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A conceptual ecological model to facilitate understanding the role of invasive species in large-scale ecosystem restoration

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ABSTRACT

We developed a conceptual ecological model (CEM) for invasive species to help understand the role invasive exotics have in ecosystem ecology and their impacts on restoration activities. Our model, which can be applied to any invasive species, grew from the ecoregional conceptual models developed for Everglades restoration. These models identify ecological drivers, stressors, effects and attributes; we integrated the unique aspects of exotic species invasions and effects into this conceptual hierarchy. We used the model to help identify important aspects of invasion in the development of an invasive exotic plant ecological indicator, which is described a companion paper in this special issue journal. A key aspect of the CEM is that it is a general ecological model that can be tailored to specific cases and species, as the details of any invasion are unique to that invasive species. Our model encompasses the temporal and spatial changes that characterize invasion, identifying the general conditions that allow a species to become invasive in a *de novo* environment; it then enumerates the possible effects exotic species may have collectively and individually at varying scales and for different ecosystem properties, once a species becomes invasive. The model provides suites of characteristics and processes, as well as hypothesized causal relationships to consider when thinking about the effects or potential effects of an invasive exotic and how restoration efforts will affect these characteristics and processes. In order to illustrate how to use the model as a blueprint for applying a similar approach to other invasive species and ecosystems, we give two examples of using this conceptual model to evaluate the status of two south Florida invasive exotic plant species (melaleuca and Old World climbing fern) and consider potential impacts of these invasive species on restoration.

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1. Introduction

Large, complex regional restoration programs such as the multi-billion dollar Everglades Restoration Initiative must include a means for determining how well restoration goals are met (Niemi and McDonald, 2004; Thomas, 2006; Ruiz-Jaen and Aide, 2005; Vigmostad et al., 2005). Uncertainties, however, are inevitable in dealing with large ecosystems and their restoration because such systems are highly complex and not thoroughly understood. In Everglades restoration conceptual ecological models (CEMs) have provided an organized framework for reaching a scientific consensus regarding key ecological linkages among ecosystem components and how those components interact, and

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identifying and reducing uncertainties that exist about how natural and human systems will respond to long-term restoration programs (Ogden et al., 2005, see Wetlands Special Issue, 2005). The southern Florida CEMs have served as thought experiments used to develop interrelated sets of ecosystem hypotheses and have assisted in identifying key research questions to guide design and implementation of comprehensive monitoring and research programs. Our CEM was used to develop an invasive exotic plant ecological indicator that is presented in a companion paper in this special issue (see Doren, Volin, and Richards, this issue).

The need to repair and rejuvenate large natural landscapes – generally termed ecosystem restoration – is usually the result of long-term and large-scale disturbance, typically of anthropogenic origin, of an ecosystem. Characteristics attributed to ecosystem structure and function, such as ecological resilience (*sensu* Holling, 1973), adaptive capacity (Gunderson, 2000), ecological memory (*sensu* Peterson, 2002), and landscape pattern (*sensu* Ludwig et al., 2000), may no longer be meaningful in a highly disturbed, human-dominated system, particularly where invasive species are part of the cause of disturbance (D'Antonio and Meyerson, 2002; Fridley et al., 2004; Hulme, 2006). CEMs can help sort out the patterns, relationships, and links in such complex and dynamic systems. Such models are especially needed for exotic species, which may generate successional trajectories that are new to the ecosystem, are especially complex or unpredictable (D'Antonio and Meyerson, 2002), but are also difficult to develop because each exotic species has unique characteristics and unique effects on the ecosystem.

Biological invasions also have unique characteristics resulting from cross-scale interactions. Such interactions challenge the ability of ecologists to understand and predict system behavior at one scale based on information obtained at either finer- or broader-scales (Holling, 1992; Platt et al., 2002; Peterson, 2002; Fridley et al., 2004; Sheley et al., 2006). Under some conditions, fine-scale processes can propagate nonlinearly to influence broader-scale dynamics, while under a different set of conditions broad-scale drivers can overwhelm fine-scale processes (Platt et al., 2002; Fridley et al., 2004). Cross-scale interactions often result in "surprises" that can have severe consequences for the environment, such as wildfires or pest outbreaks (Platt et al., 2002; Peterson, 2002; Fridley et al., 2004). Alternatively, cross-scale interactions can be exploited to accelerate recovery of vegetation after fire or removal of exotic species (Platt et al., 2002; D'Antonio and Meyerson, 2002). Spatial heterogeneity in the environment often structures the outcome of cross-scale interactions by governing the nature and scale of particular processes (e.g., fire spread as affected by fine-scale fuel connectivity; exotic species invasion, establishment, and spread as affected by initial site conditions or propagule pressure). Invasive exotic species in particular illustrate these cross-scale problems. A newly introduced exotic species may initially distribute relatively small numbers of propagules to remote locations. The fine-scale conditions (soil type, soil moisture, pH, etc.) in each location must be conducive to germination and recruitment in order for the species to establish. Once established, as the species matures and reproduces over time, additional propagules are released and colonize new sites. In the early stages of spread the establishment sites may not be widespread, and propagules may only rarely reach sites that are remote from the original foci of infestation. As more propagules are produced and distributed, however, more propagules are released over ever larger regions and time spans, providing a greater opportunity for more propagules to encounter the right fine-scale conditions and helping to create greater spatial connectivity. At this point the interactions between numbers of propagules, propagule distribution, and finer-scale site conditions intersect larger-scale patterns (e.g., landscape heterogeneity, landscape pattern, weather patterns, hydrology, rainfall, etc.) that may lead to the exponential increase in spread rates such as we now see in the Everglades with *Lygodium microphyllum* (Volin et al., 2004). At this point – a point which can take many decades to reach – invasive exotic species become what we term ecosystem engineers (*sensu* Jones et al., 1994; Crooks, 2002), and the dynamics of the exotic/ecosystem interactions change because the presence of the invasive species alters ecosystem patterns and processes on a large-scale. A CEM for invasive species needs to illustrate this temporal dynamic and the associated cross-scale interactions. This CEM may be particularly helpful in developing monitoring and research programs for invasive animal species, as less is known about individual invasive animal species or their impacts on ecosystems. This framework could provide a basis to evaluate critical ecosystem components, define small and large scale interactions and locate key points in a species' invasion that allow for eradication versus simply managing for a reduction in numbers.

In this paper we present a CEM for invasive exotic plants that can be applied to any invasive species. We then give two examples of using this conceptual model to evaluate south Florida invasive exotic plant species and potential impacts of restoration on these invasive species.

2. Methods

2.1. *Model development*

The framework for the invasive species CEM was the CEMs developed for Everglades restoration (see Thomas, 2006 and Wetlands special issue, 2005). These CEMs are hierarchical and based on identifying ecological drivers, human stressors, ecological effects and specific measurable attributes that reflect the ecological effects and their linkages (Ogden et al., 2005). Drivers are major environmental forces that have large-scale influences on the natural system (e.g., climate, hydrology, and major natural disturbances); stressors, which are also drivers, are the human induced perturbations that have large- or regional-scale influences on the natural system (e.g., water management, contaminants, exotic species); ecological effects are the biotic and abiotic responses caused by the drivers and stressors; and the attributes are a subset of the components of the natural system that represent the overall ecological conditions of the system, some of which may be useful as indicators (Ogden et al., 2005; Doren, Trexler, Gottlieb, and Harwell, this issue). The Everglades CEMs are spatially oriented and model processes in either a landscape (e.g., ridge and slough Ogden et al., 2005) or regional (e.g., Lake Okeechobee Havens and Gawlik, 2005) context.

Invasive species have effects at these large spatial scales, but modeling their position in the hierarchy requires a temporal aspect, in addition, that accounts both for invasion and the effects of invasion, as well as the particular effects of the exotic species itself on ecosystem characteristics and processes. Thus, the general Everglades CEMs required modification in order to model invasive species in the ecosystem context. We began to design our model by using input from an expert panel (*sensu* Oliver, 2002) of regional scientists and managers who work on invasive species. The model grew out of invasive species workshops that brought together scientific experts in plant ecology, invasive exotic species, biological control, landscape ecology and invasive species management and control, as well as our experience of plant invasive species biology and management.

2.2. Model application

We selected two southern Florida invasive exotic plant species, *Melaleuca quinquenervia* and *L. microphyllum*, as examples of how to apply the CEM. We then worked through the model, surveying the literature for information on each potential driver, stressor, effect and attribute, in order to arrive at conclusions about our knowledge about each species and to identify potential targets for further research, monitoring or management.

3. Results and discussion

3.1. General CEM for invasive exotics (Fig. 1)

Individual invasive species exhibit characteristics in an ecosystem that can include being a driver/stressor (Gordon, 1998; Ogden et al., 2005), having other direct effects on ecological aspects of a system, and even contributing particular attributes to a system (D'Antonio and Meyerson, 2002). We faced two challenges in developing a CEM for invasive exotic species: each invasion occurs because of individual species attributes and environmental characteristics unique to that particular invasion; and the characteristics of that particular invasion change over space and time as a result of the invasion (Vitousek, 1986; Williamson, 1996; D'Antonio and Meyerson, 2002). The unique aspect of this model, as compared to other Everglades restoration conceptual models (Ogden et al., 2005), is that once an exotic species becomes established, it plays a central role as an ecosystem engineer, further altering the environment and changing the impacts that drivers and stressors have on both native and exotic species and the environment. An additional difference in this model is that the invasive plant, as a stressor, is in turn affected by environmental factors, the biological properties of the particular invasive species (dispersal, recruitment, etc.), human factors such as use and transport, restoration activities, and control measures (Fig. 1A and B (also see ovals either side of B). Specific invasive exotic drivers and stressors and the ecological effects and attributes are discussed below.

Many species illustrate invasiveness under certain circumstances, and the species may not necessarily be exotic. An example in the Everglades is cattail, *Typha domingensis*. Cattail becomes highly invasive when an ecosystem state-change occurs; studies have documented that in the Everglades this invasiveness is directly correlated with an increase in phosphorus (Craft et al., 1995). Where indigenous species become invasive in their native habitats through some sort of ecological perturbation, the reasons are usually clear or can be discerned based on an understanding of that species' ecology. With exotic species, however, the basis of their invasiveness is usually unknown, if not unknowable, because they are new to the ecosystem and their ''invasiveness'' is often not a part of their ecology in their native ecosystem.

After introduction of an invasive species, certain triggers – environmental conditions and species interactions – are necessary for an introduced species to become invasive (arrow between A and B, Fig. 1). Once a species has become invasive, it becomes an ecosystem engineer (Jones et al., 1994; Crooks, 2002) (Fig. 1B). We then model the ecological effects and attributes of the invasion (Fig. 1C and D). Thus, our conceptual model identifies the general conditions that allow a species to become invasive in a *de novo* environment, and then, once a species is invasive, the model illustrates the possible affects exotic species may have at varying scales and for different ecosystem properties (Fridley et al., 2004; Sheley et al., 2006). We consider details of the different phases of invasion below.

3.1.1. Drivers and stressors (Fig. 1A)

Major drivers affecting the potential invasiveness of exotic species include native ecosystem drivers such as climate, hydrology, topography, soils, water quality, disturbance regimes (e.g., fire), etc. (Fig. 1A). These indigenous drivers affect how both exotic species and native species function within the ecosystem. Where invasive exotic species are present, however, different or additional drivers come into play at different points in an exotic species' establishment, recruitment and spread (Fig. 1A). In addition to an ecosystem's indigenous drivers, exotic species themselves may act as a driver/stressor, bringing individual species attributes that in a *de novo* environment may play a crucial role in determining invasibility. These drivers include characteristics that affect species introduction, such as multiple introductions or the introduction of multiple genetic strains, as well as individual species attributes that aid recruitment and establishment, such as fecundity, propagule dispersal, hybridization with native species (Rogers et al., 1982; Childs et al., 1996; Anttila et al., 1998; Ayers et al., 1999), large persistent seed banks (Newsome and Noble, 1986; Noble, 1989; Baskin and Baskin, 1998), leaf life span (Poorter et al., 2006), physical or geochemical alteration of soils or water chemistry (e.g., through nitrogen fixation), and enhanced growth rates in relation to native species (see Gordon, 1998). In addition, human use and manipulation of both an exotic species and the larger ecosystem serve as drivers, and these anthropogenic effects may either intensify exotic species attributes that encourage the leap to invasiveness (Mack et al., 2000) or negatively impact native species or habitat, thus giving exotics a disturbance advantage (Lozon and MacIsaac, 1997; D'Antonio et al., 1999).

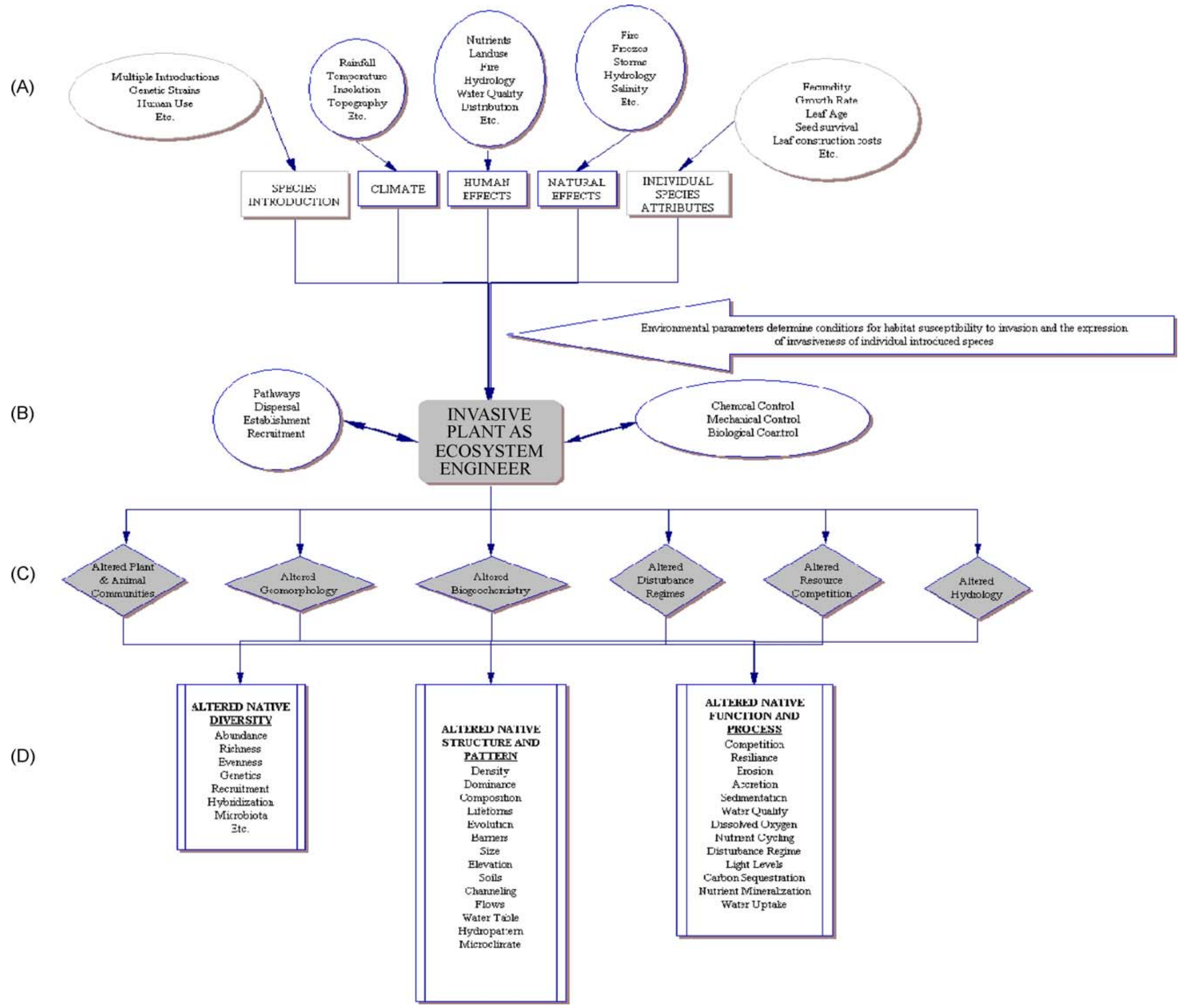

Fig. 1 – General CEM for invasive species. The model encompasses the trajectory of the invasion, evaluating the ecological causes and effects in the initial phases of invasion, as well as in the established phase. It shows the driver and stressor interactions that may lead to invasion (A), the attributes that affect an invasive exotic plant becoming an ecosystem-engineer (B), the ecological effects (C) and attributes (D), which are the ecological functions, processes, and structures that the exotic as ecosystem engineer may alter. The large arrow between A and B indicates the point at which a species becomes invasive. In section B of the figure, the two ovals indicate how the effect of control may impact the invasiveness or spread of an invasive species, and how the biology or use of the species itself may impact it ability to continue to invade. Effects and attributes that are highlighted in gray are documented by the literature.

3.1.2. *Exotic species as ecosystem engineers (Fig. 1B)*

The drivers and stressors determine the course of invasion, but once a species becomes invasive, it acts as an ecosystem engineer and can alter drivers and stressors at the landscape scale (two-way arrows with ovals, Fig. 1B). At this point in an exotic species invasion, additional drivers may have either positive or negative impacts on the species. Drivers such as multiple species introductions and commercial availability (Pemberton, USDA ARS, 2007, personal communication), human use and dispersal (Mack et al., 2000), competitive superiority (Anttila et al., 1998), multiple dispersal pathways (human and natural) (Mack et al., 2000), and extinctions of native species or extirpations through hybridization (Rhymer and Simberloff, 1996) may significantly enhance the spread and recruitment of an exotic (Ayers et al., 1999). Other drivers, such as biological control organisms (Tipping et al., 2008; Center et al., 2007), and mechanical (hand or machine removal) or chemical control (herbicide application) programs, may significantly reduce the impact of exotic species (SFWMD, 2006).

3.1.3. *Ecological effects and attributes (Fig. 1C and D)*

An invasive exotic can have a variety of ecological effects, such as altering biodiversity, geomorphology, biogeochemistry, etc. (see Gordon, 1998), that can be expressed in a variety of altered ecosystem attributes, such as changes in species richness,

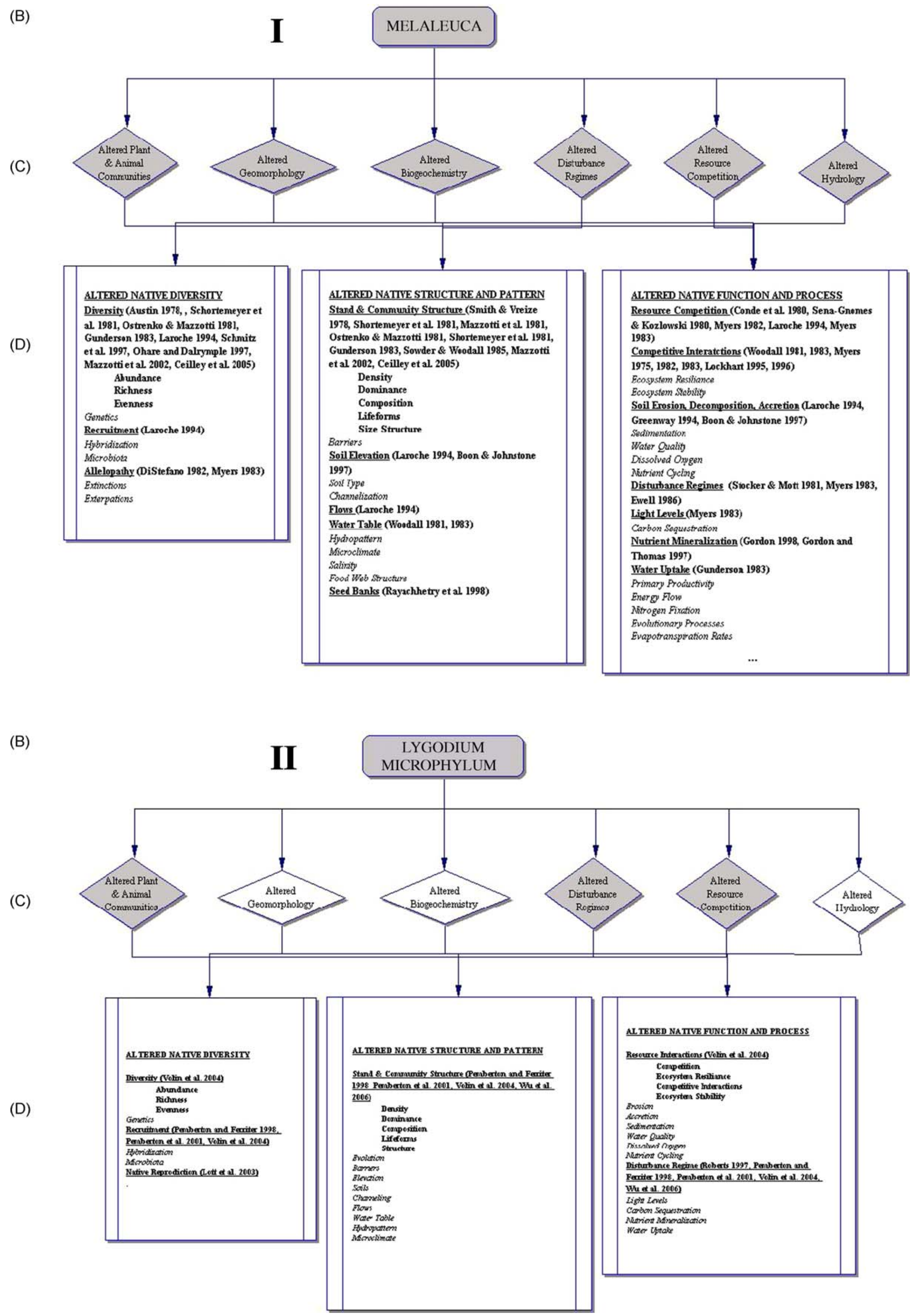

Fig. 2 – Two examples of the application of our CEM to two Everglades invasive species; we present here just the bottom half of the general model in order to highlight the major differences in ecosystem effects and attributes of the two species, as well as differences in our knowledge about these two species. Those effects and attributes that are documented by the

density, dominance, and composition of native communities (Fig. 1D). Our conceptual model identifies the general ecological effects that invasive exotic species may produce in an ecosystem. These are effects on (1) plant and animal communities; (2) geomorphology; (3) biogeochemistry; (4) disturbance regimes; (5) resource competition; (6) hydrology (Fig. 1C). Alteration of any one or a combination of these may affect native diversity, native structure and pattern and/or native function and process (Fig. 1D). Alterations of ecological attributes by invasive exotic species may work individually or in combination to cause changes in diversity, structure or function. The links between these complex interactions are extremely difficult, if not impossible, to discern empirically (Pysek et al., 1995; Fridley et al., 2004; Sheley et al., 2006).

In summary, our general CEM integrates the drivers, stressors, ecological effects and attributes that have been described for invasive exotic plant species. This model provides suites of characteristics and processes, as well as hypothesized causal relationships to consider when thinking about the effects or potential effects of an invasive exotic. In addition, the model is designed to be tailored to individual invasive species. Thus, when considering the effects of a particular invasive, only certain drivers, ecological effects and attributes may be relevant (Fig. 2). We use melaleuca (*M. quinquenervia*) and Old World climbing fern (*L. microphyllum*) to illustrate application of the model to individual species (Fig. 2). Both are invasive exotic species in South Florida that are impacting Everglades restoration.

3.2. *Example 1: application of CEM to M. quinquenervia (Fig. 2)*

3.2.1. *M. quinquenervia drivers and stressors in southern Florida (Fig. 1A)*

Because *M. quinquenervia* invasion has had a major impact on Florida wetlands that has been well documented, we have a fairly solid understanding of the drivers and stressors that have allowed this species to succeed. Melaleuca was first introduced by seed into southern Florida in the 1880s, with multiple subsequent introductions and re-introductions on both the east and west coasts (Dray et al., 2006). The tree was used as a medicinal plant, unusual landscape plant and fast-growing forest crop, so human intervention aided it in overcoming the very long initial lag phase often characteristic of woody plant invasions (Kowarik, 1995), but human usage has declined, especially in light of governmental regulation and publicity about this species' invasive nature (http://www.fleppc.org/list/list.htm). As a result of numerous different introductions over many decades from different areas of its native range, multiple genetic strains of melaleuca are found in southern Florida (Dray, 2003; Dray et al., 2006), which complicates biological control efforts. The species is native to northeastern Australia, where it occurs in coastal wetlands that are very similar to south Florida in climate and habitat (Turner et al., 1998), thus the natural effects that support and limit growth in Australia are similar for south Florida. Although it is limited to a subtropical climate in its native range, it has survived and recovered from short-term freezes in southern Florida, which suggests that it could colonize slightly colder environments (Turner et al., 1998).

An important aspect of *M. quinquenervia*'s invasiveness is its reproductive biology, as the species produces millions of tiny seeds in woody capsules that remain on the tree until triggered to release by a stress, such as fire, or by natural growth of the plant severing vascular connections; although seed release is synchronous in response to stress, there is a constant slow seed rain throughout the year (Rayamajhi et al., 2002). Seeds are able to germinate in sun and shade, as well as submerged, although 6–12 months of submergence will kill seedlings (Rayamajhi et al., 2002). Germination and seedling survival trials in southern Florida habitats indicated that only two of eight habitats supported seedling growth (Myers, 1983). The communities tested did not include sawgrass marsh or slough communities; although melaleuca has been documented to invade sawgrass marsh (Laroche and Ferriter, 1992). Similarly, melaleuca responds to canopy destruction in fire and freezing through resprouting via epicormic buds and reportedly can form root sprouts (Turner et al., 1998). *Melaleuca* has a high growth rate in certain environments in southern Florida, in which it can flower within a year of germination (Rayamajhi et al., 2002). A short-term seed bank is present, as seeds are viable for 18 months (wet soil) to 24 months (dry soil) in southern Florida (Rayamajhi et al., 2005). An aerial seed bank is available from seeds held in woody capsules on trees. Studies have shown that these seeds lose viability over time, but how long such seeds are viable has not been determined (Rayachhetry et al., 1998).

3.2.2. *M. quinquenervia as an ecosystem engineer in Southern Florida: expansion and control (Fig. 1B)*

Once *M. quinquenervia* was established in southern Florida, its individual species attributes enabled it to modify its environment to create new habitat conducive to its spread. Specifically, once established melaleuca grows in dense stands that shade out other species or prevents their survival because of allelopathic effects (DiStefano and Fisher, 1983). The species' reproductive biology and ability to regenerate vegetatively after major disturbances contributes both to its spread and to maintenance of existing stands. The dense litter built up in these stands creates a new soil type for many of the communities that it is invading, as well as raising the soil

literature are highlighted in gray (C, effect diamonds) or in bold (D, attribute boxes; references for a documented attribute follow); un-highlighted effect diamonds and attributes in italics are areas of no effect or unknown effect. Part I. Effect (C) and attribute (D) portion of the CEM used to evaluate the status of the invasive tree *Melaleuca quinquenervia* (paperbark tree or melaleuca) in southern Florida. Part II. Effect (C) and attribute (D) portion of the CEM used to evaluate the status of the invasive fern *Lygodium microphyllum* (Old World climbing fern) in southern Florida. Comparison of parts I and II show that *Melaleuca* has major effects across the ecosystem, and many ecological attributes are modified; *Lygodium* has many fewer documented effects, which could reflect its younger invasion or our lack of knowledge.

level, concurrently reducing the hydroperiod (Van et al., 2006). Although early studies based on measurements of transpiration rates across the surface of individual leaves and an estimate of total leaf area in mature melaleuca stands compared with estimates of sawgrass leaf area (Hofstetter, 1991b in Laroche, 1994) suggested that melaleuca transpiration rates might impact hydrology, this idea is based solely on unpublished data, and this hypothesis has never been adequately tested (Simberloff et al., 1997, p. 55)

Massive control efforts in southern Florida have involved primarily chemical and biological controls. Chemical control has helped to manage *M. quinquenervia* in places of special concern, such as Everglades National Park and the water conservation areas under management of the South Florida Water Management District. Restoration activities that alter hydrology could provide a type of physical control on melaleuca, as increased water depth and duration could decrease the amount of invasible habitat and the likelihood of appropriate conditions for invasion, although we do not know what water depths and durations will affect adult stands.

Research on biological control of melaleuca has been ongoing for approx. 20 years (Laroche, 1994). Numerous insect biocontrol agents have been identified and tested and two have been released; *Oxyops vitiosa*, a weevil, was released in, 1997, and *Boreioglycaspis melaleucae*, a psyllid, was released in 2002 (Pratt et al., 2003; Center et al., 2006). These two insects have had substantial impacts on the growth and reproduction of melaleuca, primarily in response to chronic herbivory (Tipping et al., 2008; Center et al., 2007; Pratt et al., 2005). The effects of the insects appear to be independent rather than synergistic (Franks et al., 2006), but seedlings and young growth of melaleuca have been reduced in areas with the insects by as much as 70% (Center et al., 2007) and leaf abscission increases almost five fold (Morath et al., 2006). In areas where the insects have been active the longest, even mature melaleuca trees are dying and native plant recovery is substantial (Rayamajhi et al., 2006).

3.2.3. *Ecological effects and attributes after M. quinquenervia invasion (Figs. 1C and D and 2A)*

The documented effects of *M. quinquenervia* on southern Florida ecosystems are shown in Fig. 2A, where effects (A and C) and attributes (A and D) are shown. As compared to native tree islands and pinelands, melaleuca stands have altered structure and pattern (stand and community structure, including the seed bank, soil elevation, flow and water table). These differences lead to changes in ecosystem function and process (resource competition, competitive interactions, soil erosion and accretion, disturbance regimes, light levels, nutrient mineralization and water relations). These altered habitat and ecosystem processes produce major changes in native diversity (diversity, recruitment and allelopathy). Although the genetic structure of invasive *Melaleuca* populations and the effects of genetic variation on biocontrol agents have been studied (Dray, 2003; Dray et al., 2003), the effects of *Melaleuca* on the population genetics of native species have not been documented, nor have hybridization events, extinctions and extirpations, and changes in the microbiota. Similarly, *Melaleuca* either does not affect a number of ecosystem structures and functions, or the effects have not been documented (Fig. 2A and D, unhighlighted attributes).

3.2.4. *Conclusions from using CEM to evaluate M. quinquenervia*

Application of our general CEM to *M. quinquenervia* invasion in southern Florida shows that our knowledge about this invasion is quite extensive, although the depth and precision of that knowledge is not always sufficient to generate hypotheses about restoration outcomes, e.g., what are the precise conditions that allow melaleuca to invade sawgrass prairie (Is a fire required? A drought?); or what are the lower limits of water depth that allow seedling and adult survival and growth? Similarly, a review of control measures in a restoration context highlights the need for considering the effects of increased water depth and duration on melaleuca stands and how these interact with other control methods and restoration effects in general. For example, increased hydroperiod may stress trees, causing them to become more susceptible to biological control agents but may also impact the reproductive cycle of the weevil biocontrol agent *O. vitiosa*, because it pupates in the soil and does not tolerate inundation (Pratt et al., 2003). Alternatively, will increased hydroperiod create new invasible habitats, as drier sites become wetter and more susceptible to invasion, and can we use hydrological models to predict the location and extent of these habitats in order to target them for increased control efforts?

3.3. *Example 2: application of CEM to L. microphyllum (Fig. 2B)*

L. microphyllum is a relatively recent wide-spread invasive exotic in southern Florida, and in the absence of control by biological, chemical and mechanical means, is predicted to become the most widespread of any current exotic plant species within the next 10 years (Volin et al., 2004). *L. microphyllum* is a vine-like climbing fern that, left unchecked, smothers native understory and overstory vegetation, eventually collapsing canopy trees or altering fire regimes by providing a fire ladder into the canopy, resulting in forest canopy death (Roberts, 1997; Pemberton and Ferriter, 1998; Pemberton et al., 2001). The exceptionally quick spread of *L. microphyllum* across the landscape of central and southern Florida has been facilitated by its highly plastic reproductive strategy. Lott et al. (2003) showed that the fern is capable of reproducing by all three mating systems possible in homosporous ferns: intra- and inter-gametophytic selfing and outcrossing. In addition, upon spore germination gametophytes initially develop as females. These initial gametophytes also produce an antheridiogen hormone that promotes less mature gametophytes to become male, thus ensuring outcrossing and spore formation (Kurumatani et al., 2001; Lott et al., 2003). Finally, the growth of *L. microphyllum* has been found to also be highly plastic under different environmental conditions, including light (low to high) (Lott and Volin, unpublished data) and hydrology (dry to flooded) (Gandiaga and Volin, submitted). Thus, it has been shown to effectively be an ecosystem engineer by its ability to alter plant communities, geomorphology, disturbance regimes and resource competition. It is unknown whether it can alter biogeochemistry and hydrology, although, unmanaged and given its eventual dominance of both understory and overstory components within an ecosystem, it is highly likely that it will.

3.4. *Comparison of application of CEM to Melaleuca and Lygodium*

Application of the general CEM to the two different invasive species points out the general usefulness of the model in conceptualizing the status of an invasion, its particular ecosystem effects and the state of our knowledge about the particular species. In the case of melaleuca invasion into south Florida, we know much more about the dynamics of the invasion, its ecosystem effects, and the results of control measures. This knowledge allows us to make better predictions about the outcome of restoration initiatives and to ask more focused questions about proposed management alternatives. For *Lygodium*, many aspects of the biology of invasion are still unknown, but the model illustrates both the similarities and differences to melaleuca invasion. The different species show different patterns of invasion, in part because of different environmental requirements and dispersal dynamics, and different patterns of effects; they also are susceptible to different control measures. Differences between the species (Fig. 2I (Melaleuca) vs. II (Lygoidum)) in ecological effects and attributes can result either from real differences in what the species are doing or from lack of knowledge. Application of the CEM in both cases reveals areas where knowledge is lacking or where there is uncertainty.

4. Conclusions

This CEM can be used to help synthesize information about an invasive species. It highlights the aspects of the biology and human use of a species that contribute to its invasive ability; these aspects also represent potential targets for control. The CEM shows what ecological effects an invasive exotic is either known or hypothesized to have (Fig. 1) and which ecosystem attributes it is known or hypothesized to affect (Fig. 2). As a restoration tool, the model can highlight which ecosystem attributes can be improved as a result of control measures and show which attributes can improve as a result of restoration activities. The model is useful as a tool to identify the most effective life-stages or habitats for control, to predict the impacts of control and management activities, and to develop hypotheses regarding key uncertainties in causal relationships that may need further study.

While some useful predictive information is becoming available for exotic species that have been the focus of specific research (Rejmanek and Richardson, 1996; Wade, 1997; Volin et al., 2004), the fundamental causes or interactions that lead an exotic species to become invasive and be an ecosystem engineer are not well understood (Pysek et al., 1995; D'Antonio et al., 1999; Fridley et al., 2004; Sheley et al., 2006) and may be unique to each invasion. Our conceptual model does not attempt to attribute all the possible causes of invasion for every species that impacts South Florida. Instead we acknowledge that, when present, an exotic species has the potential to become invasive and that many different factors interacting at different temporal and spatial scales affect that potential. Our CEM provides a method to make a species-by-species assessment of the specific elements leading to the potential to invade and the potential impacts of invasion. It also provides a model for what interactions are probable, what scale-dependent factors may be involved and what the ultimate effects may be. Such assessment can serve as a planning tool for research, control and restoration programs. We are using this model to develop understanding and consensus among scientists, managers, and policy makers about the role that invasive exotic species have in the Everglades ecosystem and how they impact its restoration. The model provides a consistent framework to assess the impacts of invasive species on an ecosystem; to evaluate their control and management; and to guide the search for and predict the effects of new interventions. While our species-specific conceptual models will be helpful in developing hypotheses related to exotic species in south Florida, the general CEM provides a blueprint for applying a similar approach to other ecosystems.

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