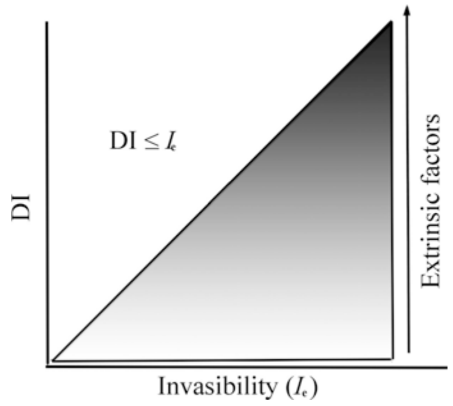

Fig. 5.1a The relationship between invasibility (I_e), extrinsic factors, and degree of invasion (*DI*). Invasibility sets the upper limit to degree of invasion, whereas extrinsic factors (e.g., propagule pressure, time, species-specific abiotic resistance) determine the realized degree of invasion below this upper limit (From Guo et al. 2015)

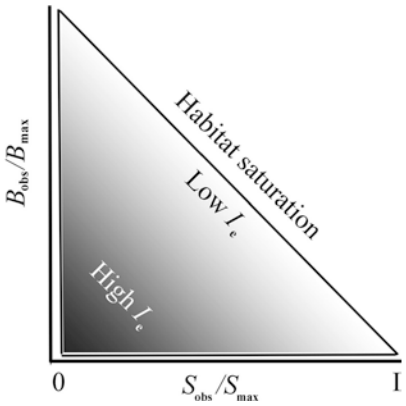

Fig. 5.1b Conceptual model for invasibility (I_e) of a plant community in terms of relative biomass (B_{obs}/B_{max}) and relative species richness (S_{obs}/S_{max}). Relative biomass increases with lower disturbance and later successional stage, whereas relative species richness is highest at intermediate disturbance (see Fig. 5.2). Where both relative biomass and relative species richness are low (high disturbance, low competition, early successional stage), invasibility is highest. Increase in either relative biomass or relative species richness reduces invasibility, which is very low at habitat saturation (From Guo et al. 2015)

The method of Guo et al. (2015) for quantifying invasibility depends on biomass and species richness data from reference areas in undisturbed condition to estimate relative values that can then be compared across ecosystems. This need for reference or historical data is a potential limitation, but even approximations of these reference values can be useful for management of invasive species. To calculate degree of invadedness, in contrast, requires only current data (Guo and Symstad 2008). The two-dimensional surface for quantifying degree of invadedness is similar to Fig. 5.1b, except that introduced species biomass and species richness relative values are calculated as a fraction of total current biomass and species richness. This has the advantages of incorporating both diversity and dominance measures of invadedness and of using unitless measures that are useful for community cross-comparisons.

In support of the model of Guo et al. (2015), Iannone et al. (2016) found that non-native species richness was negatively correlated with both tree biomass and evolutionary diversity.

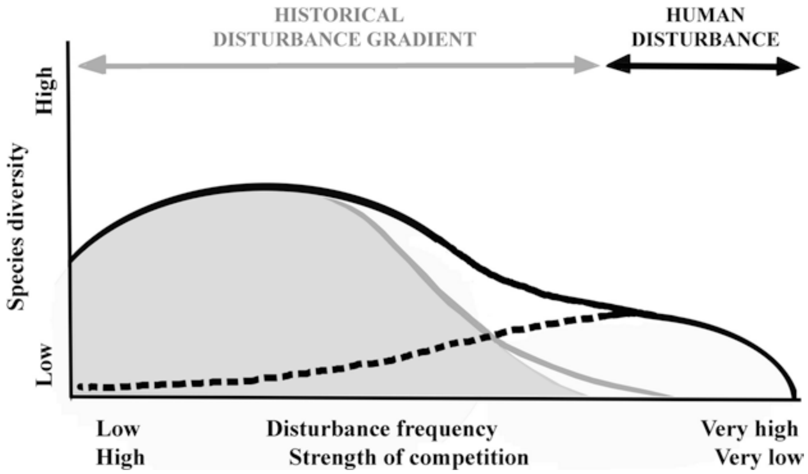

Fig. 5.2 The relationship between disturbance frequency over the natural (historical) and anthropogenic (human-caused) ranges and post-invasion diversity of native plant species (*gray line*), exotic plant species (*dashed line*), and total plant species (*black line*). Strength of competition is shown as inversely proportional to disturbance frequency. *Shaded curve* represents species diversity under the historical disturbance regime prior to any invasion (From Catford et al. 2012b)

This supports the idea that the combined effects of increased competition and increased biodiversity could reduce invasion and therefore be used to predict potential levels of invasion. Overall, this study provided evidence for biotic resistance to invasion at the landscape scale in eastern hardwood forests but also revealed some regional differences in effect.

Relative biomass is likely to impact directly the level of competition encountered by an invader and is also a reasonable surrogate for disturbance history in that reduced biomass relative to the maximum likely reflects a system in recovery from disturbance. Native species diversity, on the other hand, usually peaks at intermediate disturbance frequency. This is because after long periods with low disturbance, more competitive species become dominant and species diversity is reduced, while in the period following high disturbance, species diversity is colonization-limited. This relationship has been codified as the Intermediate Disturbance Hypothesis (IDH; Shea et al. 2004).

Catford et al. (2012b) examined how the IDH pattern of species diversity as a function of disturbance frequency could impact plant invasion (Fig. 5.2). In this scheme, disturbance frequency increases through the range of natural disturbance regimes from left to right, then enters the anthropogenic zone of more frequent (and/or more intense and/or novel) disturbance. Native species richness increases with disturbance as natural disturbance frequency increases to an intermediate level, then decreases over the remainder of the natural range. It is reduced to very low levels under anthropogenic disturbance regimes. Introduced species richness remains at low levels until intermediate levels of natural disturbance are reached, then increases through most of the range of anthropogenic disturbance, with only the most recently disturbed sites still colonization-limited. This difference between native and introduced species is predicated on the assumption that invaders are faster at colonization and better adapted to recent disturbance than native species, life-history traits that characterize many if not most invasive plant species (Rejmanek and Richardson 1996). This model predicts that maximum invasibility will occur under anthropogenically amplified disturbance regimes, but that some degree of invasion is also possible under most natural disturbance regimes. High native species diversity at intermediate levels of disturbance can compensate for reduced biomass and thus reduced competition from community dominants at intermediate disturbance levels, but moderately disturbed communities may still be more invasible than closed communities with very low levels of disturbance.

5.7 Disturbance and Plant Invasion in Different Vegetation Types

Each of the four major vegetation types in the continental United States is characterized by a suite of natural and anthropogenically modified disturbance regimes. Natural and anthropogenic disturbances in each of these vegetation types have functioned to regulate the level of invasion by introduced plant species. We use a few key examples involving major invaders to explain how disturbance and invasion interact in each of these broad vegetation types.

5.7.1 Forest Vegetation

The natural range of variability in disturbance regime in North American forests is driven primarily by fire (Attiwill

1994; Zouhar et al. 2008). All but the wettest coastal rainforests are characterized by fire return intervals that have shaped community structure, and forests typically exist in mosaics or patches with different fire histories, creating characteristic patterns of environmental heterogeneity (Churchill et al. 2013). Other natural sources of sometimes large-scale disturbance include weather-related phenomena such as long-term drought, extreme wind events, and ice storms (Lafon 2015; Millward and Kraft 2004), and outbreaks of native insects (Raffa et al. 2008). At mid-scale, geomorphic disturbances such as flooding, avalanches, and landslides can have dramatic effects, while at a smaller scale, gap formation from the death of individual trees as well as the activities of ungulates and rodents and local-scale flooding and frost-heaving can create openings in otherwise undisturbed vegetation.

The anthropogenic impacts on forest disturbance regimes have been great, beginning with the clearing of large areas for agriculture and resulting forest fragmentation. This has been exacerbated by the ever-increasing network of roads, which greatly increases the effects of forest edges on ecological processes, including invasion by non-native species. Even after abandonment and forest regrowth, the impact of human disturbance can have long-term effects. A second major impact has been through fire suppression, which has major consequences for successional trajectories in all forest types (Zouhar et al. 2008). Timber harvest and associated silvicultural activities, including control of understory vegetation, represent other major sources of anthropogenic change in disturbance regimes (Cyr et al. 2009).

Norway Maple

As mentioned earlier, intact forests are generally thought to offer substantial biotic resistance to plant invasion, and the primary limiting resource is usually light. Most forest invaders are more light-limited than the dominant tree species, and invasion is almost always initiated at forest edges where human-assisted dispersal is also more likely. A notable exception to this rule is Norway maple (*Acer platanoides*), which invades old-growth beech-maple (*Fagus-Acer*) forests in the Northeastern United States (Martin 1999; Martin and Marks 2006). This species combines exceptionally high growth rates with a remarkable degree of shade tolerance, rather than exhibiting the usual tradeoff between these two traits (Martin et al. 2010). It produces a canopy that creates conditions too shady for recruitment by the native sugar maple (*A. saccharum*), but it can easily recruit under a sugar maple canopy. It also appears to have been released from herbivores in its introduced range, experiencing only one-third the damage experienced in the native range in an experimental study (Adams et al. 2009). It also experiences significantly less herbivory than sugar maple where the two species grow together in North American forests (Cincotta et al. 2009). These studies support the enemy release hypothesis and demonstrate weak biotic resistance to invasion in these North American forests. Invasion by Norway maple has a long initial lag time because of a prolonged juvenile period under deep shade conditions, and it may be punctuated by multiple lag periods as successive generations mature, but its invasion, though slow, may be inexorable (Wangen and Webster 2006).

Kudzu

Vines or lianas, both woody and herbaceous, represent another group of important forest invaders. These may have limited shade tolerance, but they have the advantage of a climbing habit, which permits them to reach more favorable light conditions by overtopping trees. Kudzu (*Pueraria montana*) is a major invasive species in forests of the Southeastern United States, where its negative impacts are well documented (Forseth and Innis 2004). It has limited ability to establish in forest interiors, but because it can shade out and kill the trees it overtops, it can improve light conditions as it migrates further into the forest, thus reducing the effectiveness of biotic resistance through light limitation. Experimental evidence suggests that kudzu has benefitted from escape from natural enemies in its home range, enabling it to divert resources from defense to growth and thereby evolve increased growth rate and competitive ability (Yang et al. 2014). Climatic niche modeling shows that there are areas in North America where kudzu could potentially become invasive, including parts of the Western United States. (Cullen and Miller 2015). The invasion of kudzu in the Southeastern United States was greatly accelerated by a very extensive planting effort in the first half of the twentieth century (Forseth and Innis 2004). When many of these plantings were abandoned and the areas underwent natural reforestation, kudzu was already a dominant component of the resulting vegetation.

Japanese Honeysuckle

Japanese honeysuckle (*Lonicera japonica*) is another non-native vine that is a successful invader of mesic eastern US forests (Schierenbeck 2004). It has high shade tolerance and is favored by fire suppression, although it is a root sprouter that is also quite fire-tolerant. Closed-canopy forests offer some biotic resistance to invasion by this species, but it can penetrate forest interiors at low rates of spread, then take advantage of the improved light conditions in small-scale disturbances such as treefall gaps to increase its reproductive success (Horvitz et al. 1998). The fruits are bird-dispersed, which provides an avenue of introduction into forest interiors, but the species is reported to be pollinator-limited in at least some of the invaded range (Larson et al. 2002). Japanese honeysuckle was less impacted by herbivory than a native congener in an observational study and also exhibited compensatory growth in response to herbivory, which suggests that native herbivores are not an effective component of biotic resistance (Schierenbeck et al. 1994).

Garlic Mustard

Garlic mustard (*Alliaria petiolata*) is a deliberately introduced herbaceous forest invader that has undergone explosive range expansion (Kurtz and Hansen 2014; Rodgers et al. 2008). A great deal of research has been carried out on this species, and it has been proposed as a model species for the study of plant invasion (Colautti et al. 2014b). This biennial plant is quite tolerant of low light conditions and can invade forest interiors, albeit slowly. It is most successful in deciduous forests where it can complete much of its life cycle in spring before canopy closure. Once established, it benefits from natural and anthropogenic disturbances that increase light availability (Eschtruth and Battles 2014). It is not palatable to deer, and several studies have shown that its spread is accelerated by deer overstocking, which impacts more palatable natives and gives garlic mustard a competitive advantage (Eschtruth and Battles 2008; Kalisz et al. 2014). There is some indirect evidence that forest communities differ in their biotic resistance to this species, with some studies reporting large negative effects on the native understory that would be expected from a strong invader (Stinson et al. 2007) and others reporting no effect and a positive association between garlic mustard abundance and overall species richness, as would be expected from a weak invader (Davis et al. 2014, 2015). This difference could reflect intrinsic differences in the structure of the invaded communities or possibly differences in modern or historic disturbance regimes (Nuzzo 1999). It is clear, however, that this species has become a permanent member of the forests that have been invaded.

A common thread that runs through the narrative for almost all invaders of relatively undisturbed forests is that these species were introduced deliberately for horticultural purposes and were not accidental arrivals. As mentioned earlier, this makes it more likely that they will not be constrained by the light limitation in forests that would prevent invasion by the great majority of accidental introductions (Martin et al. 2009).

5.7.2 Wetland and Riparian Vegetation

Wetland and riparian ecosystems occupy the transition zone between aquatic and upland terrestrial ecosystems. They are characterized by highly dynamic disturbance regimes, with frequent, intense disturbance and broad natural ranges of variability as the norm (Middleton 1999). Consequently, the plant communities in wetland and riparian ecosystems are rarely in an equilibrium condition and are often far from equilibrium. This increases the likelihood of state changes as a result of natural disturbances (Richardson et al. 2007). These natural disturbances often involve dramatic changes in hydrologic regime, including seasonal flooding or episodic flooding associated with extreme weather events like hurricanes. Water level fluctuations due to drought or changes in flow caused by erosion and aggradation processes as well as modification of woody debris structure of stream channels and beaver (*Castor canadensis*) activity are additional sources of frequent natural disturbance. The complex community structure and high native biodiversity characteristic of these ecosystems are maintained by these natural disturbance regimes, and efforts to restore wetland or riparian communities to static, ideal states cannot be successful in the long term (Middleton 1999; Zedler and Kercher 2004). Long-term stress from drought and episodic weather events such as out-of-season frosts and windstorms are additional sources of disturbance. Finally, periodic fire is also an essential component of the disturbance regime of many wetland and riparian ecosystems, which changes surface litter and nutrient cycling and also plays a role in slowing or preventing succession from wetland to swamp forest, thus maintaining a mosaic of forested hummocks and wetland vegetation dominated by grasses and other graminoids such as sawgrass (Childers et al. 2003).

Wetlands and riparian areas have been heavily impacted by anthropogenic disturbance, much of it associated with land use of surrounding upland areas or with modifications of the hydrologic regime designed to meet human goals. Wetlands have been much reduced in areal extent in many parts of the country due to draining for agriculture or urban development. Development on adjacent uplands can also lead to sedimentation and eutrophication, often accompanied by drastic changes in community structure, as discussed earlier for conversion from sawgrass to cattail vegetation in the Everglades. Because wetlands tend to be sinks in terms of their position on the landscape, they are more dramatically affected by waterborne nutrient pollution than other ecosystems. Fragmentation reduces the connectivity of wetlands and thus their resilience in the face of disturbance, and disruption of natural fire regimes through fire suppression can lead to state changes that are difficult to reverse.

Riparian systems have been dramatically impacted by human efforts to capture water, generate electricity, and reduce the perceived negative effects of flooding. These anthropogenic disturbance factors include dam construction, stream diversion and inter-basin water transfer, and canalization, all of which have the effect of dewatering riparian areas and generating major vegetation changes in response to changed hydrologic regimes (Stromberg et al. 2007). Dam construction has had enormous impacts on almost all US rivers, with very few that are still free-flowing. Other anthropogenic disturbances in riparian areas include livestock grazing and recreational use.

Wetlands and riparian areas are often highly invaded by introduced plant species. One reason is that these areas act either as conduits of seed dispersal in the case of riparian systems or seed collectors in the case of wetlands. They are thus characterized by high propagule pressure from both native and introduced species (Stohlgren et al. 1998). And because these ecosystems are essentially subject to perpetual natural disturbance and far from equilibrium, the niche space is rarely filled, creating continuous opportunities for new species to colonize and establish (Catford et al. 2011; Chipps et al. 2006).

Saltcedar

Invasive species management in wetlands and riparian areas is complicated by the often tight linkage between anthropogenic disturbance and invasion, making it difficult to know where control efforts are best applied. Saltcedar (*Tamarix* spp.) invasion in the river systems of the desert Southwest, for example, is largely driven by changes in hydrologic regime caused by dam construction (Stromberg et al. 2007). Its rapid rise to dominance along many southwestern rivers has elicited a major control effort, but some ecologists argue that this species is in fact dominant only in a novel niche that cannot be filled by native riparian species under the current hydrologic regime (Richardson et al. 2007). Its invasion into the riparian communities of free-flowing rivers has apparently not resulted in the rapid rise to dominance seen along dammed rivers with dewatered floodplains, but instead seems to result in its integration into the native riparian vegetation with little loss of native biodiversity or cover (Stromberg 1998). In environments where light is the main limiting factor, native trees like box elder (*Acer negundo*) can effectively compete with saltcedar (Dewine and Cooper 2008). The case for saltcedar as an invasive species is therefore context-dependent and subject to considerable debate (Stromberg et al. 2009).

Paperbark

Paperbark (*Melaleuca quinquenervia*) invasion of large areas of sawgrass marsh in the Everglades is less subject to the kind of debate applied to saltcedar invasion, as it is apparently capable of invading under the natural range of variability in disturbance, though some might argue that anthropogenic influence is pervasive throughout the Everglades. This Australian native was intentionally introduced to Florida and was even seeded into parts of the Everglades, setting the stage for massive invasion and consequent state change to a wooded swamp vegetation type (Serbesoff-King 2003; Turner et al. 1998). It is a prodigious seed producer that can release seeds continuously but that also reserves a large seed bank in canopy fruits for release after fire. Seedlings can reach reproductive maturity in as little as one year, and mature trees are highly fire-tolerant. Sawgrass marshes are maintained free of less fire-tolerant woody vegetation by the natural fire regime, but this does nothing to stop paperbark invasion. In addition, this species is tolerant to drought, flooding, and moderate freezes, further expanding its niche. It is limited to subtropical climates, but could further expand its range across wetlands along the Gulf Coast States under current climate scenarios (Watt et al. 2009).

Common Reed

Another major invader throughout the wetlands of the United States, particularly on the eastern seaboard, is common reed (*Phragmites australis*). There is little doubt that this species is a strong invader that can interact synergistically with anthropogenic disturbance to create a state change to near-monoculture of common reed (Chambers et al. 1999; Kettering et al. 2012). Management is complicated by the fact that both noninvasive native genotypes and invasive Eurasian genotypes are widespread in North America. In coastal wetlands, there is good evidence that invasion and subsequent dominance by introduced genotypes of common reed are exacerbated by land-use patterns in adjacent terrestrial vegetation (Minchinton and Bertness 2003; Silliman and Bertness 2004). Removal of woody vegetation as part of shoreline development results in increased nitrogen availability and decreased salinity in coastal salt marsh, both factors that favor common reed invasion. Anthropogenic disturbance within the marsh, as simulated in removal experiments, also greatly accelerated the invasion rate. Minimizing within-marsh disturbance and maintaining buffer zones of woody vegetation between salt marshes and adjacent developed areas can be used as a means to slow the rate of common reed invasion. In a study in a riparian system, it was found that high native functional group diversity, and the presence of native pioneer species that could provide immediate competition following disturbance, could greatly reduce seedling establishment of common reed in previously uninvaded habitat (Byun et al. 2013).

5.7.3 Grassland Vegetation

Grassland was historically the dominant vegetation type across much of the Great Plains, as well as in many other parts of the country, for example, the Palouse prairie of the Pacific Northwest. The natural or historic range of variability in disturbance regime for grasslands includes periodic fire, small-scale physical disturbance, and nutrient pulses. Physical disturbance resulted from the burrowing activity of rodents, from the actions of native ungulates (e.g., pronghorn (*Antilocapra americana*), bison (*Bison bison*)), and from soil movement due to frost heaving and hydrological effects. Native ungulates can also create an uneven distribution of soil nutrients with temporary, locally enriched patches. Intensive grazing by large herds of bison probably created short-term impacts on prairie vegetation, but their wide-ranging habits kept these at relatively low frequency, so that the vegetation had time to recover. Large herding ungulates were largely absent from grasslands of the Interior West, so that intensive grazing rarely if ever took place there. Most grasslands in the United States historically experienced fire, although natural fire regimes varied widely depending on climate and soils. Grasslands also experience invasion of native woody species from adjacent vegetation types during periods of low fire frequency, especially in more mesic grasslands such as tallgrass prairie. Drought of varying length and severity is another natural chronic stress that probably caused shifts in species composition.

The arrival of European humans drastically changed the disturbance regimes of grassland ecosystems. Large-scale conversion for agriculture nearly eliminated tallgrass prairie and Palouse prairie grasslands, while other grassland ecosystems, such as the Mediterranean grasslands of California, the mountain meadow ecosystems of the Interior West, and the high desert grasslands of New Mexico and Texas, were heavily exploited for livestock production. Excessive grazing pressure pushed some of these systems beyond their ability to recover. For example, excessive grazing on montane ranges in Utah caused denuded mountainsides and severe soil erosion and flooding. The management response was to seed fast-growing introduced forage grasses for soil stabilization, primarily smooth brome (*Bromus inermis*). This has apparently caused a permanent state change in these ecosystems, which are still dominated by this introduced perennial grass nearly a century after treatment. In central California, the ecosystem response to anthropogenic disturbance was a type conversion to a relatively high-diversity mixed introduced-native system dominated by introduced winter annual grasses from the Mediterranean region, mainly wild oat (*Avena fatua*), annual ryegrass (*Lolium multiflorum*), and soft brome (*Bromus hordeaceus*), with native perennial grassland present only in remnant areas. European humans also impacted natural fire regimes in many grasslands, in most cases through fire suppression.

Anthropogenically altered disturbance regimes in grasslands opened the way for the invasion of a large suite of non-native species that can exploit these new regimes. Increased nutrient availability has emerged as a key variable regulating invasibility in many grassland studies. For example, when fire retardants are applied to intermountain grasslands during control activities, they cause an intense pulse of both nitrogen and phosphorus (Besaw et al. 2011). Experimental work showed that this resource pulse created a competitive advantage for the winter annual invaders cheatgrass and tumble mustard (*Sisymbrium altissimum*) over both native grasses and herbaceous perennial dicots and the perennial invader spotted knapweed (*Centaurea stoebe*). This effect was increased by burning. Knapweed showed a positive response to this resource pulse only in the absence of competition from the more resource-responsive annuals.

The knapweeds (*Centaurea* spp.) are among the most serious invaders of grassland and associated ecosystems in the Western United States (LeJeune and Seastedt 2001). Spotted knapweed invades and increases in response to "improper grazing" of bunchgrass communities but also apparently has the capacity to invade "well-managed rangeland" (Sheley et al. 1998). Ortega and Pearson (2005) showed that dominance by spotted knapweed in an invaded bunchgrass community in western Montana likely was the cause of reduced native species diversity rather than the consequence. In contrast, Maron and Marler (2007) found that native biodiversity in experimental bunchgrass communities was the apparent cause of reduced spotted knapweed success in post-seedling stages. This negative effect was mediated through competition for resources but persisted even at enhanced resource levels.

A somewhat similar scenario has emerged with studies of yellow starthistle (*Centaurea solstitialis*). This species is a late-season annual that is able to use deeper soil moisture than most co-occurring species, enabling it to complete its life cycle in the summer even in summer-dry environments (Roche and Thill 2001). Kyser and DiTomaso (2002) studied the effect of late-season prescribed burning on yellow starthistle populations in a remnant perennial grassland in California. Repeated burning before seed dispersal effectively eliminated yellow starthistle and triggered a strong positive response in the fire-adapted native plant community. However, when burning was discontinued, the competitive advantage shifted away from the native community, and the site was reinvaded.

Frequent fire was an especially important part of the historic fire regime in tallgrass prairie in terms of its effect on invasibility. Smith and Knapp (1999) found that invasion by introduced cool-season species at Konza Prairie in Kansas, though never a serious problem, increased with fire suppression. Burning increased the dominance of the warm-season grasses that provide strong competition to invaders. Bison grazing at moderate levels, on the other hand, increased invasion through reduction of competitive abilities of the warm-season dominants. Species richness of both native and introduced species was increased in the grazing treatment, however, suggesting that bison grazing historically was a force for the maintenance of native species diversity. In contrast, Milchunas et al. (1989) found that heavy cattle grazing in shortgrass prairie in central Colorado increased the biomass production of the dominant grass, blue grama (*Bouteloua gracilis*), a compensatory response that is probably the result of long evolution with bison. Invasibility may not be strongly impacted by grazing in shortgrass prairie, though this question was not examined. In experimental work in tallgrass prairie, both Kennedy et al. (2002) and Fargione and Tilman (2005) found that increased plant diversity decreased invasibility.

5.7.4 Shrubland Vegetation

Shrub-dominated vegetation occurs at some scale under most climate regimes in the United States, but shrubs achieve regional dominance primarily in the arid and semiarid Interior West. We focus on these shrublands, which occur over a wide productivity gradient that is related to precipitation. Most precipitation is received in winter; shrublands tend to give way to desert grasslands where monsoonal moisture dominates the precipitation regime (Brooks and Chambers 2011). The natural disturbance regime in these shrublands also varies systematically according to precipitation, which is itself usually correlated with elevation. At the low-precipitation and high-temperature end of the gradient, in the low-elevation Mojave Desert of the Southwestern United States, the historic disturbance regime was likely dominated by the periodicity and severity of long-term drought (Hereford et al. 2006; McAuliffe and Hamerlynk 2010). Fire caused by lightning strikes burned only small areas because of low productivity and the large proportion of bare ground. Even in high-precipitation years, the native desert annuals that make up much of the biodiversity in the Mojave Desert as well as any perennials that were present tended to be concentrated beneath shrubs because of the "fertile island" effect, with very little fuel production in the interspaces (Thompson et al. 2005). A similar pattern of historical disturbance is characteristic of the salt desert shrublands of the Great Basin, with long-term drought a major force for vegetation change but with fire playing a very minor role.

Other disturbance factors on a more local scale in these low-productivity deserts included the effects of overland flow from severe rainfall events on erosional and depositional processes and also more large-scale geomorphic events such as debris flows at longer intervals (Webb et al. 1987). Rodent workings are another important source of disturbance in deserts and can have a large impact on vegetation dynamics on a local scale (Kitchen and Jorgensen 1999).

In the more productive cold desert vegetation dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) at mid-elevation on the valley floors and bajadas in the Great Basin, decadal drought was probably still important as a disturbance factor. Fire was more important relative to the warm and salt deserts because of increased fuel loads, the presence of perennial bunchgrasses and perennial dicots in the shrub interspaces, and the lack of fire tolerance in the dominant shrub species. The fires were likely still relatively small and patchy, with return times measured in decades, resulting in a shifting mosaic of shrub-dominated and perennial grass-dominated vegetation (Whisenant 1990). On more productive and cooler upland sites, Wyoming big sagebrush gives way to mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) steppe, with a concomitant decrease in the importance of drought as a historic disturbance factor and an increase in the importance of, and resilience to, fire.

One historic disturbance factor that was conspicuously lacking in the arid and semiarid shrublands of the Interior West was the effect of large herding ungulates such as bison that played such an important role in grasslands to the east of the Rocky Mountains. When Europeans arrived on the scene, they brought domestic livestock in large numbers to these ecosystems, and the results were devastating (Mack and Thompson 1982). The bunchgrasses characteristic of desert and steppe vegetation were largely intolerant to grazing and were quickly eliminated, while the biological soil crusts that formed a continuous cover in the interspaces were readily destroyed by trampling. The stress of unregulated livestock grazing continued for decades in these ecosystems and caused a reduction in resilience that has resulted in dramatic vegetation changes. Another source of anthropogenic disturbance was clearing for rainfed agriculture that ultimately failed, leaving a legacy of huge tracts of abandoned farmland (Morris et al. 2011). Mining and energy development have created major disturbances and have also left a web-like network of roads over much of the desert, providing corridors of disturbance for plant invasion and also an invitation to off-road vehicle recreational use (Gelbard and Belnap 2003).

The introduction of livestock grazing into the shrublands of the Interior West created the "perfect storm" for plant invasion and the subsequent shift to an alternative stable state. The winter annual grasses that became the primary invaders were pre-adapted to livestock grazing and other forms of intense disturbance in their native Eurasian range. They were largely introduced incidental to agriculture, for example, as contaminants in grain seed, and they could readily disperse with livestock as the animals were allowed to range freely across the landscape (Mack 1981). They encountered environmental conditions similar to the steppe and desert habitats of Eurasia, and experienced little biotic resistance due to the destruction of both the perennial understory and the biological soil crust that could deter recruitment from seed. The depleted understory quickly became dominated by these grasses, chiefly cheatgrass and medusahead rye (*Taeniatherum caput-medusae*).

Once these disturbance-responsive annual grasses became dominant in the understory, the shrub overstory could not suppress them effectively, especially in years of above-average precipitation, when they formed a dense, continuous layer of highly flammable fine fuel. As a result, wildfire, always part of the disturbance regime in these systems, became the ascendant disturbance, resulting in the loss of shrub cover and conversion to communities that are hardly more than annual grass monocultures that burn repeatedly (Brooks et al. 2004; D'Antonio and Vitousek 1992). In this case of the interplay of chronic livestock grazing and resulting lowered resilience, annual grass invasion, and a subsequently altered fire regime were necessary to push the sagebrush steppe ecosystem over to an alternative stable state over millions of acres in the Intermountain West (Chambers et al. 2014). In an experimental study, cheatgrass increased in response to both perennial biomass reduction and burning, but the synergistic effect of both of these factors together increased its seed production by an order of magnitude relative to each factor alone (Chambers et al. 2007).

A similar process has played out with red brome (*Bromus rubens*) as the invader over large areas in the Mojave Desert, where wildfire has also become the ascendant disturbance factor in a system that basically evolved without fire and therefore has little fire resilience (Brooks and Chambers 2011). Increased fuel loads in the interspaces in high-precipitation years are the main drivers of these fires, which kill many desert shrub species outright and reduce the competitive ability of those that do manage to resprout. Even in highly fire-adapted shrubland ecosystems such as the California chaparral, disturbance of the understory and subsequent invasion of non-native winter annual grasses have increased the frequency of fire beyond the capacity of chaparral species to regenerate post-burn, so that these ecosystems too are undergoing conversion to annual grass-dominated systems (Keeley 2001; Zedler et al. 1983). Another anthropogenic disturbance potentially driving these changes to alien annual dominance is nitrogen deposition (Brooks 2003).

Most invasive plants in deserts have been accidentally introduced and are disturbance-responsive species, but there is also a potential for deliberately introduced species to become invasive in desert ecosystems, as they could be pre-adapted for success even in relatively undisturbed xeric environments. Invasive forage grasses such as buffelgrass (*Pennisetum ciliare*) are good examples (Stevens and Falk 2009).

5.8 Disturbance and Invasions of Consumer Organisms

Much of the literature on the invasion process has focused on invasive plants, and these studies are emphasized in the preceding discussion. It would be a mistake, however, to discount the importance of invasive species that are consumers rather than producers, including vertebrate animals, specialist insects, plant pathogens, and generalists such as earthworms. It is well known that specialist invaders, for example, the white pine blister rust pathogen (*Cronartium ribicola*; Kinloch 2003) and the hemlock woolly adelgid (*Adelges tsugae;* Eschtruth et al. 2006), can have profound and far-reaching negative effects on ecosystem structure and function that can rise to the level of an irreversible change of ecological state. What is less obvious is how invasive consumer organisms are impacted by disturbance regimes.

The concept of invasibility has been applied mainly to plant invaders (Lonsdale 1999), but the same principles can potentially be applied to the factors regulating the colonization and spread of invasive consumer organisms. Disturbance is less likely to be a direct regulator of consumer invasion than of plant invasion because plant establishment depends directly on the physical space or resource that is made more available by disturbance. In a comprehensive literature review, Lozon and MacIsaac (1997) concluded that disturbance was far less likely to be implicated in consumer invasions than in plant invasions. Notwithstanding, the broader concept of invasibility, which includes disturbance as one factor, can be useful in understanding invasions of consumer organisms.

5.8.1 Invasive Plant Pathogens

Non-native pathogen invasion is a widespread and global problem that is continually increasing (Fisher et al. 2012; see Chap. 2 of this volume for discussion). Though many introductions likely occur, there fortunately are still relatively few examples of invasive plant pathogens that have caused widespread ecosystem change in the United States (Aukema et al. 2010). These include white pine blister rust on five-needle pines (*Pinus* spp.; Richardson et al. 2010), chestnut blight (caused by *Cryphonectria parasitica*) on American chestnut (*Castanea dentata*; Anagnostakis 1987), and sudden oak death (caused by *Phytophthora ramorum*) on a variety of broadleaf trees in California (Grünwald et al. 2012; Rizzo and Garbelotto 2003).

The many ecological roles that fungi play within ecosystems, including nutrient acquisition, nitrogen cycling, and soil formation, make their connections to biological invasion and disturbance complex (Van Der Heijden et al. 2008). Little research exists on factors that drive successful introductions of plant pathogens, though studies have examined how native plant pathogens successfully infect their native hosts (Ennos 2014). Further, only a handful of studies examine how native pathogens fare under disturbance. Much of the research on biological invasion of fungi is focused on how, through anthropogenic introductions, fungi can be the drivers of disturbance as invasive or emerging plant pathogens or as fungal mutualists helping invasive plants with co-establishment in a new environment by improving their fitness and success (Desprez-Loustau et al. 2007). These topics are beyond the scope of this chapter.

Establishment or persistence of invasive plant pathogens depends on several basic principles for transmission to occur between the initial infected host and subsequent infections (Gilligan and van den Bosch 2008). Duration of the infection period is critical because infection must be sustained to ensure high propagule pressure to infect additional susceptible hosts; otherwise, the invasion will fail (Ennos 2014). Important to invasibility as well is the ability of the pathogen to persist during unfavorable environmental and various host demographic conditions (Gilligan and van den Bosch 2008). These can directly affect the ecology of the pathogen, as there are specific abiotic and biotic conditions that are required for success of a particular pathogen (Ennos 2014). Woods et al. (2005) showed that *Dothistroma septosporum*, the causal agent of the red band needle blight, required sustained wetness at 15–20 °C for successful spore dispersal and germination. In sites where these conditions are not met, the pathogen cannot thrive. Spatial and genetic heterogeneity of the host population can also be directly linked to the ability of a pathogen to become invasive (Burdon et al. 2006), as invasive pathogens can spread more quickly in single-species plantings such as poplar or pine plantations than in diverse, species-rich natural forest. Additional factors that can influence invasibility and rate of spread include transmission rate, host density, host susceptibility, and weather conditions (Gilligan and van den Bosch 2008).

Success by invasive pathogens is also thought to be driven by a lack of resistance in native hosts, the ability of fungal pathogens to evolve quickly, and their ability to produce many reproductive propagules (Gladieux et al. 2015). Host jumps occur through anthropogenic invasion events where pathogens are moved to new environments and are in contact with a susceptible host for the first time (Burdon et al. 2006). Native hosts have not evolved genetic resistance against new, invasive pathogens. Environment plays an important role as well. When ecosystems are subject to chronic stress due to drought or other factors, plants become more susceptible to invasive pathogens because their defense mechanisms are weaker. This could allow for host jumps that might not occur if plants were not under chronic stress conditions (Burdon et al. 2006).

Host jumps can also occur through pathogen evolutionary change resulting in the ability to be pathogenic on a new host present in the invaded range. One evolutionary mechanism is hybridization between two pathogens, allowing for a broader host range. Hybrids of *Melampsora medusae* (North American origin) and *M. larici-populina* (European origin) in New Zealand have resulted in offspring with a broader host range within *Populus* species than either parent (Burdon et al. 2006; Spiers and Hopcroft 1994), thus facilitating the spread of a new invasive pathogen.

5.8.2 Invasive Insects

As with plants and plant pathogens, most insect introductions likely fail to establish due to abiotic factors or other forms of environmental mismatch (e.g., lack of suitable host species) and also to Allee effects, i.e., processes that tend to cause extinction from initially low population size (Liebhold and Tobin 2008). Presumably, biotic resistance operates to keep most non-native insects at levels that have little impact, but cases where this biotic resistance fails can result in invasions with major ecological effects (see Chap. 2 of this volume for discussion).

Hemlock Woolly Adelgid

Biotic resistance to herbivorous insect invasion involves at least three basic mechanisms: host resistance, native natural enemies, and vegetation patterns, including the distribution of host plants relative to non-host plants on the landscape. The effectiveness of these mechanisms can vary even for the same insect invader. For example, the host-specific hemlock woolly adelgid from Japan has become a high-impact invader in eastern forests, where the hemlock species have little or no resistance, and natural parasitoid populations are inadequate to keep the invader in check (McClure and Cheah 1999; Wallace and Hain 2000). A related but genetically distinct species native in Western North American hemlock forests has only a minor effect, largely because western hemlock species have co-evolved with this insect and have some resistance (Havill et al. 2011). Native parasitoids are also more abundant and effective in western hemlock forests (Kohler et al. 2008). Predation by parasitoids has the potential to be a major component of biotic resistance to herbivorous insect invasion (Owen and Lewis 2001). This concept is the basis for the development of biocontrols for insect pests of plants, including hemlock woolly adelgid (Van Driesche et al. 2008).

Locally, the hemlock woolly adelgid is dispersed passively by wind. Experimental work has shown that even this passive mode of dispersal can result in dispersal distances of >1200 m in spring before deciduous trees leaf out and reduce wind speeds; even in summer with closed canopies, dispersal distances can exceed 400 m (Turner et al. 2011). The role of vegetation pattern in limiting rate of spread has been established for another passively dispersed insect, maritime pine bast scale (*Matsucoccus feytaudii*), a host-specific pest of *Pinus pinaster* in Europe (Rigot et al. 2014). These researchers found that the rate of spread was slowed by patches of non-host deciduous trees surrounding pine patches, an example of associational resistance on a landscape scale (Barbosa et al. 2009). The rate of spread was increased by high connectivity between patches of pine but also by the presence of non-forested open areas. This effect of openings could be interpreted as a result of disturbance that lowered biotic resistance to invasion.

Emerald Ash Borer

Insects that have an actively flying dispersal stage are much less likely to be slowed in rate of spread by heterogeneous landscapes and can achieve much larger dispersal distances. Emerald ash borer (*Agrilus planipennis*) has had a devastating impact on highly susceptible North American ash (*Fraxinus*) species (Herms and McCullough 2014). Mated females can disperse up to 10 km in their lifetime, enabling them to locate even widely dispersed host trees, and human-aided "host jump" dispersal through long-distance transport further accelerates the rate of spread (Muirhead et al. 2006). Few negative impacts of native predators or parasitoids on emerald ash borer have been reported (Duan et al. 2012). Trees that are stressed by other factors may be attacked first, and in the native range of emerald ash borer in China and Russia where the ash species have evolved resistance, only stressed trees are strongly impacted. In the Eastern United States, even otherwise healthy trees are frequently killed. Open-grown trees in landscape plantings are more likely to be killed than trees growing in shaded conditions, but this associational resistance is weak. The rapid spread and high ecological impact of emerald ash borer represents an invasion into "defense-free space" (Gandhi and Herms 2010), which represents the worst-case scenario for impacts of an insect invader—a case where biotic resistance does not seem to operate at all. Introduction of emerald ash borer natural enemies from the native range is one of the few remaining options for control in wildland settings (Duan et al. 2013). Habitats that support *Fraxinus* species are also likely to support emerald ash borer, meaning that abiotic constraints are not likely to limit its spread.

Gypsy Moth

Biotic resistance to generalist herbivore insect invaders presents a different scenario. Undoubtedly, the best studied of these is the gypsy moth (*Lymantria dispar*), a species that is known to feed on hundreds of species of woody plants, though it has a feeding preference for oaks (Elkinton and Liebhold 1990). Natural enemies and habitat heterogeneity both play a role in limiting spread of this species, or at least in regulating its patterns of outbreak and decline. Different classes of natural enemies operate to regulate gypsy moth abundance when it is at high versus low abundance. Host-specific pathogens play a major role at high densities, causing population crashes following epidemic outbreaks (Hajek et al. 2015). One of these, the Nuclear Polyhedrosis Virus (NPV), appears to have traveled with gypsy moth from its native range (Hajek et al. 2015), while the other, a fungal pathogen (*Entomophthora maimaiga*), reappeared as a natural control many decades after a biocontrol introduction from the native range in Japan (Andreadis and Weseloh 1990). Thus, these pathogens do not represent biotic resistance in the sense that they are native to the invaded ecosystem. Population regulation at low levels has been found to involve native rodent predation on the immature stages (Liebhold et al. 2000). The deer mice (*Peromyscus* spp.) that eat caterpillars and pupae are generalists that also rely heavily on oak mast (acorn production) and that prefer acorns to caterpillars as a food source. Caterpillar mortality levels are a function of rodent abundance (which in turn is correlated with weather patterns) and exhibit high spatial synchrony. This could be an explanation for the observed spatial synchrony of gypsy moth outbreaks (Liebhold et al. 2000).

Rates of spread for gypsy moth are uneven, resulting in patchy distributions that are not necessarily associated with underlying environmental heterogeneity. Jankovic and Petrovskii (2013) showed that Allee effects at low densities and disease (NPV) at high densities coupled with a diffusion dispersal model can generate these patterns. Because gypsy moth females are flightless and attract males through pheromones, the difficulty of mate-finding at low densities can cause local establishment failures, limiting the effectiveness of human-assisted long-distance dispersal. The moths disperse locally only as ballooning first instar larvae, which limits their primary dispersal distance, and epidemic disease at gypsy moth outbreak levels as described earlier also affects spread dynamics.

Habitat heterogeneity has also been shown to affect rates of gypsy moth spread. Topographic relief increases reproductive asynchrony and thus further increases the difficulty of finding mates, increasing the Allee effect (Walter et al. 2015). On the other hand, forest fragmentation that increases the relative importance of forest edges on the landscape increased gypsy moth mating success via its effects on male flight behavior and the aerodynamics of pheromone plumes (Thompson et al. 2016). This could be interpreted to mean that disturbance that creates fragmentation and forest edges could be a factor accelerating gypsy moth spread.

Generalist Insect Predators

Generalist predators are another class of insect invaders. These have a propensity for occupying areas disturbed by human activity, which makes them more noticeable to humans (Snyder and Evans 2006). Important generalist predators are invasive ants and to a lesser extent vespid wasps, mantids, and ladybird beetles. Many species are almost completely restricted to anthropogenic disturbances; these include the "tramp ants" that are rarely found far from human habitation (Holway et al. 2002) and mantids that can occupy old fields but cannot move into nearby forested areas (Snyder and Evans 2006). Even species like fire ants (*Solenopsis invicta*) that can invade natural systems are favored by natural disturbances that resemble the floodplain disturbances that are characteristic of their habitat in the native range (Snyder and Evans 2006). Therefore, the biotic resistance presented by undisturbed native vegetation is probably a factor in reducing the importance and spread of these generalist predators in North America. However, there are exceptions to the generalization that biotic resistance can reduce ant invasion and subsequent negative impacts, particularly on oceanic islands in the tropics (Hoffman and Saul 2010; O'Dowd et al. 2003; Wetterer 2005).

Native ant species can also present biotic resistance to introduced ant species through interference competition, though the outcome is often the opposite due to the aggressive nature of many of the introduced species. But while short-term negative impacts on native ants have been reported, in one long-term study, native ants returned to pre-introduction levels in spite of the continued presence of fire ants, a clear case of biotic resistance (Morrison 2002).

5.8.3 Invasive Earthworms

Earthworms are among the most abundant soil macroinvertebrates in temperate and tropical ecosystems. They are ecologically and taxonomically diverse, exhibiting the capacity to occupy different habitats ranging from truly arboreal to deep mineral soil horizons and have approximately 3,000 described species worldwide (Edwards et al. 2013). Earthworms are often termed ecosystem engineers (*sensu* Jones et al. 1994) because of their ability to physically alter the environments they inhabit. They are responsible for the processing of surface and mineral-associated soil organic matter, and through their burrowing and feeding activity, they are known to increase soil porosity, water infiltration, gas diffusion, and soil aggregate formation and to contribute to increased plant productivity (Edwards et al. 2013). See Chap. 3 of this volume for a more complete description of earthworm effects on biogeochemical processes.

Earthworms also occupy a critical position in terrestrial food webs and represent an important channel through which nutrients and energy flow from detrital pools to higher trophic levels, as they are consumed by other invertebrates, birds, herptiles, and mammals (Blackman et al. 2012; Catania 2008; Gorsuch and Owen 2014; Maerz et al. 2005; Richardson et al. 2015). There are numerous "peregrine" earthworm species that have been transported and introduced around the globe, and of these, there are perhaps 45 species introduced into North American soils (Hendrix et al. 2008). When non-native earthworms become established, they have been shown to significantly alter ecosystem properties ranging from plant population dynamics (e.g., Gundale 2002) to biogeochemical cycling (e.g., Cameron et al. 2015).

In North American soils, there are two distinct scenarios that must be considered when discussing earthworm invasions. These have to do with the fact that much of the continent was covered in glacial ice sheets as recently as 10,000 years ago. In the first case, following the retreat of glaciers, the underlying soils developed in the absence of earthworm influences, whereas in the second case, soils of mesic environments that did not experience glaciations were continuously inhabited by native earthworm species (James 2004). These different starting conditions have had a strong influence on the impacts and invasion patterns that have been observed for invasive earthworm species introduced primarily from Europe and Asia (Frelich et al. 2006; Hendrix et al. 2008).

Disturbances and Invasive Earthworms in Glaciated Soils

The earliest records of European and Asian earthworms in the glaciated portion of North America come primarily from agricultural soils, from extensive surveys conducted along roadsides, and generally from areas that otherwise experienced some form of human disturbance (Reynolds 1995). These records suggest that human-mediated transport of earthworms has been responsible for establishment of invasive populations, and the dumping of ship ballast, movement of horticultural materials, and use of non-native earthworms as fish bait have all been implicated as important vectors of the invasive species (Callaham et al. 2006a; Hendrix and Bohlen 2002). More recently, however, it has become clear that invasive earthworms are now actively colonizing less disturbed or even pristine forested habitats of the glaciated portions of the continent (Frelich et al. 2006).

The introduction of invasive earthworms into less disturbed habitats is still thought to be driven primarily by human activities (i.e., disturbances), and in one study the age of roads constructed in northern boreal forests was a strong predictor of the extent of earthworm invasion (Cameron and Bayne 2009). These authors also showed that the distance of a particular forested habitat from active agriculture was related to earthworm invasion, and they further developed a predictive model showing the relationship between road density and the likely extent of new earthworm invasions. Another study found that road building and harvesting in a small portion of a forested watershed were enough disturbance to allow earthworms to become established throughout the watershed, and that the earthworms were passively dispersed along stream corridors into areas otherwise unaffected by the harvesting activity (Costello et al. 2011). In addition to this general pattern of association with roads, earthworm invasions can also occur in essentially roadless areas such as the Boundary Waters Canoe Area Wilderness where recreational use is high.

Disturbances and Earthworm Invasions in Non-glaciated Soils

The relationship between soil profile-disrupting disturbances and the advent of non-native-dominated earthworm communities have long been recognized (Stebbings 1962), as early observers noted the loss of native species from and the incursion of European species into agricultural soils of the Midwest. Indeed, in soils where native earthworm species might be found (i.e., in soils south of the most recent glacial maximum, including the Southeastern States and some soils along the Pacific coast (James 1995, 2004)), it is extremely rare to find pure assemblages of native earthworm species in soils that experience regular tillage or other profile disruption (Hendrix et al. 2008). However, these profile-disrupting disturbances need not affect large areas of land, and other researchers have found that roads built through otherwise undisturbed habitats can serve as corridors for the introduction of non-native earthworms into less disturbed habitats (Kalisz and Dotson 1989; Kalisz 1993). In other parts of non-glaciated North America, workers have observed a relationship between land-use history and the prevalence of non-native earthworms in soil invertebrate communities, with a clear indication that perturbations to vegetation and soil result in a dominance of the earthworm community by European species (e.g., Callaham et al. 2006b; Sanchez de Leon and Johnson-Maynard 2009; Winsome et al. 2006). This and other evidence has led to the development of ideas around the influence of disturbance gradients and the resulting likelihood that a particular community will include non-native invasive earthworms (Fig. 5.3). Included in this line of reasoning is the observation that native earthworms and/or other macroinvertebrates in the forest floor may offer some biotic resistance to the invasion of non-native earthworms. Snyder et al. (2011) found that earthworm invasions in the field were associated with lower diversity and abundance of millipedes. In laboratory microcosms, Snyder et al. (2013) found that millipedes prevented the earthworms from producing cocoons, and this may limit or slow invasive spread into forests.

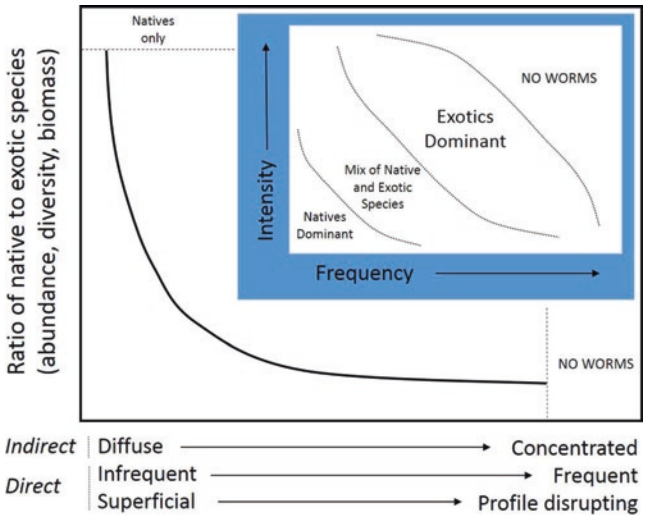

Fig. 5.3 Conceptual diagram showing the relationship between the composition of the earthworm community (ratio of native to non-native species) and disturbances. Observations from the field support the hypothesis that in soils where both native and non-native earthworms occur, the ratio of native to non-native earthworm abundance is related to disturbance level. The *inset* provides a more nuanced view of the nature of these relationships and acknowledges the interplay of disturbance frequency and intensity. Disturbances (*x-axis of main plot*) can be indirect or direct. An example of an indirect disturbance is the establishment and spread of an invasive plant, which modifies the environment to be favorable for invasive earthworms. An example of a direct disturbance would be annual tillage of an agricultural field (Modified from Hendrix et al. 2008)

Invasive Earthworm Interactions with Other Invasive Species

There is growing evidence that introduced earthworms and invasive plants may be involved in a synergistic “invasional meltdown” relationship (*sensu* Simberloff and Von Holle 1999). This has been suggested in shrub invasions of ecosystems both in the Great Lakes region as well as in the riparian forests of the Southeastern United States. In deciduous forests of the Great Lakes, European buckthorn (*Rhamnus cathartica*) is an invasive shrub that is currently expanding its range, and there have been observations of greater densities of non-native European earthworms beneath the canopy of this species in some cases (Heneghan et al. 2007; Wykoff et al. 2014). Furthermore, in other studies where European buckthorn was removed through management activities, the density of European earthworms declined (Madritch and Lindroth 2009). Similarly, in southern riparian forests where Chinese privet (*Ligustrum sinense*) has invaded extensive areas, the abundance of non-native invasive European earthworms increased, but these densities were reduced five years after removal of the shrub (Lobe et al. 2014). Removal of the shrub was also associated with the recovery of native earthworm populations, and the authors hypothesized that the plant’s influence on soil pH may be the underlying mechanism driving these earthworm species responses (Lobe et al. 2014).

Invasive Earthworms and Fire

Studies on the potential interactions between fire and invasive earthworms have been few, but due to the sometimes profound effects that fires can have on soils and vegetation, there is the expectation that there should be at least indirect effects on earthworms. In North American tallgrass prairies, fire is considered a necessary component of the ecosystem, and when fires are suppressed, the vegetation will shift away from grasses and toward woody species (Knapp et al. 1998). In one study explicitly examining the effects of prescribed fire on prairie invertebrates, Callaham et al. (2003) found that native earthworms were favored by fire, but that when fire was excluded for 20+ years, European earthworms dominated the community. In a study of earthworm/fire interactions in boreal forests of North America, Cameron et al. (2015) suggested that introduced earthworms interact with soil carbon in such a way that losses of forest floor carbon attributable to wildfires should decline as European earthworm invasions progress in these forests. In still another earthworm/fire interaction study, Ikeda et al. (2015) explored the use of prescribed fire as a way to manage invasion of southern forests by litter-dwelling Asian earthworm species, and found that experimental fires did not have significant direct effects on adult worms, but that the fires had strong negative impacts on the cocoons of the invasive species, potentially limiting their population levels in the following year. There have also been documented cases of completely neutral effects of fire on invasive earthworms (Scharenbroch et al. 2012).

5.8.4 Invasive Terrestrial Vertebrates

Introduced terrestrial vertebrates in the United States are well documented to cause major ecological harm (see Chap. 2 of this volume). The conditions upon which successful vertebrate invasions are predicated were examined in a meta-analysis that included invasions in both Europe and North America (Jeschke and Strayer 2006). Frequency of introduction and "human affiliation" were identified as the most important factors. In contrast to the case with invasive plants, traits associated with life history were relatively unimportant in invasion success; instead, the direct and indirect effects of human activities were much more likely to predispose a vertebrate species to invasion success than any specific set of biological attributes.

The close association of many invasive vertebrates, for example, rats (*Rattus* spp.) and English sparrows (*Passer domesticus*), with humans implies that anthropogenic disturbance favors their increase and that relatively undisturbed natural systems must possess some biotic resistance to invasion. But there is little evidence to suggest that disturbance of a natural system reduces its resistance to invasion by these "human commensal" species, unless this disturbance results in a major land-use change to a human-dominated landscape (Jeschke and Strayer 2006). Invasive vertebrates that pose a more direct threat to natural ecosystems are more often species that were introduced for hunting or that represent escapes from the exotic pet trade. The invasibility of a natural system to an introduced vertebrate that is preadapted to the environment does not seem to be contingent upon level of disturbance. This conclusion is supported by Lozon and MacIsaac (1997), who reported that only 11% of examined studies on terrestrial vertebrate invasions mentioned disturbance as a predisposing factor.

European Starling

The European starling (*Sturnus vulgaris*) is a classic example of a human commensal invasive species that does tremendous damage to US agriculture (Linz et al. 2007). Starlings also have negative impacts on natural systems, specifically in competition with native cavity-nesting birds (Purcell 2015). In a study in the steppe of central Washington, starlings visited sagebrush steppe habitats but did not nest there (Brandt and Rickard 1994). Purcell (2015) showed that starlings forage in mowed areas in preference to areas with taller vegetation, which could explain why they preferred abandoned agricultural land to sagebrush steppe in the Washington study. She suggested that managing vegetation height might be a way to protect native cavity-nesting birds from the negative impacts of starlings.

Wild Boar

An example of an invasive vertebrate that was introduced for hunting is the wild boar (*Sus scrofa*). This species can thrive over an extremely wide range of environmental conditions, as evidenced by both its large native range in Eurasia and its ability to invade both tropical and temperate ecosystems worldwide (Barrios-Garcia and Ballari 2012). The spread of wild boars is favored by the expansion of agriculture because of the rich food source represented by agricultural fields, and wild boar abundance in natural systems depends on the availability of preferred foods rather than on the level of disturbance. The main effect of wild boars on natural ecosystems is through their rooting activities, which can have a major negative impact on herbaceous vegetation. There is evidence that plant communities that are adapted to frequent surface disturbance are more resilient to wild boar rooting disturbance, with even some positive effects reported (Baron 1982; Kotanen 1995). This represents a form of biotic resistance in that it potentially reduces the negative impacts of this invader, but there is no reported mechanism of biotic resistance that prevents its establishment and spread.

Burmese Python

The Burmese python (*Python bivittatus*), one of the largest snake species in the world, represents a new category of vertebrate invader that has resulted from the rapidly expanding market for exotic pets. These kinds of animals are not human commensals and do not depend on anthropogenic disturbance for their success in either the native or the introduced range. Consequently, when they are released deliberately or accidentally into the wild in ecologically suitable areas, they are able to establish and spread rapidly across a broad spectrum of disturbance regimes. Burmese pythons apparently have few or no natural enemies in their introduced range in south Florida, and their dramatic negative impact on native mammals has manifested itself very rapidly (Dorcas et al. 2012). The spread of Burmese pythons in the United States is limited by cold temperature and dry conditions, but climate modeling, based on the occupied native range, indicates that they could spread across the South and even along the Pacific Coast under the current climate regime and could spread even farther north in response to climate change (Rodda et al. 2009).

5.9 Disturbance and Invasive Species Management

The strong link between anthropogenic disturbance and invasion, especially for plants, suggests that managing to reduce anthropogenic disturbance in vegetation not yet impacted by strong invaders is the most straightforward and cost-effective tool for reducing the probability of such an invasion (Firn et al. 2008; MacDougall and Turkington 2005; Marvier et al. 2004). This generalization applies primarily to species that are disturbance-dependent, but as anthropogenic disturbance also increases the probability of propagule arrival, decreasing disturbance can also reduce the probability of arrival of an invader that does not depend strongly on disturbance to establish. These authors emphasize the difficulty and expense of attempting to manage the ever-growing cadre of invasive organisms one species at a time through active control. Extraordinary investment of time, resources, and funding in active control of invasive species has often yielded equivocal results (e.g., Martin and Blossey 2013 for common reed). It should be more cost-effective to address the underlying facilitator of most plant invasions, namely anthropogenic disturbance, more directly. While many human-related activities that create disturbance in natural vegetation are probably difficult to regulate or eliminate, this tactic should be considered and used to the maximum extent possible. It may become more of a priority to limit human impacts if a known strong invader has already established along disturbance corridors in the area.

Weed-Shaped Holes

An often-overlooked source of disturbance in invasion biology is the disturbance created by weed control activities themselves. These activities create “weed-shaped holes” that are prime sites for invasion by secondary weeds and also for reinvasion (Buckley et al. 2007). Pearson et al. (2016) in a meta-analysis found that a large majority of weed control efforts that are successful in terms of controlling the target weed are subsequently beset by the problem of secondary weed invasion and experience very limited recovery of native vegetation. The importance of minimizing anthropogenic disturbance especially in areas adjacent to weed-infested patches has also been emphasized (Firn et al. 2008; Marvier et al. 2004), along with the obvious need to target secondary weeds in the initial control effort, to fill the “weed-shaped hole” with invasion-resistant native vegetation as quickly and efficiently as possible, and to protect it from subsequent disturbance (Pearson et al. 2016).

Identifying Problematic Invaders

Another difficult problem for managers is determining which introduced species are likely to be strong invaders with potentially major impacts on invaded plant communities (Ortega and Pearson 2005). As discussed earlier, the majority of non-native species that arrive and establish along disturbance corridors in a particular vegetation type are unlikely to have a major impact due to a combination of abiotic and biotic resistance and intrinsic species traits (e.g., growth rate, seed production). Given the globalization of world trade and the range of broad-scale anthropogenic disturbances such as global warming and nutrient pollution that are largely beyond management control, it seems inevitable that the species composition of natural vegetation will include increasing numbers of introduced species (Davis et al. 2008). Ecologists predict the emergence of “novel ecosystems” that will include species combinations that have never before coexisted (Hobbs et al. 2009).

The inevitability of colonization by non-native species does not mean, however, that efforts to prevent invasive species from pushing ecosystems into less desirable alternative stable states should be abandoned. Monitoring the abundance of individual species through time, perhaps in plots already established for some other purpose, can provide this kind of information (Strayer et al. 2006). The lag-time phenomenon in biological invasions adds to the difficulty of distinguishing the weak from the strong, however, because it may take a long time for a potentially strong invader to manifest itself with respect to a particular ecosystem. However, a potentially strong invader has probably shown its true colors in similar ecosystems elsewhere, and this is one of the best predictors of subsequent invasion behavior.

5.10 Knowledge Gaps and Research Needs

Many of the review papers cited earlier that address the history and impacts of even important and apparently well-studied invaders remark on the surprising lack of experimental studies or even rigorously collected quantitative field data that address the question of the underlying causes of invasion into a particular ecosystem. Ecologists have tended to focus on theoretical questions and to use whatever native or non-native species were tractable for addressing those questions, and even when these studies produce results that are useful to managers, they often are not readily accessible. Recently, the focus on “model invasive species” (e.g., Colautti et al. 2014b) attempts to address this somewhat piecemeal approach, but it hinges on the assumption that knowing everything there is to know about a few species will cast light on the invasion process for many others. One alternative, namely in-depth experimental and field studies of each invasive species of interest, is clearly not practical, given the urgency of the problems and the decisions that managers must make to address them. A more useful approach for basic research might be to classify environmental factors that drive species invasion and perform studies designed to elucidate the relationship between these drivers and consequent invasion for multiple invasive species.

The work of Guo et al. (2015) and Iannone et al. (2016) suggests another approach that might provide information on invasibility and invasiveness more quickly than experimental studies, and this approach could be applied to specific ecosystems, as well as to specific invasive species. As discussed earlier, long-term data sets available from the Forest Inventory and Analysis Program (www.fia.fs.fed.us/) were used to address the relationship between vegetation characteristics and both invasibility and invasion by non-native plants in general. The conceptual model of Guo et al. (2015; Fig. 5.1a, 5.1b) could also be used as a framework for addressing questions about the distribution and abundance of individual species relative to these vegetation characteristics. There may be other long-term data sets, for example, from LTER (Long Term Ecological Research Network) sites and USDA Forest Service Experimental Forest and Range sites that could be used for this purpose in non-forested systems. With careful matching, a suitable reference data set for the undisturbed stage could be selected for a particular site and then compared with current biomass and species richness data as an estimate of invasibility (Fig. 5.1a). Relative cover of individual non-native species on multiple dates could be used as a measure of the progress of the invasion through time. Although this approach is strictly correlative and cannot establish causal relationships, it could give managers some valuable information about the ecological behavior of both weak and strong invaders. The practicality of this approach depends on the availability of suitable data to address the management question at hand. A first step would be to determine whether existing data sets could be used in this way.

5.11 Key Findings

- The probability of establishment and spread of invasive plant species generally increases with increased disturbance and decreases with increased native biodiversity.
- Invasive plants that were deliberately introduced for horticulture are more likely to invade undisturbed forests than accidentally introduced weedy species.
- The probability of insect pest and plant pathogen invasion is not closely tied to either disturbance or native biodiversity but instead depends more on availability and spatial distribution of suitable hosts.

5.12 Key Information Needs

- Better methodology for assessing invasibility (vulnerability to invasion) and degree of invadedness for different ecosystem types.
- Improved understanding of the role of dispersal corridors and propagule pressure in mediating the pattern and speed of invasion.
- Experimental studies that address specific environmental drivers that affect groups of invasive species in a similar way, enabling generalization beyond individual species.
- Improved understanding of the ecological differences between invasive species and non-native species that do not become invasive, including development of models predicting the likelihood of invasion into specific ecosystems based on species functional traits.

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