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Invasive plants in conservation linkages: a conceptual model that addresses an underappreciated conservation issue

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Conservationists have frequently touted the merits of increased landscape connectivity, usually focusing on the efficacy of conservation linkages (corridors) for maintaining viable populations of target species. An often-mentioned, but still greatly understudied, concern is that increased landscape connectivity via linkages may also aid the movement of undesired species. This paper provides conceptual guidance for research on one major aspect of this gap: invasive plants in conservation linkages. To guide research goals and methods, I develop a conceptual model describing eight interaction types between invasive plants and linkages, i.e. the ways that invasive plants can exist in and move into, through, and out of conservation linkages. Each interaction type within the model has three main components: linkage, matrix, and focal species. I discuss several aspects of these components, including a) differentiating among matrix types, b) understanding edge effects within the linkages, and c) incorporating relevant invasive species' ecology (primarily dispersal ecology). Spatially-explicit documentation of invasive plant distribution is essential to understanding these interactions. By focusing on landscape-scale patterns in real-world systems, this model will enhance landscape-level knowledge of invasion ecology and aid land managers in identifying and prioritizing research and management decisions regarding invasive plants in conservation linkages.

For more than twenty years, conservation biologists have explored the merits of increased landscape connectivity, usually focusing on the efficacy of conservation linkages for maintaining viable populations of target species (Noss 1987, Simberloff et al. 1992, Beier and Noss 1998, Bennett 1999, Haddad et al. 2003, Crooks and Sanjayan 2006, Haddad and Tewksbury 2006, Boitani et al. 2007). Conservation linkages (also known as corridors) are intended to combat the negative effects of widespread, pervasive habitat fragmentation and isolation by facilitating native plant and animal movement between habitat patches (Beier and Noss 1998, Anderson and Jenkins 2006, Crooks and Sanjayan 2006, Damschen et al. 2006). World-wide, studies of linkage design and function for a wide variety of species and habitats have proliferated (Wikramanayake et al. 2004, Williams et al. 2005, Beier et al. 2006, 2011,). However, all of these modeling, observational, and experimental studies only mention potential negative or undesired effects of linkages (Proches et al. 2005). An often-mentioned but rarely studied concern is that increased landscape connectivity via linkages may aid the movement of undesired species (e.g. invasive plants) or events (e.g. fire or spread of disease) (Simberloff et al. 1992, Beier and Noss 1998, With 2004, Anderson and Jenkins 2006, Hulme 2006, Beier et al. 2008, Fausch et al. 2009, Sullivan et al. 2011, Brudvig et al. 2012).

This paper directly addresses an important aspect of this gap: the relationship between invasive plants and conservation linkages. I propose a decision-making approach that will aid managers in identifying and prioritizing appropriate research and management actions given their focal conservation linkage, invasive plant species, and surrounding matrix. I developed a conceptual model that consists of eight types of interactions between linkages and invasives. I then elaborate on the most salient knowledge gaps using major components of the conceptual model. This examination of the potential negative consequences of using conservation linkages does not imply that linkages are a net negative for conservation efforts. Indeed, current evidence favors conservation of linkages for native plants and animals as well as ecosystem processes (Tewksbury et al. 2002, Crooks and Sanjayan 2006, Damschen et al. 2006, Doerr et al. 2011). However, a fuller understanding of the negative effects of linkages can better maximize their net positive effects.

Background and rationale

Definitions

A conservation linkage is 'connective land intended to promote movement of multiple focal species or propagation of ecosystem processes' (from Beier et al. 2008). Here I use the term 'linkage' due to its broad definition and to avoid confusion with other uses of the term 'corridor' (e.g. 'transportation corridor'). 'Invasives' refer to plants that are non-native, have invasive characteristics, and are a management priority for control.

Why invasive plants and linkages?

Many invasives are not detectably impacted or are positively impacted by habitat fragmentation (but see With 2002, Minor et al. 2009, Alofs and Fowler 2010). This is likely due to their ability to disperse and colonize at high rates and their association with edge habitat, which increases with fragmentation (Richardson and Pysek 2006, Nehrbass et al. 2007, Nathan et al. 2008, Andrew and Ustin 2010). Therefore, movement of invasives in conservation linkages may differ significantly from that of many native plants (Crooks and Suarez 2006, Damschen et al. 2006, Hulme 2006).

To conceptualize the ways in which invasive plants may interact with conservation linkages and the ecological variables that influence these interactions, I integrated several facets of invasion and landscape ecology. Invasive plants are of special concern with respect to conservation linkages due to a) linkages' high edge-to-area ratios and b) the role of matrix habitat.

Edge habitat often has been positively associated with plant and animal invasion (Brothers and Spingarn 1992, With 2002, Bartuszevige et al. 2006, Theoharides and Dukes 2007, Cilliers et al. 2008) through a variety of mechanisms, including increased light and wind exposure. Although many existing and planned linkages have relatively high edge-to-area ratios, potentially increasing their susceptibility to invasion (Panetta and Hopkins 1991, Deckers et al. 2004, Hansen and Clevenger 2005), only one published study has directly addressed the relationship between edges and invasive plants in linkages – a study of plant spillover from experimental connected (via corridors) and unconnected habitat patches into the surrounding matrix (Brudvig et al. 2009). There, connectivity and distance from edge helped determine how many native plant species spilled into the matrix, but exotics were not affected by either factor.

Invasive plants turn another aspect of connectivity on its head: the role of the matrix. Matrix is defined here as the habitat adjacent to a linkage (Fig. 1) and is often highly heterogeneous (see below). Matrix structure, configuration, and ecological characteristics can affect connectivity for native focal species (Ricketts 2001, Goodwin and Fahrig 2002, Rodewald 2003, Donald and Evans 2006, Hilty et al. 2006, Schmitz et al. 2007, Prugh et al. 2008, Magle et al. 2009, Diaz et al. 2010, Rico et al. 2012). However, these studies examine how matrix affects only native species, and generally assume that the focal species' source patches are the connected habitat patches and/or the linkage while the matrix is unsuitable habitat. With invasives, however, the population source is often the matrix itself (Cook et al. 2002, Pysek et al. 2002, Rodewald 2003, Murphy and Lovett-Doust

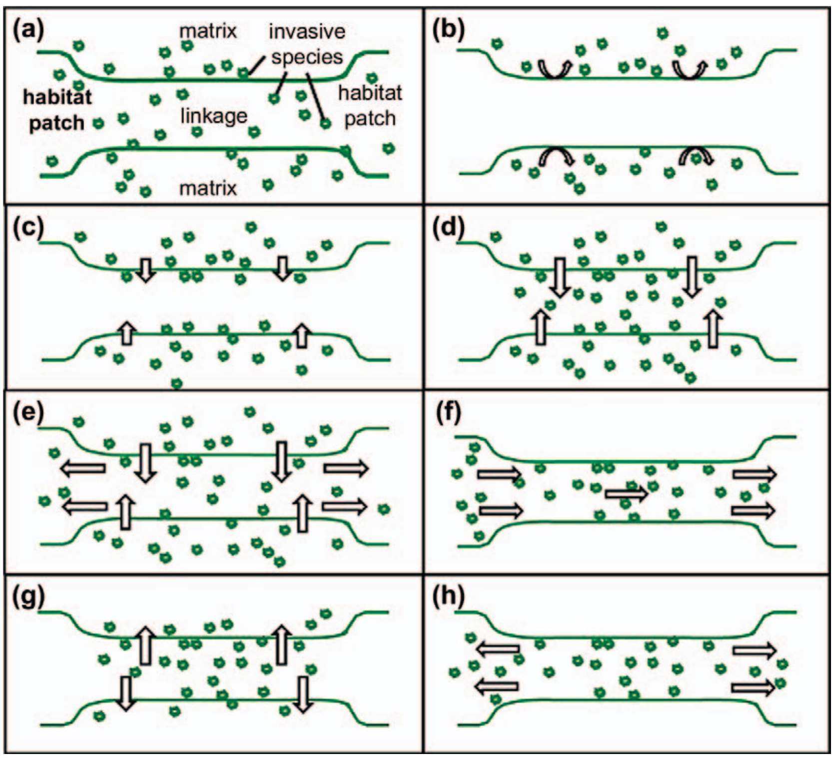

Figure 1. Interaction types between invasive species and conservation linkages. Arrows denote direction of invasion; green shapes denote invasive plant species occurrence. (a) Invasion throughout the landscape (neutral model). (b) Invasion from matrix does not penetrate linkage boundary (barrier). (c) Matrix invasion stays along linkage edges (partial habitat). (d) Matrix invasion penetrates throughout linkage (complete habitat). (e) Matrix invasion spreads through linkage into habitat patches ('drift-fence' conduit). (f) Invasion from habitat patch through linkage moves into connected, uninvaded patch ('classical corridor' conduit). (g) Invasion from linkage spreads into surrounding matrix (source 1). (h) Like (g), but invasion spreads from linkage into habitat patches (source 2).

2004, Kupfer et al. 2006, Nascimento et al. 2006, Foxcroft et al. 2011).

Existing work on invasive plants and linkages

Expanding theory and practice with respect to invasive plant ecology and landscape ecology of conservation linkages can aid crucial management decisions. Despite the potential importance of plant invasion in linkages, I found only two empirical studies of the effects of linkage features on invasive plant connectivity. Damschen et al. (2006) demonstrated that native plant species richness, but not invasive plant richness, increased with increased connectivity. Conversely, Deckers et al. (2008) showed that increased hedgerow connectivity in an agricultural setting enhanced the invasion potential of a non-native tree species. These contrasting results emphasize that more empirical research is needed to determine the patterns and processes of plant invasion into and through linkages. We also lack conceptual guidelines. Here I propose a conceptual model framework to guide research and decision-making.

Conceptual model

The conceptual model describes the ways that invasive plants can exist in and move into, through, and out of landscape linkages, i.e. interaction types between invasive plants, linkages, and surrounding matrices (Fig. 1). It can also be applied to many native species, plants and animals, but the specific arguments used below are tailored to invasive plant concerns. By focusing on landscape-scale patterns in real-world systems, the model suggests research approaches that can enhance landscape-level knowledge of invasion ecology and aid land managers in prioritizing, designing, and/or managing conservation linkages.

Interaction types in the conceptual model

I propose eight interaction types, illustrating each with topics to guide management decisions (Fig. 1): 1) neutral model, 2) barrier, 3) habitat (subdivided into two habitat functions), 4) conduit (subdivided into two conduit functions), and 5) source (subdivided into two source functions). A diagnostic key (Fig. 2) illustrates the decision-making process managers can use to determine how an invasive plant species (or group) may be interacting with the matrix and linkage based on observational data. The details of each interaction type and methods of detection are described below.

The majority of references cited in the sections below are not from linkage-oriented studies of invasive plants, which are almost non-existent. Rather, literature on habitat fragmentation and invasive plant ecology is cited to detail which interactions types listed below are likely to be operating in linkages, supported by a few key linkage studies and reviews (Table 1).

Neutral model

In the simplest scenario, there are no differences between invasive plant distribution in the matrix, linkage, and connected habitat patches (Fig. 1a and Fig. 2). Neutral models, using random or fractal algorithms, are useful for comparison with real-world distribution patterns to determine the degree and type of spatial structure of species' populations across the landscape (With 1997, With and King 1997). A neutral model for a focal landscape will help researchers and managers verify or rule out potential patterns listed in Fig. 1.

In situations where the neutral model applies, the problem of controlling focal invasive plant species transcends matrix-linkage-patch landscape configuration. If the focal invasives are ubiquitous then the abiotic or biotic attributes of the linkage or matrix largely will not matter to the invasion pattern or process. Note that some invasive plants could have been in the matrix, connected patches, and/or linkage well before the linkage was constructed or managed. The interaction types discussed here will be most useful for evaluating and prioritizing management actions for invasives that either arrived or underwent rapid expansion (active invasion) after linkage creation. However, just because an invasive plant has established does not mean invasion processes cannot continue or change due to factors such as changing disturbance conditions (Johnstone 1986, Chabrerie et al. 2007).

Barrier

Ideally, a conservation linkage would function as a barrier to invasive plants coming in from the surrounding matrix (Fig. 1b). Foxcroft et al. (2011) provide evidence that a protected park boundary served as a barrier to non-native plants coming in from the matrix. Since edge effects are often important in invasive plant establishment and different matrix types may alter distribution patterns (sections Habitat and Matrix characteristics), managers might examine how the patterns change across the matrix-linkage boundary as a measure of boundary permeability (Ries et al. 2004, Foxcroft et al. 2011). Various analytical methods can detect spatially-explicit changes in plant patterns across potential boundaries (Fortin and Drapeau 1995, Fagan et al. 2003, Kent et al. 2006, Fitzpatrick et al. 2010 and Table 1). The boundary function of the linkage edge may depend on the type and configuration of the adjacent matrix. Identifying areas that have hard edges versus softer edges (Lopez-Barrera et al. 2007) and then narrowing down the various abiotic and biotic causes will help managers determine 'danger zones'. The distinction between barrier and partial habitat (Fig. 1c) may be difficult to ascertain (see also Fig. 2). Both types of interactions will likely have more invasives in the matrix than the linkage, so a close examination of the linkage-matrix boundary would be key.

If the linkage is indeed functioning as a barrier to focal invasive plant species (either in its entirety or from certain matrix types), managers might justifiably relax their concerns about invasion into their conservation land. Of course, that could change if the matrix habitat changes (e.g. wildland matrices are developed into suburban housing) or with the arrival of a new invasive plant species.

Habitat

More mobile species may move through linkages in a few hours or days, but for slower-moving or sessile species (like plants), conservation linkages may serve initially as habitat,

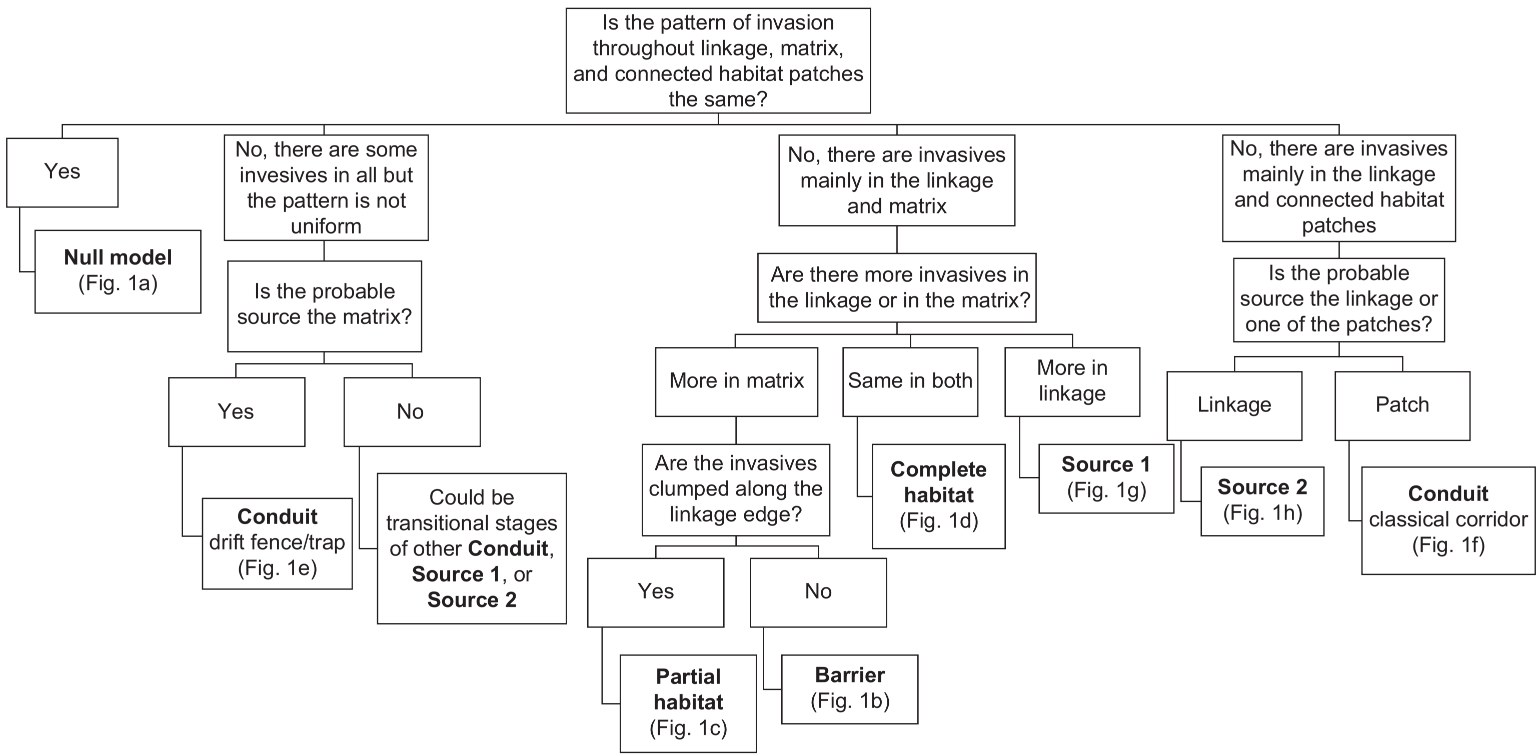

Figure 2. Diagnostic key for determining the likely interaction type between a conservation linkage and focal invasive plant species (or group). Further detail for each type (from Fig. 1) is provided in the text.

Table 1. Literature used in background for the eight interaction types (grouped into five categories below) presented in Fig. 1. Most of the literature does not come from studies or reviews about conservation linkages but is supportive (in other contexts) of the potential for linkages to serve one of the detailed functions with respect to invasive plant species (or groups).

Classes of interactions	Key topic	Author and date	Type and focus of work	Relevance to linkages and invasives
Neutral	Developing neutral/null models	With 1997	review on neutral models in conservation ecology	definitions of neutral/null models; different types of neutral models; application to defining connectivity and species' perceptions of the landscape
		With and King 1997	review on neutral models in landscape ecology	
Barrier	boundary detection	Fortin and Drapeau 1995	review of boundary detection methods with empirical example	how to choose appropriate boundary detection method based on type of available data; overview of boundary detection methods, inc. wombling, moving split windows, and spatial clustering; ways to address spatial autocorrelation
		Fagan et al. 2003	review of boundary detection methods	
		Kent et al. 2006	review of spatial statistics for plant ecology	
		Fitzpatrick et al. 2010	modeling study on specific boundary method using empirical invasive species example	
	boundary permeability	Ries et al. 2004	review on edge ecology	different mechanisms of boundary function; importance of edge physical structure; how to quantify boundary permeability; importance of the relative amount of edge in a linkage and ways to measure it
		Hilty et al. 2006	review book on corridors	
		Lopez-Barrerra et al. 2007	observational study of edge effects on seed dispersal across forest boundaries	
		Foxcroft et al. 2011	observation study of edge effects on invasive plant spread into parks	
Habitat (partial and complete)	determining habitat quality	Hilty et al. 2006	review book on corridors	benefits of increased habitat in linkage; methods for differentiating between habitat and conduit function patterns; importance of physical scale when collecting and analyzing spatially-explicit data
		Kalwij et al. 2008	observational study of invasive plants and roads	
		Christen and Matlack 2009	observational study of invasive plants and roads	
		Sullivan et al. 2009	observational study of invasive plants and roads	
	edges vs interiors	Anderson and Jenkins 2006	review book on corridors	relationship between habitat area and distance to edge in community composition; impact of edge habitat, patch/linkage size, and invasive species on conservation goals; how width of linkage might alter edge effects; reasons for differences between edge vs interior in invasive species richness and abundance
		Hilty et al. 2006	review book on corridors	
		Theoharides and Dukes 2007	review on plant invasion factors and stages	
		Ewers et al. 2007	observational study of interacting edge effects in forest corridors on an invertebrate community	
Conduit (drift-fence and classical corridor)	conduit types	Townsend and Levey 2005	observational study of pollen transfer in experimental linkages	how to differentiate between drift fence and traditional corridor hypotheses
	determining spatially-dependent structure	Tikka et al. 2001	observational study of plants and roads	demographic models used for comparison of different dispersal patterns to determine conduit function; use of chronosequences for snapshot data; using parallel and perpendicular transects in a linkage from edge to establish dispersal capability and patterns; role and meaning of spatiaul autocorrelation for conduit function
		Christen and Matlack 2006	observational/modeling study of invasive plants and roads	

(Continued)

Table 1. Continued.

Classes of interactions	Key topic	Author and date	Type and focus of work	Relevance to linkages and invasives
		Christen and Matlack 2009	observational study of invasive plants and roads	
		Calabrese and Fagan 2004	review on connectivity measures	
		Minor and Urban 2008	review on graph theory and modeling example using birds	
	graph theory	Minor et al. 2009	observational/modeling study of invasive and native plants' connectivity in fragmented landscape	background on graph and network theory; how to think about connectivity for conservation using graph theory; combining spatially-explicit habitat data with dispersal data; examples of application, analysis, and interpretation; how species spatial structure can differ based on dispersal mode
		Alagador et al. 2012	modeling study on habitat linkages using graph theory	
		Luque et al. 2012	preface to special issue on connectivity in Landscape Ecology	
		Kirchner et al. 2003	observational study on rare aquatic plant dispersal along corridors	
	genetic structure	Dyer et al. 2012	observational study on native tree pollen connectivity across habitat types	examples of application, analysis, and interpretation; how graph theory can be incorporated into genetic connectivity; need to incorporate both demographic data and genetic connectivity data to establish current functional connectivity
		Luque et al. 2012	preface to special issue on connectivity in Landscape Ecology	
		Rico et al. 2012	observational/modeling study of grassland community genetic connectivity	
Source (1 and 2)		Marshall 1989	observational study of weed ingress into agricultural fields	
		Smith et al. 1999	experimental study of weed ingress into agricultural fields	
		Sosnokie et al. 2007	observational study of weed ingress into agricultural fields	distribution patterns to show spillover effect; incorporation of landscape context and dispersal mode when determining spillover; examples of application, analysis, and intepretation
	spillover effect	De Cauwer et al. 2008	experimental study of weed ingress into agricultural fields	
		Brudvig et al. 2009	observational study on native plant spillover in experimental linkages	
		Cordeau et al. 2011	experimental study of weed ingress into agricultural fields	

while movement occurs across generations (Anderson and Jenkins 2006, Hilty et al. 2006) (Fig. 1c, d). This parallels studies demonstrating that man-made linear features (roads, trails, etc.) can function more as habitat for invasives than as dispersal conduits (Kalwij et al. 2008, Sullivan et al. 2009). Within linkages, differences in species' diversity and abundance may differ along the edge versus the interior (Anderson and Jenkins 2006, Hilty et al. 2006, Ewers et al. 2007) with invasive plants more abundant in edges than in interiors (Theoharides and Dukes 2007). Differentiation between partial and complete habitat is relevant for management and should be obvious from invasive distribution patterns (Fig. 2). The most easily-observable distinction between habitat and conduit interaction types would be if the invasive plant is also present in the connected habitat patches (Fig. 2). However, just because a species has not yet invaded the connected habitat patches does not mean that the linkage may not function as a conduit. Figure 2 functions as a starting guide for land managers but once the observational pattern has been examined, processes must be examined as detailed below.

The distinction between habitat function and conduit function (see also section Conduit) deserves further explanation. If an invasive plant proliferates in part or all of a linkage, it does not necessarily mean that the linkage is facilitating movement of that species. The conduit function implies directed dispersal, evidenced by diminishing abundance away from source populations (Levin et al. 2003, Levey et al. 2005, Christen and Matlack 2006, Kalwij et al. 2008). Determining the source population will often be a top management priority when examining the functional relationship between linkages and invasives. The clearest indication of a conduit function would be the presence of 'wave spread' (Christen and Matlack 2006) from the source population into and along the linkage. First, the effects of habitat heterogeneity must be separated out (Christen and Matlack 2006, Sullivan et al. 2009) and then an examination of patterns parallel and perpendicular to the linkages will help determine if invasion is being directed by the linkage (cf. Christen and Matlack 2006, 2009). A linkage that is functioning as a conduit should exhibit non-random patterns of distribution. This snapshot observational method of differentiating between habitat and conduit would be a straightforward first step, followed by direct examination of movement via seed traps, genetic studies, or other methods (section Conduit) if time and resources permit.

The same methods used to detect boundaries (section Barrier) can detect differences between edges and interiors to distinguish between habitat interaction types (Fig. 1c vs 1d). If a focal linkage is functioning as habitat for a particular species or suite of invasive plants, its conservation value could be compromised due to the negative direct and indirect impacts of invasive plants on the native species the linkage is meant to serve (Panetta and Hopkins 1991, Hilty et al. 2006).

Particular management strategies will depend on which linkage characteristics contribute to habitat quality for a given species. Eradicating local populations might have only short-term effects if the source population (here, the matrix) remains intact or the habitat quality in the linkage remains high. If the linkage serves as partial habitat for focal invasive plant species, managers could concentrate their control efforts along the edges of linkages. The balance between management strategies targeting the matrix versus linkage populations will depend on the stage of invasion of the species and its life history (Epanchin-Niell and Hastings 2010). For example, for species in the spreading phase controlling satellite populations within the linkage might be a more immediate strategy (Catford et al. 2009).

Conduit

Conservation linkages are meant to facilitate, directly or indirectly, the movement of native plants and animals. Invasive plants also may move into one or both of the connected habitat patches from the matrix (Fig. 1e) or move via linkages from one connected habitat patch to the other (Fig. 1f) (Hilty et al. 2006). These two possible conduit functions represent the 'drift fence' (Fig. 1e) and the 'traditional corridor' function (Fig. 1f), well-illustrated by Townsend and Levey (2005). Deckers et al. (2008) documented a traditional corridor function in their study of invasive plant movement, via bird dispersers, in a hedgerow system. Figure 2 highlights the fact that interaction types other than habitat or barrier will likely require more of an inspection of processes (determining source populations and direction of movement) behind the observational patterns. Nonetheless, there may be observational distinctions between the 'drift fence' and 'traditional corridor' types (Fig. 2).

There are several ways managers can determine if there is actual movement into and/or through the linkages. If multiyear, longer-term studies are not feasible, spatially-explicit snapshot data can be analyzed based on random versus spatially-dependent patterns of richness and abundance (cf. section Habitat and Tikka et al. 2001, Christen and Matlack 2006, 2009). Arrays of seed traps in the matrix, linkage, and connected habitat patches could help determine where and at what abundances seeds are being dispersed. Another (albeit resource-intensive) way to determine actual conduit function would be to monitor multi-year spatially-dependent genetic changes in species populations (cf. Rico et al. 2012) or snapshot data of genetic structure across populations (cf. Kirchner et al. 2003, Christen and Matlack 2006, Dyer et al. 2012). Graph theory also has become increasingly popular in connectivity research, for both animal and plant species, combining spatially explicit habitat data and dispersal data (Calabrese and Fagan 2004, Luque et al. 2012). Minor and Urban (2008) provide a research framework for using graph theory for understanding habitat connectivity, and Minor et al. (2009) examined native and invasive plant connectivity between fragmented habitat patches using graph theory.

Management control efforts will also depend on whether the linkage is functioning as a drift fence (Fig. 1e) or a traditional corridor (Fig. 1f) since the source populations differ. As noted above (section Habitat), control strategies targeting satellite populations or habitat quality characteristics might also be effective. The key determinant for deciding management focus would be the mechanisms behind the conduit pattern observed. For example, if the species is being transported along the linkage by birds (Deckers et al. 2008), managers might want to alter management of the linkage with regards to that dispersal vector and not just to the locations where the plant species establishes (see also section Species' ecological characteristics).

Source

Conversely, a linkage may be the source of invasive plant invading previously uninvaded matrix (Fig. 1g, h). Invasives along the edge or throughout the linkage could invade the matrix and/or the connected habitat patches (a combination of Figure 1g and 1h is also possible). Spillover may be of most concern where the matrix habitat has a highly controlled plant species composition, such as in agricultural landscapes (Sosnoskie et al. 2007, Brodt et al. 2009 but for a note of encouragement, see Marshall 1989, Smith et al. 1999, De Cauwer et al. 2008, Cordeau et al. 2011). There are observational differences between the two source interaction types (Fig. 2). However, if a focal linkage is undergoing active or changing invasion, the source may not be apparent. This is where process (mechanisms underlying observed patterns) comes into the forefront, and methods such as seed traps, also suggested above, would help identify those mechanisms.

If the linkage is functioning as the source for invasive plants, then management efforts should be concentrated at those source populations within the linkage, especially if presence of invasives is impacting other conservation goals of the linkage system. Control or eradication should also be attempted in the matrix or the connected habitat patches, depending on the interaction type.

Knowledge gaps and components within conceptual model

After examining and analyzing the spatial pattern of invasive plant distribution and abundance within the focal linkage landscape, researchers and managers should focus on the processes behind the patterns. This involves looking at the main components in the interaction types in Fig. 1: the linkage, the matrix, and the focal species. All three are fundamental to assessing landscape connectivity (Taylor et al. 2006). To assess actual functional connectivity of a linkage for a particular species, relevant landscape structure and species-specific movement ecology should be incorporated (Taylor et al. 2006, Damschen et al. 2008, Lizée et al. 2012, Rico et al. 2012). Rico et al. (2012) present a conceptual model for studying functional connectivity for plants in fragmented landscapes, emphasizing collecting data on the likely source populations of a species (pre-dispersal characteristics), landscape structural elements (e.g. matrix types) and dispersal mode (dispersal characteristics), and actual establishment (post-dispersal characteristics).

Below I provide the most relevant characteristics of these three components in the context of critical knowledge gaps about how linkages and invasive plants interact. Additionally, I highlight decision-making 'shortcuts' that will aid managers in prioritizing management actions when trying to understand and control plant invasions in their linkages.

Matrix characteristics

1) How will matrix identity impact invasive plant processes in a linkage system?

Many conservation linkages will likely be imbedded in multi-use landscapes, and thus the matrix cannot be simply treated as uniform 'non-linkage'. Differing types of matrix can differentially influence invasive pattern and process within the linkage, such as the nature and depth of edge effects (in non-linkage contexts: Mesquita et al. 1999, Jules and Shahani 2003, Murphy and Lovett-Doust 2004, Harper et al. 2005, Porensky 2011). Multiple studies have demonstrated that increasing levels of human disturbance impacts, usually negatively, native and non-native plant species in adjacent linkages and/or fragmented habitat patches (Boutin and Jobin 1998, Schmitz et al. 2007, Brady et al. 2009, Cutway and Ehrenfeld 2010, Ernoult and Alard 2011, Jamoneau et al. 2011). The level of structural contrast between matrix and linkage habitat can also affect whether the differing matrix types are enabling or preventing species movement between matrix and linkage or serving as a source/sink (Kupfer et al. 2006); specifically, decreasing structural contrast may enhance functional connectivity for plants (Prevedello and Vieira 2010). Focusing on levels of human disturbance and/or structural contrast are decision-making shortcuts for this information gap.

2) What are the most appropriate spatiotemporal scales for determining matrix effects on invasive plant processes?

For some species and questions, the matrix types directly adjacent to a linkage may be the only ones worth examining (Hilty et al. 2006). However, if, for example, an invasive plant is transported readily by a wide-ranging animal that crosses matrix habitat, then one should examine invasive plant patterns in matrix types at greater distances from the linkage. Due to the dynamic nature of human use of fragmented landscapes (e.g. new housing developments), managers should keep in mind that the matrix could change and impact conclusions based on the previous matrix type (Fagan et al. 2003, Jules and Shahani 2003). The history of the matrix should likewise be incorporated. For example, if one of the matrix types is suburban housing, the length of time since development may be of relevance to invasive plant patterns.

Linkage characteristics

1) How will edge effects alter how linkages and invasive plants interact?

Edges remain a central focus in landscape ecology due to their roles in mediating ecological flows between patch mosaics, impacting dispersal and habitat quality (Cadenasso and Pickett 2001, Cadenasso et al. 2003, Ries et al. 2004). Edge effects are not fixed and will vary among even closely-related species (Young et al. 1995, Cadenasso and Pickett 2001, Ries and Sisk 2004). However, some generalizations can be made across landscapes that are floristically and structurally similar (Cilliers et al. 2008). If managers have similar matrix types adjacent to similar linkages, they might be justified a decision-making shortcut by attributing findings from one matrix-linkage study to another area. Ries and Sisk (2004) present a predictive model of edge effects that enables researchers to better understand the mechanisms behind observed edge-response patterns of abundances. The model is based on resource (quality) differences between habitat patches and within the edge itself (Ries and Sisk 2004, Ries et al. 2004). As a general rule, edge effects may be most severe when there is a sharp structural contrast between matrix and linkage (Anderson and Jenkins 2006, Hilty et al. 2006). Quantifying edge effects will help managers understand not only which interaction type (Fig. 1) prevails for which species but also why that particular interaction type occurs (process behind pattern).

2) What are the effects of interacting edges within linkages?

Researchers should also recognize the impact of having interacting edge effects within a type of landscape feature (i.e. a linkage) that is highly 'edgy'. Edge interactions can occur when the two edges of the linkage are physically close enough for their individual edge effects to interact in additive or even synergistic, i.e. non-intuitive ways. Interacting edges can significantly alter the shape and depth of edge effects, depending on the width of the linkage/patch, total linkage/patch area, and strength and direction of simple edge effects (Ries et al. 2004, Ewers et al. 2007, Harper et al. 2007, Porensky 2011, Porensky and Young 2013). If the simple effects of edges on invasive plants are impacted by interacting linkage edges, management focus and strategies will have to alter to reflect those process-changing interactions.

Species' ecological characteristics

1) How do differing dispersal syndromes and dispersal distance change how invasive plants interact with linkages?

Because the conceptual model presented here focuses on movement, understanding dispersal ecology, the most crucial aspect of movement ecology for plants, of focal invasives is essential (Damschen et al. 2008, Holyoak et al. 2008, Nathan et al. 2008). Minor et al. (2009) found that the configuration of fragmented habitat patches impacted the connectivity for non-native and invasive plant populations less than it did for native plants, likely due to greater dispersal ability of the invasives. Some invasives capable of occasional long-distance dispersal may be relatively unaffected by landscape fragmentation (With 2002, Minor et al. 2009), but there may be a tradeoff between dispersal distance and colonization ability if species with short-range dispersal modes establish more rapidly in landscapes with clumped suitable habitat (With 2002).

Many of the explanations why invasive plants can spread so quickly and thoroughly can be reduced to specific aspects of landscape structure in conjunction with dispersal mode (With 2002, Deckers et al. 2008, Christen and Matlack 2009, Flory and Clay 2009). For example, Deckers et al. (2008) found that an invasive tree's distribution pattern clusters around larger trees that are seed sources or around hedgerow intersections; this is due to the perching preferences of the species' main disperser (birds). That particular dispersal syndrome makes those hedgerows function as conduits for invasives, not just habitat.

The few studies involving linkage features (for conservation or not) and plant species (invasive or native) suggest that bird- and mammal-dispersed species may be most strongly affected, usually positively, by the presence of linkages (Damschen et al. 2008, Brudvig et al. 2009, Andrew and Ustin 2010). In addition, Damschen et al. (2008) found that both bird-dispersed and wind-dispersed plant species are impacted by experimental corridors, albeit in different time-dependent ways. In their experimental corridor system, richness of bird-dispersed species increases in habitat patches linked by corridors, independent of edge amount. Given adequate time and resources, studying invasive plant dispersal would entail research on the movement patterns or processes of their dispersal agents, both biotic and abiotic. Managers might choose to make a decision-making shortcut by focusing on animal- or bird-dispersed invasive plant species as these may be the most impacted by linkage characteristics.

2) How do stage of invasion and life history change the interaction type?

There will be differences in research goals and applicability of the conceptual model for a nascent versus an established invader (Brady et al. 2009, Andrew and Ustin 2010). For example, an established, widespread invasion can obscure the influence of different matrix types, especially if the landscape is highly fragmented (Brady et al. 2009). Additionally, landscape structure may influence demographic factors more strongly than dispersal factors at certain stages of invasion (With 2002, 2004). For example, although well-distributed suitable habitat for an invasive plant can aid dispersal, aggregated habitats might enhance that species' establishment and reproduction success (Bergelson et al. 1993). Additionally, invasive plant species with different life histories could interact differently with landscape-level habitat patterns. For example, an invasive plant species with an annual lifecycle and high fecundity may spread more quickly through a linkage than its perennial counterpart with lower fecundity even if both are dispersed by the same vectors.

Applicability of conceptual model

Although this paper focuses on invasive plants, the interaction types and main components presented in the conceptual model can be applied to other invasive species, including animals and pathogens. In fact, the model and discussion above also may help researchers and managers determine the pattern and process behind native plant and animal movement in conservation linkages. Because a biotic dispersal agent's movements may strongly facilitate invasive plant spread (Malo and Suarez 1997, Buckley et al. 2006, Deckers et al. 2008), the model's interaction types should also be viewed with that type of movement capacity in mind. Researchers and managers can narrow down the range of possible types due to the dispersal agent, focusing their data-collection and/or modeling efforts.

Studying non-experimental landscape linkages may limit one's ability to differentiate the impacts of potentially enhanced connectivity from intercorrelated factors, such as increased habitat area or edge. Replicated experiments may be the best method for rigorously testing the mechanisms behind observed patterns (Damschen et al. 2006). However, landscape-scale experiments are difficult (Kupfer et al. 2006, De Cauwer et al. 2008). Some encouraging studies suggest that confounding factors may be manageable. In a meta-review of corridor studies, Gilbert-Norton et al. (2010) found that even when corridor effectiveness studies do not control for area effects, their results are usually still valid. Using similar landscapes with the same focal species but without conservation linkages can serve as controls (Haddad and Tewksbury 2006).

Final thoughts

This paper is meant to not only provoke further thought on the theoretical aspects of linkage connectivity but also to give researchers and land managers decision-making guidance and tools to assess the issue of invasive plants in conservation linkages (Fig. 2). Understanding not only what is happening in the focal landscape (patterns) but also why (process) will help managers predict future invasions and manage current ones. Research based on the model presented here may suggest innovative management practices, such as intentionally fragmenting conserved lands within a linkage to halt the dispersal of invasive plants, i.e. an invasive 'firebreak' (With 2004, Alofs and Fowler 2010). Such research may also support the recommendations of Minor and Gardner (2011) that managers adjust their invasive control methods depending mainly on dispersal ecology, in particular the probability of long-distance dispersal. Focusing on enhancing habitat quality for natives (thereby reducing the abundance of invasives), via restoration or edge management, may be another effective general approach to reducing the extent that conservation linkages function as habitat or conduits for invasives (With 2004, Crooks and Suarez 2006). This research and management work necessarily entails the involvement of multiple, diverse stakeholders (Bennett 1999, Bennett 2004, Sanderson et al. 2006, Franklin and Lindenmayer 2009, Aune et al. 2011, Beier et al. 2011) whose lands may function as sources of invasive plants or may be affected by invasives in the linkages.

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