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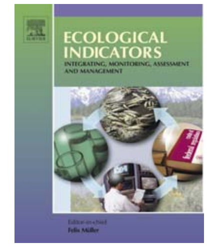


# A conceptual ecological model to facilitate understanding the role of invasive species in large-scale ecosystem restoration

*Robert F. Doren* [a,*], *Jennifer H. Richards* [b], *John C. Volin* [c]

[a] *Florida International University, Southeast Environmental Research Center, Miami, FL 33199, United States*
[b] *Florida International University, Department of Biological Sciences, Miami, FL 33199, United States*
[c] *University of Connecticut, Department of Natural Resources Management and Engineering, Storrs, CT 06269, United States*

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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 eco-regional 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.



## 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

* *Corresponding author*. Tel.: +1 305 348 6721.
E-mail address: dorenr@fiu.edu (R.F. Doren).
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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 non-linearly 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.,