Ecosystem resistance to invasion and the role of propagule supply: A California perspective

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Abstract

The concept of ecological resistance includes both abiotic and biotic features of a recipient environment that influence the success of propagules of a species that has not previously occurred on a site. Despite broad interest in this topic by ecologists and land managers, we lack an understanding of what factors contribute to ecological resistance and how processes influencing resistance interact with the supply of propagules to determine invasion success. Here we present a simple conceptual framework for examining how variation in propagule supply should interact with ecosystem resistance to influence the rate at which exotic invaders enter a habitat. We suggest that when resistance is low, it takes very few propagules for an invader to become established and that rates of invasion will be fast regardless of propagule supply. As resistance increases, however, it takes proportionally more propagules for the invader to establish. When resistance is high invasion will occur only when propagule pressure is high or when invaders themselves can alter resistance as they get a toehold in the community. When resistance is controlled largely by biotic factors we believe that it can be overcome by high rates of propagule supply even if initially appears to be strong, because over space and time biological sources of resistance are likely to be variable allowing windows when a site has moved to a region of the propagule supply axis where many fewer propagules are required for invasion to occur. By contrast, strong abiotic resistance is less likely to be overwhelmed by high propagule pressure and if determined largely by soil factors, is likely to be relatively constant over space and time. We also suggest, that some invaders of harsh environments are successful because of their own ability to modify abiotic conditions thus decreasing the number of propagules needed to promote further invasion. We review examples of resistance in California plant communities and where possible show how resistance interacts with propagule supply. Overall, we found very few studies that measure or consider the role of propagule supply and how it interacts with resistance factors and we believe that such studies are badly needed if we are to advance our understanding of controls over biological invasion.

Introduction

In his seminal book, *The ecology of invasions by animals and plants*, Elton (1958) called attention to the devastating impacts that biological invasions have on native species. However, he also pointed out that most introduced species actually fail to establish self-replacing populations. To explain this establishment failure, he introduced the concept of “ecological resistance,” the natural processes or ecosystem properties that negatively influence invasion success. In the time since Elton’s landmark book, interest in the success and impact of non-indigenous species has skyrocketed, yet our understanding of ecological resistance remains fragmentary. A better understanding of resistance is important for predicting communities that will be most susceptible to future invasions and for advising managers on how to enhance ecological resistance. Maximizing ecological resistance may be a means by which to constrain the spread and subsequent damage done by unwanted invaders.

Interest in ecological resistance has spurred efforts to understand which communities are most invaded and impacted by non-indigenous species. Recent surveys indicate that several Mediterranean ecosystems including those in California contain some of the highest numbers of non-indigenous species on the planet (Macdonald et al., 1988; Mooney et al., 1986; Kruger et al., 1989; Usher et al., 1988). Possible explanations include: ecological resistance may be weak in some Mediterranean communities because of regular disruption by natural or anthropogenic disturbances. Alternatively, resistance may be substantial but may be overwhelmed by a large supply of exotic species to these regions because of high human activity. This high propagule pressure might also be explained by the fact that since Mediterranean systems are distributed worldwide, and since many of their invaders come from other Mediterranean habitats
(Mooney et al., 1986; Fox, 1990; Rejmanek et al., 1991), there is simply a large pool of species well adapted to similar climatic conditions and that pool is being very actively moved. Without knowing more about the flow of propagules among regions, it is impossible to evaluate the importance of ecological resistance in any given area.

The basic theme of this manuscript is that variation among communities in their susceptibility to invasion can be attributed to biotic and abiotic factors, and to the supply of invader propagules (Lonsdale, 1999). Here we examine our knowledge of how these factors affect the success of non-indigenous plant species in California’s Mediterranean ecosystems focusing largely on plant invasions since plants are the focus of our individual research. Our major goal is to review empirical evidence about resistance in California and develop a conceptual framework linking resistance and propagule supply that generates predictive, testable hypotheses regarding community susceptibility to invasion.

Our decomposition of the controls over invasion into propagule supply, abiotic factors and biotic factors is not without precedence in community ecology. Plant ecologists, for example, have debated whether populations are limited by the arrival of seed or the availability of suitable or “safe” sites (Harper, 1977; Crawley, 1990; Turnbull et al., 2000). Meanwhile, marine ecologists have grappled with competition-predation (Menge & Sutherland, 1976) versus “supply-side” explanations for community patterns (Gaines & Roughgarden, 1985; Roughgarden et al., 1988). Because of the parallels between these issues and invasibility (sensu Rejmanek, 1989), we feel that approaching the invasion of Mediterranean systems from a general community perspective is fruitful.

General framework

Elton’s original use of the term “ecological resistance” included both abiotic features of the environment and biotic features of the community occupying a site. Beginning with Elton, community susceptibility to invasion has largely been treated as a yes/no issue: communities are either deterministically resistant or susceptible to the invasion of a particular species (Fig. 1). Realistically, however, communities vary continuously in their susceptibility to invasion, making invasion success a probabilistic process (Fig. 1). A single community can vary in its location on a resistance continuum depending climate, disturbance, herbivory and natural succession (Davis et al., 2000). “Natural” and anthropogenic disturbance will tend to push a community towards the susceptible end of the continuum (Hobbs, 1989; Hobbs & Huenneke, 1992; D’Antonio et al., 1999), while managers desire to push or keep communities nearer the resistant end. Where a community lies on this continuum dictates the number of arriving propagules that it takes to establish a population. Viewed in this way, propagule supply rates play an important role in determining the ultimate success of invaders. Where environmental resistance (biotic or abiotic) is strong, propagule supply must be great for invasion to occur. By contrast, where resistance is weak or temporally variable, propagule supply need not be as great to overcome resistance. Since the invaders’ reproductive biology is an important determinant of propagule pressure, we might see a
wider range of invader reproductive traits in less resistant habitats. Alternatively, less resistant habitats may rapidly switch to being more resistant if a competitively superior invader arrives early.

In California, invasive non-indigenous species are well known to be abundant near the coast, in counties with large urban areas, and near roads, disturbance corridors and structures (Mooney et al., 1986; Knops et al., 1995; Zink et al., 1995; Randall et al., 1998). Thus, human disturbance and propagule pressure are likely major contributors to the invasion of California ecosystems. Nonetheless, there is intense human contact with some California systems that are not very invaded suggesting that California ecosystems vary in the strength of mechanisms that influence invasion resistance.

Abiotic factors affecting invasion success in California ecosystems

The important role of abiotic factors in limiting the entry of exotic species into new areas has been strongly emphasized by several researchers (e.g. Simberloff, 1986, 1989; Baker, 1986; Ehler, 1998; Alpert et al., 2000). Indeed, it is assumed that climate matching (a coarse scale abiotic factor) is a precondition of successful invasion (Baker, 1986). Potential abiotic constraints on invasion include harsh or toxic soil conditions, prolonged summer drought, repeated scouring or submergence by water, and severe climatic conditions such as those in deserts or high montane habitats.

In California, an example of abiotic resistance appears to be the limited success of European annual species on serpentine-derived soils while they thrive on adjacent unaltered soils (McNaughton, 1968; Mooney et al., 1986; Harrison, 1999a,b). Harrison (1999a) surveyed a wide range of serpentine outcroppings in northern California and found that the cover of exotic species was positively related to the Ca++ content of the soil. Low Ca++ patches of serpentine soil had very few exotics despite being surrounded by a sea of European annual species on unaltered soils. Interestingly, small patches of serpentine showed a much stronger positive correlation between soil Ca++ and number of exotic species than large patches of serpentine, potentially because they are more susceptible to propagule swamping. On a small serpentine outcropping in central California, Huenneke et al. (1990), found that harsh conditions on serpentine could be alleviated somewhat by fertilization which then allowed for invasion by exotic grasses.

Most evidence for the role of abiotic resistance in limiting invasions into California's Mediterranean ecosystems is based on species lists. For example, of all of the major eco-regions in California, the California deserts (Mojave, Colorado/sonoran, and montane deserts) contain the lowest number of exotic species per km² (mean=27). This cannot strictly be due to distance from the coastal sources of propagules, because regions such as the Sierra Nevada foothills are at least as far from areas of introduction (Los Angeles or San Francisco) as many parts of the Mojave desert (24 species/km²) but they contain significantly more exotics per km² (mean for Sierra Foothills=85, Randall et al., 1998).

Lonsdale (1999) examined species lists from around the world and also concluded that deserts contain distinctly fewer exotic species than most other habitats (except islands) and Alpert et al. (2000) looked at evidence from a range of spatial scales and concluded that water stressed environments have reduced levels of invasion. Those species that have established in California deserts often alter the abiotic environment during invasion (Kemp & Brooks, 1998) and therefore modify abiotic resistance. For example, exotic annual grasses such as Bromus spp. create litter that decays slowly. This litter traps moisture, enhancing conditions for seed germination of the invaders (Evans & Young, 1970; Young & Evans, 1985) thus partially ameliorating abiotic stress.

The number of exotics per km² declines with elevation in the Sierra Nevada (Mooney et al., 1986; Randall et al., 1998) suggesting that severe winter conditions may limit the invasion of upper montane environments. However, the relative roles of propagule pressure versus abiotic factors in driving patterns of invasion across elevational or climatic gradients has yet to be examined. Also unexplored is the potential role of abiotic disturbance such as flooding or fire in reducing the invasion of exotic plants many of which are not adapted to such disturbances. Burns & Sauer (1993) suggest that chaparral fires have been important sources of abiotic mortality for introduced conifers in coastal mountain plantations. Other factors may also account for the lack of spread of these plantation trees (see below).

With the exception of studies on Serpentine soils (e.g. Huenneke et al., 1990; Hobbs & Mooney,
1991), little experimental work has examined the role of abiotic factors in limiting invasions in California. While manipulation of abiotic features is a difficult management action, better understanding the role of abiotic features in influencing invasion success could aid our understanding of where restoration and exotic species control is most likely to be effective. Likewise, identifying those invaders capable of reducing abiotic resistance as they invade may help to prioritize species for control.

**Biotic factors affecting invasion success in California ecosystems**

Elton (1958) and others (e.g. Simberloff, 1986, 89; Lawton & Brown, 1986; Ehrlich, 1989) have focused largely on competition and predation/parasitism in their consideration of biotic mechanisms of resistance. Nonetheless biotic resistance can result from any of the following: (1) Competition including, [a] preemption or priority effects whereby established native species keep out potential invaders and [b] competition among seedlings or regenerating individuals of native and exotic species after disturbance. In this latter case, it is the relative ability of native versus exotic species to colonize or regenerate that influences invasion. This dichotomy has not typically been included in discussions of resistance mechanisms. (2) Predation or parasitism by native or previously established organisms may prevent invader propagules from establishing and reproducing. (3) Attack by indigenous pathogens. (There is no published information on this topic for California plants so we will not discuss it further). (4) Limited availability of required mutualists. In the latter case, resistance may arise from a depauperate mutualist biota or competition from native species that limits the availability of mutualists (e.g pollinators or dispersers) for the invaders. Experimental tests for biotic resistance mechanisms are few. Perhaps this is because in their purest form they would involve introducing potential invaders into native-dominated habitats where they are currently rare or absent while manipulating the biological environment. Nevertheless, several experimental studies have examined mechanisms influencing invasion by exotics that are already established in California and these provide useful insights into the role of community structure in affecting invasions.

**Competition**

Peart (1989) introduced seeds of non-native species into patches where existing grassland species had been killed by insecticide but the soil was undisturbed. Virtually no establishment occurred if the resident species weren’t killed. D’Antonio (1993) introduced seeds and seedlings of *Carpobrotus edulis* near to and away from shrubs to test for facilitative or interference effects of shrubs in a dune and coastal scrub habitat. Weak competitive effects were present in some years, while in other years shrubs had no effects or were facilitative. Evidence for the role of competition at broader scales comes largely from anecdotal observations and descriptions of communities where invaders are generally lacking (Baker, 1986). Several investigators have observed that mixed conifer forests, hardwood forests and dense chaparral are depauperate in introduced species in California (Baker, 1986; Mooney et al., 1986; Randall et al., 1998). It is assumed that competitive suppression by light limitation is the cause although the role of herbivores or pathogens has not been examined.

Most often, the role of competition in limiting invasion by exotics is inferred from studies of disturbance or species removals or from negative correlations between vegetation stature and presence of exotics (Mooney et al., 1986; Rejmanek, 1989). D’Antonio (1993) and Peart (1989) introduced propagules of non-native perennial species into manually disturbed and undisturbed coastal grassland in California and found that seedlings germinated but survived poorly in undisturbed plots presumably because of competition from grassland species. By contrast, on artificial and natural rodent disturbances the invaders survived quite well. Likewise, Schiffman (1994) found that disturbances associated with kangaroo rats promoted a community of annual exotics in an interior grassland that otherwise had a reasonable component of native annual species.

Most invasion/disturbance studies do not document the mechanism through which disturbance promoted invasion but alteration of the competitive environment with resident species is likely to be important. Disturbance can facilitate invasion by other mechanisms such as direct stimulation of the seed bank. While these studies suggest that preemption type competition can suppress invasion, they likewise point to the important role that native sources of soil disturbance play in promoting inva-
sion. In many California grasslands, rodents and other vertebrates are a constant source of soil disturbance (Schiffman, 1999) turning over up to 25% of the soil per year (Hobbs & Mooney, 1991, Schiffman, 1999). Thus, these environments may lack strong biotic mechanisms of resistance because they are and have been disturbed by animals for centuries (Schiffman, 1999). Furthermore, many of the native species in these communities apparently lack the regenerative ability of introduced species. Perhaps when resistance comes down solely to regenerative ability, communities are always susceptible to invaders with superior regenerative powers.

In contrast, disturbance does not favor exotic invaders in communities in which many of the native species are better at regeneration. For example, Kotanen (1995) found that disturbance by feral pigs, which reduced native perennial grass cover in a northern California meadow, favored both native and exotic annual species, all of which had a dense seedbank. Eventually native perennial species from the surrounding area recolonized the disturbances. Interestingly, disturbances in some of these same meadows are now being invaded by Holcus lanatus, a persistent perennial grass from northern Europe that also has very rapid colonization and growth capabilities.

Apparently, the invasion of better colonizing and highly persistent exotic species has not yet happened in California chaparral—a vegetation type with numerous native species capable of rapid regeneration after fire. Though annual exotic species often colonize after fire, they do not persist: chaparral has remained dominated by native perennial species (Mooney et al., 1986) because after fire these species readily reestablish from seed or by resprouting. We cannot however, assume this situation will persist indefinitely. The South Africa fynbos is replete with native perennial species capable of rapid regeneration after fire, but has been invaded by Australian shrub species that have more prolific post-fire regeneration. Thus far in California the only sites where chaparral vegetation has been replaced by exotic species are those where fire frequencies have been greatly increased (Zedler et al., 1983; Haidinger & Keeley, 1993). Also in a restricted form of maritime chaparral exotic perennials have been able to invade and persist after fire because of fast growth rates compared to the natives (Zedler & Sheid, 1988; D’Antonio et al., 1993) but this is an exceptional circumstance where a very open form of chaparral occurs on sandy soils.

Several authors have noted that some apparently undisturbed communities are readily invaded (Rejmanek, 1989; D’Antonio et al., 1999). These studies should not be treated as cases of communities with no resistance. Rather, resistance may be strong but persistent propagule pressure could have gradually led to invasion. Conversely, they may be situations where invaders have altered resistance mechanisms as they invade. Careful experimental work would be required to distinguish the various possibilities.

**Herbivory**

D’Antonio (1993; D’Antonio et al., 1993) found that native animals could strongly limit the success of the South African succulent, Carpobrotus edulis, in coastal dune, grassland and scrub habitats in central California. Vila & D’Antonio (1998) made similar findings for invading Carpobrotus taxa in northern California coastal sites. D’Antonio (1993) found that one of best habitats for growth of C. edulis in the absence of herbivores was a coastal scrub site with dense shrubby vegetation. Despite the high shrub cover, competi-

| Table 1. Sources or mortality and number of propagules required for invasion of three California coastal habitats by the South African succulent, Carpobrotus edulis. Sites and invasion experiments are described fully in D’Antonio, 1993. Mortality data are percent of seedlings outplanted to field sites that died from particular causes. Number of seeds needed for establishment are based on germination rates of seed in microhabitat where survival occurs, typical abundance of that microhabitat across transect through each site, and survival rates estimated on natural and outplanted seedlings in each habitat. |
|---|---|---|---|---|
| **Habitat** | **Competition** | **Abiotic** | **Herbivory** | **Number of seeds required** |
| Backdune | 0 | 22 | 78 | 10,000 |
| Grassland | 53 | 0 | 44 | 1,111 |
| Coastal Scrub | 0 | 0 | 100 | 77,000 |
tion had only a weak effect on seedling survival and growth. Still, seedling establishment rates were near zero because of intense herbivory. Propagule supply was estimated to have to be very high in order for establishment of the invader to occur (Table 1). The herbivores abundant in this study were brush rabbits, *Sylvilagus bachmanii*, a species shown to have a strong influence on understory structure at the ecotone between shrublands and grasslands in California (Bartholomew, 1970; Halligan, 1974). Other shrubland-associated animals such as seed-eating birds have been found to reduce seed densities of Scotch Broom in coastal California (Bossard, 1991) and mammalian herbivores in the same system reduced growth and reproduction of the same invader (Bossard & Rejmanek, 1993). Cushman (unpublished data) has experimentally demonstrated that vertebrate herbivores reduce the abundance of both exotic annual grasses and an aggressive South Africa grass in coastal dunes in northern California.

**Mutualists**

Recently, Richardson et al. (2000) and Simberloff & Von Holle (1999) have pointed out that mutualistic interactions involving introduced and native species are common and the ease with which they are acquired by invaders will enhance invasion rates. There is however, some limited evidence that availability of mutualist partners such as pollinators may slow invasion for some outcrossing plant species in California (Parker, 1997; Parker & Haubensak, in press). Parker and Haubensak (in press) found that for both French and scotch broom in some coastal California settings pollinator availability could greatly limit seed set. This in turn can affect population growth rates (Parker, 1997). It was not clear, however, whether pollinator limitation resulted from competition between the brooms and simultaneously flowering native species or an asynchrony between pollinator activity and flowering time. Although both broom species are abundant in several regions of the state, these pollination studies suggest that seed production in some habitats could be much greater than current levels.

While invasion by introduced plantation conifers into the surrounding vegetation can be limited by the availability of ectomycorrhizal mutualists in South Africa (see Richardson et al., 2000), this possibility has not been examined in California. Native conifer and ericoid diversity are high; hence mycorrhizal inoculum may also be diverse. Yet Horton et al. (1999) and others have shown that native conifers can be limited in their invasion of shrublands by the availability of appropriate mycorrhizal inoculum. Burns & Sauer (1992) reviewed the history of conifer introductions into the San Gabriel Mountains in southern California and found that none of the 40+ introduced species planted there have spread beyond their original plantations. They claim that this is due to competition from the dense surrounding vegetation, harsh abiotic conditions and/or the relatively greater ability of native species to recover from fire. But this failure may also result from the lack of compatible mycorrhizal inoculum away from planted stands. It is unlikely that invasion is limited solely by low propagule pressure since for many of the species thousands of individuals were planted in the original stands.

**Species diversity**

Numerous recent studies have focused on the relationship between biological diversity and the invasibility of Mediterranean systems. Diversity may increase community resistance through any of the mechanisms listed above, though the most commonly cited mechanism is competition. Specifically, higher plant species richness is hypothesized to better preempt available resources and thereby reduce the likelihood of invasion—an argument based on species packing and Lotka-Volterra type models (see Levine & D’Antonio, 1999). Though several experimental studies have found that diversity can enhance resistance to invasion in some California ecosystems on a plant neighborhood scale (Levine, 2000; Dukes, 2001; Lyons et al., in review), these effects are not strong enough to drive community-level patterns (Levine, 2000). Indeed the most diverse California ecosystems often contain the most invaders or are most easily invaded (Peart & Foin, 1985; Knops et al., 1995; Robinson et al., 1995). A similar result has been found in a global analysis of invasive species (Lonsdale, 1999). It seems that factors co-varying with diversity and not diversity itself are responsible for driving these community-wide patterns (Levine & D’Antonio, 1999). Levine (2000) found that patterns of invasion in a riparian community in northern California are much more strongly related to patterns of propagule dispersal than to local scale resistance associated with high species diversity.
Summary of evidence for resistance

Perhaps the most striking aspect of this review is the paucity of experimental studies of mechanisms responsible for resistance in California environments. In particular, there are no studies that simultaneously manipulate propagule supply rates and sources of resistance, or that measure rates of seed arrival and per capita seed success in different environments. We found that native vertebrate activity can be very important in both promoting and limiting plant invasions and its importance to invasions is underappreciated. While competition has been demonstrated to be significant at the local scale in invasions, it may be less important at the community scale because of the widespread occurrence of soil disturbance in many California environments.

Evidence for the importance of propagule supply

Although the number of arriving propagules is an obvious factor influencing the rate of invasion of a system, few studies have explored the importance of propagule supply to invasion into California ecosystems, particularly by plants. The already discussed studies of Harrison showing that small serpentine patches are more invaded than large ones and of Levine, showing that downstream assemblages along the Eel River are more invaded than those upstream, provide some of the best evidence for the role of propagule supply in California. We could find no study that directly measured the supply of propagules to an entire ecosystem or across several sites and attributed patterns of invasion to variation in supply rates.

Evidence from other systems for the importance of propagule supply comes largely from the purposeful introductions of birds and biological control agents. This work has demonstrated that the number of introduced propagules is the greatest predictor of invasion success (Newsome & Noble, 1986; Crawley, 1989; Hopper & Roush, 1993; Veltman et al., 1996; Duncan, 1997; Green, 1997). Nevertheless, the application of these studies to natural communities and those in California is questionable for several reasons. These introductions are typically into highly altered ecosystems such as agricultural fields or urban parks. Furthermore, because of the very nature of biocontrol introductions, suitable prey items are typically abundant. Thus, it is no surprise that ecological resistance is weak. Still, a few studies of purposeful introductions do suggest that native consumers can deter the establishment of potential invaders so resistance is not always nil in these settings (Goeden & Louda, 1976; Crawley, 1990; Mack, 1996; Ehler, 1998). Given that a number of factors influence patterns of invasion, only some of which relate to ecological resistance, controlled experimental studies of the mechanisms underlying the success or failure of biological invasions are badly needed.

Conceptual model for approaching resistance

While we have evidence for the importance of abiotic and biotic resistance, the links between these factors and propagule supply remains unclear. In the following discussion we present a simple conceptual framework for examining how variation in propagule supply should interact with ecosystem resistance to influence the rate at which exotic invaders enter a habitat. We separate abiotic and biotic resistance because we believe that they interact slightly differently with propagule pressure.

By reducing invader performance, abiotic resistance may slow the invasion process or when extreme, may completely restrict invasion (Fig. 2a). For abiotic forms of resistance, there are likely to be thresholds of conditions above which the probability of establishment and persistence for a given invader is essentially zero (see discussion of serpentine soils below). In this case no level of propagule supply will result in invasion (Fig. 2a). However, abiotic resistance may vary over time providing windows of establishment. For example, in a serpentine grassland, Hobbs and Mooney (1991) found that during wet years gopher disturbance could promote the invasion of serpentine grassland by non-native grasses. Presumably this was because the harsh abiotic conditions were lessened by increased water availability. In contrast, during average years, gopher disturbance did not promote invasion onto serpentine.

Biotic resistance mechanisms may be strong in any year or place but are more likely to be variable over time and space since natural variation in herbivore populations, disturbance regimes and plant vigor are common. As with abiotic resistance,
High Propagule Supply
Medium Propagule Supply
Low Propagule Supply

Increasing Abiotic Resistance

High Propagule Supply
Medium Propagule Supply
Low Propagule Supply

Increasing Biotic Resistance

Fig. 2. Interaction of propagule supply (different lines within a graph) and ecological resistance to invasion (x axis). Abiotic resistance may involve thresholds above which no level of propagule supply can overwhelm resistance (without evolution of new genotypes). We suggest that biotic resistance factors are less likely to lead to this sort of threshold response and that high propagule supply can overwhelm even relatively high biotic resistance.

By contrast, when biotic resistance is strong, increasing propagule pressure should have a strong effect on invader establishment (Fig. 2b). High propagule supply should increase the likelihood of plants finding refuges from herbivory or competition so unlike abiotic resistance, under high biotic resistance, increasing propagule supply has a large effect on the likelihood of invasion.

Once an invader is established in a site and begins to reproduce there, seed production from within the habitat eventually overwhelms the influx of propagules from outside and greatly exceeds seed supply prior to initial colonization. With respect to the model, the invader population can rapidly climb the propagule supply curves (Fig. 2) and the invasion process should accelerate. The speed at which this happens will be a function of the reproductive biology, dispersal and dormancy characteristics of the invaders. For example, invader seeds that require scarification or passage through an animal gut have a low chance of germinating if they fall passively beneath the parent plant (D'Antonio, 1990). For these species, influx from outside the habitat may continue to be important for many years after initial invasion. This is also true for invaders that take many years to become reproductive, during which time control can be enacted. By contrast, passively dispersed species, particularly those with short juvenile periods, may only need to disperse outside the adult canopy to establish. Such populations may quickly accelerate propagule supply.

Adding impact to the model

In discussions of community invasibility or lists enumerating exotic species within a given region, all established non-native species are treated as equals. In California, fewer than 10% of the 1000+ invasive non-native species are listed by the California Exotic Pest Plant Council (CalEPPC) as damaging to wildland ecosystems in California (Randall et al., 1998; D’Antonio & Haubensak, 1998). In other words, many of the invasive non-native species in California coexist with residents on a small scale and appear to have little effect on their biomass. By contrast, those species on the CalEPPC list reduce native species populations either through some form of interference or by altering ecosystem processes (including disturbance regime). High impact invaders should be
those species that either preempt resources freed up by disturbance and persist and/or slowly overgrow native species causing death or preventing the further recruitment of native species, or ones that erode resident community resistance once they are established. The former species rely on a disturbance trigger or death event to promote their dominance and overwhelm the survival and/or regenerative capacity of the native species. The latter group may erode resistance by promoting a change in disturbance regime (e.g. increased fire frequency D’Antonio & Vitousek, 1992; Mack & D’Antonio, 1998), which then causes rapid community change. Alternatively, invaders may alter conditions for germination and/or growth of natives, causing slower, but still significant community change. Examples include the erosion of resident species’ priority by direct competition, or the accumulation of litter that negatively affects native species germination or survival (e.g. Facelli et al., 1988). As we display graphically in our model, if resistance is eroded, the number of propagules required for further invasion is reduced (Fig. 3). In this way, erosion of resistance by invaders can create positive feedbacks between the invader and its own persistence or spread. The existence of such feedbacks has been hypothesized but rarely demonstrated. Feedbacks can be complex and involve groups of invaders rather than individual species. For example, N fixing shrubs can increase soil nitrogen (Vitousek et al., 1987; Stock et al., 1995; Maron & Jeffries, 1999) while reducing native herbaceous cover through shading. After their death or removal, the original abiotic conditions have been altered and the new conditions (high soil N) contribute to success of other fast-growing invaders that can rapidly put N into biomass and seed production. Previous research on species impacts has not directly linked invasibility with generation of impact and erosion of resistance.

**Research Needs**

Our review suggests that research is badly needed in the following three areas: 1) Relating mechanisms of resistance at small spatial or temporal scales to larger scale patterns. 2) Examining the link between variation in propagule pressure and resistance. 3) Clarifying the relationship between invasibility and species impacts.

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1). **Issues of scale.** In a riparian plant community in northern California, the second author showed experimentally local scale resistance occurs but does not drive community-wide patterns (Levine, 2000). To what extent is this result a function of the specific mechanism (in this case competition) responsible for resistance? Competition is inherent-
ly a local process subject to spatial variability in disturbance, propagule arrival and abiotic factors and thus it may poorly control the resistance of an entire habitat. By contrast, mobile generalist herbivores have effects that might be more evenly distributed across a habitat and thus herbivory by generalist species may more strongly control community level invasion patterns. The extent to which local scale abiotic stress affects invasibility of entire habitats will depend on microsite variation within a habitat and temporal variation in resource availability that might override locally induced microsite heterogeneity. Further exploration of these scale issues is essential to establishing the relevance of the current literature (which focuses on small scale studies of resistance) to invasion patterns in entire ecosystems.

2. Propagule supply. We know almost nothing about actual seed rain into most sites and since it is very hard to measure, we need to develop and refine the proxies that we use for it. In addition, models linking seed supply and resistance could generate testable insights into controls over habitat invasion by particular types of invaders. Empirical studies manipulating propagule pressure or simply measuring the per capita probability of success under different scenarios of resistance (including manipulation of spatial and temporal variation would be insightful).

3. Invasibility and impact. Invasibility studies and discussions based on species lists all too often do not separate high from low impact species. Since less than 20% of invaders appear to have an impact on wildland populations or ecosystems (Simberloff, 1981; D’Antonio & Haubensak, 1998), it is important to examine mechanisms controlling invasion for high impact species. We have suggested some hypotheses relating impact to resistance and propagule pressure and these await further experimentation on a range of species. In particular, the extent to which high versus low impact species influence the interaction of resistance and propagule supply needs to be rigorously examined.

Management implications and conclusions

A greater understanding of resistance mechanisms and propagule pressure could be used in many different management contexts. Resistance mechanisms extend the period of time during which an invader and native species coexist, which widens the temporal window available for control and potentially reduces the extent of site alteration associated with invasion. Likewise, managers must ensure that their own practices do not disrupt resistance that is already working in a site. Alpert et al. (2000) suggest ways in which managers might manipulate abiotic features of the environment to increase stress (more or less similar to ‘abiotic resistance’ in our terminology) and reduce invasibility.

The identification of abiotic features that influence resistance can help set priorities for restoration. For example, native perennial dominated grasslands that are not on serpentine soils still exist in California (e.g. Keeley, 1993; Stromberg & Griffin, 1996). A greater understanding of abiotic conditions that correlate with cover and diversity of native grassland species in non-serpentine sites would aid in the identification of sites with high potential for restoration.

Furthermore, since disturbance can either increase or decrease the strength of community resistance depending on the relative responses of native and exotic species, the management of disturbance regimes can have profound impacts on community resistance. Management practices that introduce new disturbances to a system might erode community resistance. Where human caused habitat disturbance is unavoidable, disturbance should be timed or handled in ways that decrease an invader’s ability to benefit from them. Techniques that increase the competitiveness of natives in new disturbances, including boosting native propagule pressure, should be more fully explored.

The interaction of resistance mechanisms with propagule supply is critical to better predicting invasions. Little empirical data is available on the ways in which invasion rates respond to an increase in propagule number. Research is needed on patterns of seed rain away from population centers of invasive plants into potential habitats. Estimates of spread rates will allow managers to allocate resources to areas that are immediately threatened, and away from sites which are likely to remain uninvaded for a longer time. More generally, a better understanding of the mechanisms controlling the spread and success of invasions is an important research goal for protecting native biological diversity in California habitats.
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