



## Analysis

# The Role of Restoration and Key Ecological Invasion Mechanisms in Optimal Spatial-Dynamic Management of Invasive Species<sup>☆</sup>

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## ARTICLE INFO

## Keywords:

Spatial  
Dynamic optimization  
Meta-population  
Dispersal  
Species interactions  
Species competition  
Bio-invasions  
Invasive species  
Ecology  
River network  
Restoration  
Habitat  
Riparian

## ABSTRACT

To increase the ecological realism in an economic analysis of invasive species management in a river network, this paper identifies optimal spatial-dynamic management while accounting for specific invasive species strategies, including long-distance dispersal, exogenous arrivals, propagule pressure, and seed fitness. Although a stylized framework, the inclusion of native species permits analysis of trade-offs between the management actions of invasive species control and of habitat restoration for a range of settings and species characteristics. In general, more aggressive invasive species and more invasion-susceptible ecosystems require greater investment in habitat restoration despite its relative expense. Explicitly modeling invasion strategies reveals that the specific ecological mechanism of invasion defines the location of management activities in the river network, and the choice between invasive species control and habitat restoration. The analysis of this bioeconomic model develops insights that help managers to harness the power of native-invasive species establishment interactions in stemming bio-invasions across time and space.

## 1. Introduction

Most economic frameworks for the management of invasive species (IS) simplify the ecological processes or mechanisms of species invasion, and focus on the use of IS control (also called removal) as the sole management action. The framework developed herein incorporates an ecological model of dispersal and interspecies establishment competition that affect the choice of the location of management actions as both native and invasive plant species propagate across heterogeneous habitat. While still a stylized model, modeling native species and ecological components of IS strategies permits analysis of key management issues: the use of restoration as a management tool; trade-offs between control and restoration in a spatially explicit and heterogeneous landscape; and optimal management across various types of IS that use different ecological processes to outcompete native species.

Similarly, the IS economics literature recognizes the need for spatial and dynamic invasion characteristics in IS models but primarily focuses

on species dispersal – the spread of seeds or populations from one location to another – as the main process driving invasion. Examples of this emphasis include Sharov (2004) and Brown et al.'s (2002) use of stochastic radial spread rates to determine optimal barrier zone size and spread rate; Epanchin-Niell and Wilen's (2012) model of an invasion that spreads to nearest neighbors in one step per time period; and Chadès et al.'s (2011) directional dispersal in a network setting. Collectively, this literature demonstrates that the characteristics of optimal management depend on the type of dispersal modeled.

Beyond this emphasis on dispersal, however, the ecology literature emphasizes additional characteristics of successful invasions, including native-invasive species interactions (Eschtruth and Battles, 2009), the relative number of introductions (propagule pressure), and heterogeneity in the invasibility of the ecosystem (Colautti et al., 2006). Invasive species may compete with native species to establish through superior seeds (seed fitness) or through the quantity of seeds dispersed (fecundity) that increase propagule pressure. Some invasive species

<sup>☆</sup> This research was supported by the National Science Foundation (0832804, 1331932).

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compete through long distance seed dispersal or by entering systems from outside sources (exogenous arrivals), which also contribute to increased propagule pressure. These ecological aspects of invasion interact with the distribution and abundance of native species within the landscape to determine invasion pathways over time (Eschtruth and Battles, 2009; Colautti et al., 2006). Muneeppeerakul et al. (2007b) develops a model of these species interactions in a riparian setting with directional dispersal, and related articles use that model to address relationships between biodiversity, landscape structure, and directional dispersal in the absence of management activities (Muneeppeerakul et al., 2007a; Muneeppeerakul et al., 2008).

A limited number of economic analyses include aspects of IS ecology beyond rates of spread, including density dispersal of invasive pests in spatial bioeconomic models (Aadland et al., 2015; Sims and Finnoff, 2013); species competition and habitat health in non-spatial models (Finnoff and Tschirhart, 2005; Finnoff et al., 2008; Albers and Goldbach, 2000; Albers et al., 2006; Sanchirico et al., 2010; Albers et al., 2010); and spatial heterogeneity (Burnett et al., 2007; Burnett et al., 2008; Kaiser and Burnett, 2010). Based on the riparian ecological model in Muneeppeerakul et al. (2007b), Hall et al. (2017) uses the same ecological and decision framework presented here to examine spatial considerations, such as dispersal beyond nearest neighbors, directionality in spread, and network geometry; temporal characteristics, such as multiple year ecological processes; and the interaction of spatial and dynamic aspects of decisions with uncertainty.<sup>1</sup> While that companion article emphasizes spatial-dynamic optimization, this article uses those results as a foundation for investigating the impact on management of the ecological characteristics of invasive species as compared to native species. Although within a stylized bioeconomic framework, the analysis here contributes further to this literature by more fully incorporating several aspects of the ecological process of invasion – including dispersal, species interactions during establishment, and heterogeneous habitat invasion risk – into a dynamic optimization framework. Here, optimal policies – management tools and their location – reflect the characteristics of the invader: more restoration overall when facing aggressive IS or IS arrivals from outside the system; more upstream and midstream management action with long-dispersing IS; more upstream and midstream restoration with highly fecund IS; and more midstream restoration with high seed fitness IS.

This paper's focus on a subset of ecological mechanisms of invasion in a heterogeneous environment begins by explicitly modeling an IS's tendency to outcompete native species in propagation on degraded habitat sites. In keeping with the ecological literature, the framework incorporates both invader traits and reach ecosystem invasibility (Lonsdale, 1999; Facon et al., 2006; Richardson and Pyšek, 2006). The metapopulation model comprises heterogeneous sites whose individual habitat state depicts that site's ability to resist invasion. Locations with a healthy ecosystem of native species cannot be invaded until those native species populations die, creating available habitat on which invasive and native species compete to (re)establish.<sup>2</sup> Following the ecology literature's description, a degraded habitat site is “empty” or “open” and can transition to either a native-dominated habitat or an invaded habitat. By explicitly modeling the invasibility characteristics of locations, this framework captures the opportunistic character of invasive species that establish in a degraded site as a starting point for

<sup>1</sup> This paper also employs the same computational solution method and parameter set as Hall et al. (2017), which facilitates comparisons of results across the papers, but this paper emphasizes several ecological characteristics of the native and invasive species in the system.

<sup>2</sup> In this framework, both native and invasive species can die-back to a level that creates habitat openings that are filled by either native or invasive species. Hall et al. (2017) considers the implications of this lifecycle on policy as compared to models that assume that an invaded site remains an invaded site forever in the absence of management. In one example, the natural lifespan of the species determines the time at which the species “die” and create habitat openings, but other factors such as mass wasting of riverbanks can also contribute to making sites invadable at a point in time.

invading the system. Further, explicitly incorporating heterogeneous habitat invasibility in the framework demonstrates the role of the uninvaded portions of the system in determining optimal policy, in contrast to the IS economics literature's focus on the invaded area itself and its probability of spread to immediate neighbors. For example, optimal management actions typically occur within the invasion when the system is ecologically healthy but management typically occurs outside of the invasion when the system is highly degraded.

Although land managers and ecologists use and discuss habitat restoration as a possible management action, the IS economics literature largely ignores this possibility (Shafroth et al., 2005; Harms and Hiebert, 2006). Explicitly modeling native species and habitat quality permits exploration of the use of restoration to alter the habitat state and the important feedback loop between management actions and ecology (Finnoff et al., 2005). During restoration, native plants are planted on degraded sites. On invaded sites, at higher cost, invasive species are first removed before the natives are planted. The planting of natives in a location forms a barrier to invasion of that particular reach for the life of the native species. Restoration also provides off-site benefits because native plants produce seeds that disperse to other degraded sites where they compete with IS seeds for establishment. These benefits from restoration interact with the configuration of healthy, degraded, and invaded portions of the ecosystem in determining the location and type of management actions to employ. Although more costly than control, optimal policies often include restoration in locations with a high risk of invasion and locations from which restoration's native plants can disperse seeds to reduce system-wide risk of invasive species spread.

Using novel computational solution techniques, we incorporate these important ecological drivers of invasion into an economic spatial-dynamic optimization framework for a river network. The analysis explicitly addresses choices between restoration and control, the policy impact of different IS invasion mechanisms, and species interactions during establishment in a network landscape and determines the efficient allocation of limited management resources over space and time to limit costs associated with invasive species. Section 2 describes the components of the bioeconomic model and the solution method. Section 3 presents the results; and Section 4 concludes following a discussion of the intuition behind, and implications of, the results.

## 2. Model

The bioeconomic model contains three primary components: an ecological model; an economic optimization model; and a solution method. Managers make spatially and dynamically optimal management decisions in each period based both on the state of the network at that time and on all future possibilities. Optimal policy comprises the location within the river network and the type of management action applied in a time period, given an annual budget constraint and the species distribution in the network. Management actions available include control (removal) and restoration, which can be used in any combination within the budget constraint, but management actions can fail. Each management unit consists of one reach in the river network. Because the model used is identical to the model in Hall et al. (2017), the following framework description is drawn from that article.

### 2.1. Ecological Model

We employ a simplified version of the ecological model in Muneeppeerakul et al. (2007b) because it incorporates several aspects of invasive and native species interactions in a riparian setting. Reducing the number of species to a two-species metapopulation model of an invasive species and a native species in a river network explicitly incorporates key ecological components of the invasion process including dispersal, habitat availability, and competition for establishment. The section begins with a description of the spatial river structure, which

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