The Disturbed Resource-Flux Invasion Matrix: a new framework for patterns of plant invasion

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Abstract

Attempts to classify certain habitats as vulnerable to invasion or plant traits as invasive have met with limited success and applicability. Clearly, not all plant invaders are able to exploit all habitats and not all habitats are equally susceptible to invasion. Here we argue that it is critical for a successful model for invasions to incorporate both environmental and species traits and present just such a framework. Although disturbance has been targeted as a crucial event which renders habitats vulnerable to invasion, disturbances are often integral parts of ecosystems (e.g. floods, tree-falls, fire, etc.) and are not always associated with invasion events. We argue that disturbances that are associated with invasions alter historical patterns of turnover, or flux, of resources in an ecosystem. Given this perspective on the relationship between invasions and disturbances, and the need to integrate species traits with those of invaded ecosystems, we have developed an approach to characterize plant invasion patterns that we call the 'Disturbed Resource-Flux Invasion Matrix' or DRIM. This is a 16-cell matrix that classifies habitats by the quality of changes in physical and chemical resource flux either increasing or decreasing flux relative to historical patterns. Within each matrix cell, it is then possible to apply basic ecological principles to target species traits that can facilitate successful invasion of habitats experiencing that particular kind of disturbance. We present examples from the literature of how habitats and species can be classified according to the DRIM, and demonstrate the application of this theoretical model.

What is a plant invasion?

Plant invasions occur when a species expands into a new range intentionally or unintentionally due to human activities and is accompanied by adverse economic, ecological or effects (Mack 1996). The annual economic impact of invasive plants has recently been estimated at $123 billion in the United States alone (US Department of Interior 1999). Ecological costs are more difficult to measure but no less pervasive; native plant and animal species have been displaced and ecologically sensitive areas have been irreparably damaged (for examples see Cronk and Fuller 1995; Hink and Ohmart 1984; Elton 1958). Because they often grow in virtual monocultures, invasive plants reduce biodiversity and decrease the aesthetic value of natural areas. Documented ecological effects of invasive plants include competitive suppression of native species (Busch and Smith 1995; Huenneke and Thomson 1995; D'Antonio and Mahall 1991; Melgoza et al. 1990), altered fire or water regimes (Cronk and Fuller 1995; Hobbs and Huenneke 1992), and changed nutrient status of soils (Mooney and Drake 1989).

Due to the tremendous costs of plant invasions, many ecologists and weed scientists have contributed to the ultimate aim of preventing biological invasions by developing models to understand and predict invasions. In developing these models, much effort has been expended towards identifying the common traits of successfully invasive species or invaded habitats (Barrett and Richardson 1986; Harper 1965; Baker 1964). However, despite decades of attempts to classify certain habitats as vulnerable to invasion or particular species traits as invasive, most predictions have met with limited success or applicability, especially for plants (Stohlgren et al. 1999; Crawley 1987).

We argue that the exclusive focus of many approaches on either the species or the habitat limits our understanding of the ecology of plant invasions because it ignores or down-plays the interactions between the two components of invasion (but see Drake 1983; Sugihara 1983). Because different habitats are invaded for different reasons, there cannot be a suite of universally successful invading plant traits. A trait that might be advantageous to an invader in one habitat may not be successful in another. Invaded habitats are not equally vulnerable to all invaders. Invasions occur in habitats that differ widely in biodiversity, climate and geography. Therefore, it is clearly the fit of the species to the environment that makes invasions possible.

Here, we contribute to the resolution to this problem by first describing a new classification system for potentially invaded habitats. This perspective allows us to then make specific predictions about the traits of species that will successfully invade these different kinds of habitats. We believe this approach constitutes a substantial shift in ways of thinking about invasion and may possibly contribute to preventing invasions before they occur.

The role of disturbance

Many invasion biologists have targeted disturbance as a crucial factor that makes habitats vulnerable to invasion, since disturbance disrupts strong species interactions, creating empty niches that invaders can occupy (Burke and Grime 1996; Hobbs and Huenneke 1992; Hobbs 1989; Crawley 1987; Egler 1983; Forcella and Harvey 1983; Pickard 1984; Elton 1958). Alternatively, by increasing colonization opportunities, disturbance may simply provide a 'foothold' from which an invasion can proceed (Parker et al. 1993; Mack

1985). However, because not all disturbed habitats are invaded, it is clear that disturbance alone is not always followed by invasion (Crawley 1987).

Disturbance is conventionally defined as a *discrete* event in time that, by *increasing* resource – particularly substrate – availability, disrupts ecosystem, community or population structure (White and Pickett 1989). However, this definition does not encompass all invasion-related disturbances. Disturbances are integral parts of ecosystems (e.g. floods, tree-falls, fire, etc.) and do not necessarily increase the probability of invasion success; natural disturbances have even been shown to prevent or slow invasions (Mooney and Drake 1989; Mack 1989). Invasion-facilitating disturbances are not always discrete events in time (e.g. introduction of cattle grazing or flood control), may be chemical in nature, not merely physical /structural (e.g. urban nitrogen deposition or commercial fertilizers), and may even reduce resource or substrate availability (e.g. removal of herbivores from a habitat, reducing vegetative turnover).

Our experience and readings have suggested that invasions are likely to occur when historical patterns of disturbance to a habitat have been changed; individual disturbance events themselves may not affect the susceptibility of a habitat to invasion. Disturbance-mediated changes in ecosystems that render them vulnerable to invasion are characterized by either increases or decreases in resource availability. We therefore refine our definition of invasion-facilitating disturbances. These kinds of disturbances result in a change in historical disturbance regimes, altering the rate or intensity of the turnover rate, or flux, of resources in a habitat. Such resources can include space, nutrients, or light.

Resources that are affected by changes in disturbance regime fall into two distinct categories – physical (e.g. substrate) and chemical (e.g. nutrients). In addition, these changes are not uni-directional; disturbances can increase or decrease resource availability. Changes to the disturbance regime that increase physical flux increase the rate of removal of biomass and increase substrate availability. Decreases in physical resource flux change the historical dynamics of the ecosystem, reducing the rate of biomass removal and therefore substrate availability. Changes in chemical flux rates are not as readily associated with increases and decreases in resource availability as in changes in physical flux. When chemical flux decreases, resources are usually bound up and therefore less available;

however, increases in chemical flux may or may not render these resources more available. Increased flux can either lead to accumulation of excess pools of nutrients creating toxic conditions, or to increased rates of nutrient cycling, reducing the ability of most plants to exploit these resources before they are transferred to a less available state or bound up in the tissues of other species. Therefore disturbance regimes must be considered in terms of both physical and chemical changes in the habitat.

Changes to disturbance regimes may directly or indirectly result from human activity. For instance, the channelization of rivers directly reduces flooding, but by increasing understory fuel supply, may indirectly increase fire frequency and/or intensity. Infrequent natural events such as unusually intense hurricanes may also be agents of invasion (Horvitz et al. 1998). In addition, it should be noted that a species introduction could itself be a serious disturbance to physical or chemical conditions (Zink et al. 1995; Hobbs and Huenneke 1992). Thus, an invasion that appears to be unassociated with any obvious human interference to the disturbance regime may actually have been facilitated by a change in flux caused by a previous non-invasive plant introduction that altered nutrient or substrate turnover rates. The important issue is whether the native flora and fauna are adapted to the novel patterns of physical and chemical resource turnover or if the change is so extreme that the habitat is rendered vulnerable to invasion.

The Disturbed Resource-Flux Invasion Matrix

Given this perspective on invasion-related disturbances, and the need to link invasive species traits with those of invaded ecosystems, we have developed an integrative method to characterize plant invasion patterns, which we call the 'Disturbed Resource-Flux Invasion Matrix' or DRIM (Figure 1). This matrix is a framework that organizes categories of habitat change, which then can be used to show the invader plant traits best adapted for specific kinds of disturbances. Because alterations to a disturbance regime can have different, overlapping effects (or no effect), the matrix includes all combinations of physical and chemical changes in flux. These changes (i.e. increases and decreases in physical and chemical flux) can be combined into sixteen possible scenarios, taking into consideration that a habitat may experience an increase or decrease in
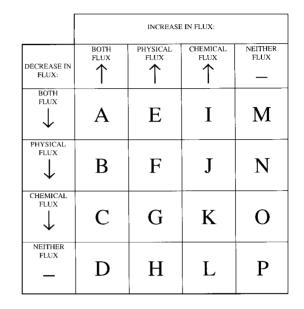
	INCREASE IN FLUX:			
DECREASE IN FLUX:	BOTH FLUX ↑	PHYSICAL FLUX ↑	CHEMICAL FLUX ↑	NEITHER FLUX —
BOTH FLUX ↓	A	E	I	M
PHYSICAL FLUX ↓	B	F	J	N
CHEMICAL FLUX ↓	C	G	K	O
NEITHER FLUX —	D	H	L	P

Figure 1. The Disturbed Resource-Flux Invasion Matrix (DRIM). This matrix is used to classify habitats by alterations to the disturbance regime that have changed physical and chemical resource flux, such that traits of successful invaders can be determined. Cells include the possibility of simultaneous increases and decreases when a habitat has more than one disturbance change, such as a habitat which experiences the decrease in one process of physical flux – i.e. cessation of natural fires – with an increase in another process of physical flux – i.e. increases in herbivory.

(1) physical or (2) chemical flux, (3) both physical and chemical, or (4) neither. Thus our matrix has 4 (increase) × 4 (decrease) = 16 cells allowing for all combinations of the above effects. A habitat is assigned to a cell based on whether the change to its disturbance regime led to an increase (↑) and/or decrease (↓) in the flux of physical and/or chemical resources. Note that this matrix also includes a cell of no change (cell P in Figure 1; no increase or decrease in chemical or physical flux). A habitat may experience a simultaneous increase and decrease in physical or chemical flux if one type of disturbance-mediated flux increases, such as trampling, is combined with one that decreases flux, such as herbivore removal.

Within each of the cells in the DRIM, it is then possible to begin to target species traits that may facilitate successful invasion of habitats experiencing that particular kind of disturbance. This characterization of species traits can be done using general ecological principles. Invader traits can then be categorized in terms of (1) reproduction, (2) environmental tolerance, and (3) suppression ability (the ability

to suppress growth of neighbors; 'competitive effect' *sensu* Goldberg 1990). We subsume the ability to withstand suppression by neighboring plants ('competitive response' *sensu* Goldberg 1990; Tilman 1988) into the 'environmental tolerance' category, which also includes the ability to withstand biotic and abiotic stress. The reproduction category includes traits associated with both establishment and persistence; e.g., perennial vs. annual, sexual vs. vegetative reproduction, and dispersal ability. By *a priori* characterizing a successful invader's life history within each of the 16 habitat type cells, we can make testable generalizations regarding invasion patterns, addressing both species and habitat traits. These generalizations can then be tested through both analyses of existing literature as well as through experimentation.

Assumptions of the model

We have made several assumptions about species and habitats involved with invasions that are necessary for this model to be useful. First, we assume that it is possible to identify the primary resource flux changes that have occurred in a habitat, and that the direction and type of these changes is more important in facilitating invasion than the magnitude or specific nature of the change in flux. It is likely that for most habitats, the predominant changes to resource flux can be identified and therefore basic invader traits defined. While our ability to correctly identify the relevant flux changes is a concern, with increased knowledge about the particular habitat in question, the model's applicability will inevitably be augmented. Although there are many different types of physical and chemical disturbances, by generalizing about the direction of the flux changes and the adaptations necessary to exploit them, we can improve the applicability of our model and avoid devising one universal strategy, which we have argued is inappropriate for the complex phenomenon of biological invasion. Our model is based on the direction and not the magnitude of flux changes because this parameter would be very difficult to quantify for most habitats and will occur on different scales for different species. Furthermore, the same traits are likely to be possessed by successful invaders regardless of the magnitude of flux changes or their source. For example, a ruderal strategy of reproduction and dispersal will be advantageous when there is an increase in physical flux, regardless of whether the substrate is made available by trampling or flooding. Specific traits related to the cause of flux change (such as fire tolerance) can be generally included under a broad category of adaptations to abiotic stress.

Second, our perspective assumes that before human interference, there is a certain level of dynamic equilibrium of ecosystems (MacArthur and Wilson 1967) that resists invasion. In some cases, this may be literally true; an invading species that has not evolved in a particular ecosystem may require a disruption of its ecological balance for a niche to be created/opened for the invader to exploit. However, the DRIM assumes only that a change has taken place. This is implicit, since invasions always result in a change in species composition or density. Therefore, the question is whether there is some change to the habitat prior to the invasion that allows the invasion to occur (cells A–O) or if the invasion itself is the only vector of change (cell P).

Third, we assume that in most cases invasiveness is a behavior shown by species only under certain circumstances. Invasiveness is not an evolved species trait, but results when species possessing particular suites of traits encounter habitats that are amenable to invasion by species with those traits. Many invasive species have distinct invasive and noninvasive ranges where resource fluxes, and therefore population dynamics, and interspecific interactions are likely to be measurably different. Explicit comparisons of population ecology and resource flux in different portions of an invasive species' range are necessary to test the validity of this assumption.

Understanding invasions of specific habitat disturbances using the DRIM

Grazing by deer
We can use the matrix to examine specific instances of invasion in terms of the intersection of habitat change and species characteristics. For example, non-native deer grazing in oak woodlands subjects the ecosystem to increased physical flux with few other measurable changes (cell H, Figure 1, Cross 1981). One might expect successful invaders of habitats with this kind of increased physical flux either to have broad propagule dissemination and rapid life cycles, or strong resistance to physical flux, i.e. persistent root systems or fire resistance, as in many herbaceous perennials. Competitive ability is not likely to improve invasiveness in this kind of a habitat, since physical turnover will preclude competitive suppression. Cross (1981) found that deer grazing created safe sites for invading

perennial *Rhododendron ponticum* by removing competitors. Although it is a weak competitor (and requires disturbance for establishment), *Rhododendron* is probably successful in this system because it is not palatable to deer and can exploit the disturbance created by herbivory. In other forests, workers have found that *Rhododendron ponticum* invasion is highly correlated with soil disturbance, yet another form of increased physical flux (Thomson et al. 1993). Thus, this species has the profile of an invader that will be successful in cell H habitats (Figure 1), regardless of the specific nature of the disturbance regime change.

Road beds

In some cases, the most important result of a physical disturbance will be its effect on chemical flux. When both physical and chemical resource turnover increases (cell D, Figure 1), we might expect successful invaders to grow and reproduce quickly and be adapted to the accelerated turnover of chemical resources. In tall grass prairies, Parker et al. (1993) found higher, nearly toxic levels of phosphorus, potassium, and higher pH in old road beds where soil was more compressed than in undisturbed sites. Disturbed sites were dominated by two invasive biennials, *Daucus carota* and *Melilotus alba*, whereas native species dominated the undisturbed sites. *Daucus* and *Melilotus* were present in high densities *only* in the areas where there had been past disturbance, although seeds were available throughout the habitat. These invasives were also the only species that were positively correlated with phosphorus, potassium, and pH. Both *Daucus* and *Melilotus* are biennial, wind-dispersed species, and therefore well adapted to physical disturbance. Further, the authors suggested that the native species may not tolerate the high mineral concentrations found in the disturbed areas, while the species which were successfully invasive thrived on these soils.

River channelization

Sometimes changes to disturbance regimes are very complex and lead to many overlapping effects. In the Southwestern United States, disturbance regimes of riparian ecosystems have been subject to extreme modifications during this century, resulting in both physical and chemical changes. Damming and straightening of rivers has reduced over-bank flooding which hinders mechanical turnover (i.e. decrease in physical flux) while also increasing salinity, reducing microbial activity and therefore nutrient cycling (i.e. decrease

in chemical flux; Crawford et al. 1993). Meanwhile, the resulting dry conditions and build-up of detritus in riparian forests increases fire intensity and frequency, which provides an increase in both physical and chemical flux (Busch and Smith 1993). This riparian ecosystem therefore may be considered as cell A example: alterations to the disturbance regime have caused simultaneous increases and decreases in both physical and chemical flux.

We might expect habitats that have experienced cell A disturbance to be successfully invaded by vegetative reproducers with high stress tolerance. An invader of this type of habitat must respond to increases in flux (due to fire), as well as tolerate decreases in flux (from lack of flooding). One of the most pervasive invaders of the Southwestern riparian habitat is the woody shrub, *Tamarix* spp. (mainly *T. ramosissima*). *Tamarix* can vegetatively spread along the dry riverbanks, tolerating both the drought and low nutrient availability that results from the lack of flooding, as well as the physical and chemical effects of increased fire frequencies (Busch and Smith 1995). However, as a seedling, *Tamarix* is a poor competitor with native trees (Sher et al. unpublished). *Tamarix* was introduced in the 1800s, but did not become invasive until after widespread river damming and channelization in the early 1900s (Crawford et al. 1993; Horton 1977; Robinson 1965). Comparisons of flooded versus dammed riparian stretches also show that this species will be invasive only under altered disturbance regimes (Stromberg 1998), and its invasion of other areas, such as Australia, is also associated with combinations of alterations to physical and chemical flux (Griffin et al. 1989).

Note that increased physical flux may override the importance of decreased physical flux for defining invader traits. In general, competitive ability is not likely to be an important trait of successful invaders in habitats with increased physical resource flux, since by definition, this type of disturbance removes competitors (as in the deer and river channelization examples above), even if a decrease in a different physical disturbance left them standing. Therefore, competitive pressure will be expected to decrease for all habitats in the columns that include increase in physical disturbance (cells A–H, Figure 1) regardless of co-occurring effects. However, effects of combined decreases and increases in physical disturbance can at least in some cases be considered in terms of net loss or gain of substrate. In contrast, there will be no such net effects

of corresponding increases and decreases in chemical flux, since traits associated with each differ. In the above example, the increase in chemical flux as caused by fire will favor plants that have traits to exploit this resource pulse, while the decrease in chemical flux requires salt tolerance, a different kind of trait. Thus, overlapping increases and decreases in resource-flux will create profiles for invaders that differ from invader profiles for habitats with single, dominant effects.

Invasions independent of disturbance

The frequency of invasions that occur in the absence of habitat change (cell P) is an important question that merits investigation. Strong competitive ability should be associated with successful invaders of habitats that fall in this category. However, understanding invasions of habitats with no change in resource flux may require a closer look at the role of dispersal, particularly by humans, and the disturbance that the introduction itself creates. Clearly, when introductions are frequent or large, they are more likely to be successful regardless of other habitat changes (Green 1997). However, even those who advocate dispersal (i.e. seed availability) as a main component of invasion patterns acknowledge that dispersal alone will only be successful in some habitats (Tilman 1997). For some particularly insular habitats such as bodies of water or islands, a very small introduction event can disturb the ecosystem merely by establishing self-sustaining populations (Mooney and Drake 1989; Vitousek et al. 1987). Some have argued that successful establishment is enhanced because of low initial species diversity, implying the existence of empty niches (Tilman 1997; MacAurthur and Wilson 1967; Elton 1958).

The relative importance of invasions that will occur in cell P habitats *versus* habitats subject to change is a part of a much larger debate regarding the role of disturbance in invasions (e.g. Crawley 1987), which is beyond the scope of this paper. However, our redefinition of disturbance-mediated invasions as facilitated by changes in historic resource flux and our suggestion that different types of invader traits will be necessary in habitats with observable changes in turnover may contribute to that discussion.

Where to go from here?

The DRIM provides a model within which previous work on invasions can be organized and understood, and provides a focus for future work. In the past, the most pervasive approaches to understanding and predicting invasions have been strictly observational and focused on traits of invasive species (e.g. Barrett and Richardson 1986; Harper 1965; Baker 1964). Many such predictions conflict and predict that invaders possess contradictory traits (i.e., mostly vegetative reproduction *versus* high, frequent sexual reproduction). The DRIM seeks to resolve this apparent conflict by suggesting that invader strategies will depend on the state of resource flux within the habitat.

Lists of invaders have already been used in *post-hoc* multivariate analyses to develop models that predict which traits are most commonly associated with invasiveness (Williamson 1996; Rejmánek 1996; Pvsek et al. 1995). The most obvious way that predictions made within the DRIM can be tested is by conducting such multivariate trait analyses by habitat-disturbance type. In this way, observational research may help us classify plant traits for each of the cells, which may in turn allow us to better understand the observations. Negative data points, i.e. failed invasions, will also be necessary to determine the consistency of habitat-species trait matches. As many introductions fail (Simberloff 1981), it is likely that closer examination of more data of this kind will be highly revealing. There is currently a paucity of such documentation. However, a close examination of current and historical species lists across habitats and locations may at least show us where invasions have failed to occur in the past. Comparisons of specific habitat differences in terms of resources can then be used to test the hypothesis that the species requires a profile of habitat conditions related to changes in resource flux to act invasively.

The DRIM's most appropriate application, however, may be to focus experimental efforts. Experimental approaches to examining invasives and traits of invaded habitats are beginning to come to the fore, but rarely have they integrated invader and habitat traits. For example, the competitive ability of invaders is being experimentally investigated (Sher et al. unpublished; Burke and Grime 1996; Busch and Smith 1995; Huenneke and Thomson 1995; D'Antonio 1993; D'Antonio and Mahall 1991; Melgoza et al. 1990). However, these studies have revealed a wide range of competitive abilities in invaders, highlighting the fact that universal invading traits will not exist across habitats. Thus, measuring and comparing traits of invaders within different kinds of habitats will be necessary to understand the relative importance of these traits. The DRIM classifies these habitats with specific regard to

invasion and therefore simplifies this necessary next step.

Acknowledgements

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