Forest Ecology and Management 324 (2014) 196–204

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of co-occurring non-native invasive plant species on old-field succession

Sara E. Kuebbing *, Lara Souza [1], Nathan J. Sanders [2]

Department of Ecology & Evolutionary Biology, University of Tennessee, Knoxville, United States

ARTICLE INFO

Article history:
Available online 27 November 2013

Keywords:
C-score
Community disassembly
Invasive plants
Level of invasion
Old-field succession

ABSTRACT

Old fields are diverse forb-dominated ecosystems transitioning into woody-dominated forested ecosystems. However, the susceptibility of old fields to high levels of plant invasion can lead to the co-occurrence of multiple non-native invasive plant species at the fine-scale of plant neighborhoods, which can alter native species co-occurrence patterns and successional trajectories into forest communities. Community disassembly by invasive species occurs when the presence of one or more invaders shifts co-occurrence patterns of native species from structured to random. Disassembly can imply a loss of existing co-evolved interactions among native species, which has ramifications for community dynamics and trajectories of invaded ecosystems. Here, we quantify relationships among multiple invasive plant species and two indicators of community succession in old-field plant communities in East Tennessee: co-occurrence patterns of native and non-native species and successional trajectories. First, we examine how biotic and abiotic factors shape the abundance of invasive species, as well as native and invasive functional groups across old fields. Second, we ask whether invasive species influence co-occurrence patterns among native species and whether invasive species are associated with altered herbaceous:woody foliar cover ratios. We found that biotic and abiotic predictors associated with invasive species were not consistent in identity or direction of association, indicating that predicting which sites or suite of biotic and abiotic variables are associated with invasive species will be challenging. Importantly, as the number of invasive plants increased in 1-m^2 plots, native species co-occurrence patterns shifted from structured to random, whereas invasive species co-occurrence patterns remained random irrespective of the number of invasive species. Plots containing three or more invaders had significant changes in native and invasive herbaceous:woody foliar cover ratios. The herbaceous:woody foliar cover ratio of native species was 4× lower and of invasive species was 2× greater compared to plots with one or two invaders, and this shift was in part explained by an increase in foliar cover of non-native woody species. Our data suggest that increased number of invasive species in old fields alters both native species interactions and the trajectories of old-field communities, which could influence the developing understory community as old fields transition into forests. We recommend that management of fields during succession should focus on decreasing the total number of invasive species to restore species co-occurrence patterns and prevent altered successional trajectories, including accelerated succession of non-native woody species.

1. Introduction

Old-field communities are successional ecosystems in transition from herbaceous-dominated abandoned agricultural land into woody-dominated forests. In the eastern United States, approximately one-third of pre-European settlement forests were cleared for cultivation (Smith et al., 2003) and approximately 50 million acres of once forested agricultural lands have been abandoned and are reverting back to forest (Cramer et al., 2008; Hobbs and Cramer, 2007). Agricultural abandonment creates local- and landscape-scale legacies, which include the creation of post-agricultural soil conditions that can select for a different suite of understory species (Dupouey et al., 2002; Koerner et al., 1997; Motzkin et al., 1996; Verheyen et al., 1999) or a fragmented landscape that prevents dispersal of some forest herbs (Bellemare et al., 2002; Dyer, 2010; Matlack, 1994; Singleton et al., 2001). Additionally, old-field species, both native and non-native, that

* Corresponding author. Address: 569 Dabney Hall, University of Tennessee, Knoxville, TN 37996, United States. Tel.: +1 865 974 3065.
E-mail address: skuebbin@utk.edu (S.E. Kuebbing).
[1] Present address: Department of Microbiology & Plant Biology and Oklahoma Biological Survey, University of Oklahoma, Norman, United States.
[2] Present address: Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, DK-2100 Copenhagen, Denmark.

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.10.031

establish in post-agricultural areas can directly impact the understories of future forests. Old-field species may persist in forest understories after canopy closure (Bazzaz, 1968; Dyer, 2010; Motzkin et al., 1996) or they may interact with newly colonizing understory herbs to influence final understory forest composition (Endels et al., 2004). Understanding how these disturbance legacies might alter transitions from field to forest is important for predicting the understory plant composition of future forests (Flinn and Vellend, 2005).

Old-field ecosystems harbor many native and non-native species (Bazzaz, 1996; Fridley et al., 2007; Souza et al., 2011a). The legacy of cultivation—alteration of plant biomass, tillage, and fertilization—can decrease seeds of native species in the soil seed banks and lead to higher probability of invasion by non-native species (Cramer et al., 2008). Similarly, disturbances like periodic mowing in old-field ecosystems could influence the establishment and growth of non-native species (Davis et al., 2000; MacDougall and Turkington, 2005), but the effects of disturbance in old-field plant communities tend to be species specific (Averill et al., 2010; Brandon et al., 2004; Renne et al., 2006). In a survey of 250 1-m^2 quadrats across 17 old fields, Souza et al. (2011a) did not find a single plot without non-native species and 90% of surveyed plots had non-native invasive species. Of those plots containing non-native invasive plants, ~47% had two or more non-native invasive species. Because non-native, invasive plant species can modify community structure and composition across a wide variety of ecosystems (Vilà et al., 2011), it is also important to study them in the context of succession from old field to forest.

Non-native invasive species can directly affect native communities by altering species richness, evenness, or diversity in recipient communities (Vilà et al., 2011; Wardle et al., 2011). Some invasive species, however, might have more subtle effects on community structure, such as altering co-occurrence patterns among species, which may not necessarily coincide with short-term declines in richness, evenness, or diversity (Sanders et al., 2003). This change in species co-occurrence patterns is termed "community disassembly" and occurs when a non-native invasive species causes association patterns of native species to shift from non-random (i.e., segregated or aggregated) to random (Sanders et al., 2003). Disassembly has been documented in ant and plant communities, where highly segregated or aggregated communities lose their structure after the arrival of a non-native invasive species (Gotelli and Arnett, 2000; Sanders et al., 2003; Santoro et al., 2012).

The presence of one or more invasive species in old fields could influence co-occurrence patterns among native species and successional dynamics of old fields in two ways. First, if invasive plants are associated with disassembly of old-field native plant species, this could suggest an alteration of interspecific interactions among native species (Sanders et al., 2003). Plant community organization can be strongly influenced by interspecific interactions (Brooker et al., 2008; Callaway and Walker, 1997; Freckleton et al., 2009; Goldberg and Barton, 1992), particularly during old-field succession (Connell and Slatyer, 1977; Fortner and Weltzin, 2007; Huston and Smith, 1987; Jensen et al., 2012; Li and Wilson, 1998). The alteration of interactions at early successional stages could lead to unpredictable paths of forest succession or, alternatively, to an ecosystem where succession is arrested and dominated by non-native grasses or shrubs (Cramer et al., 2008; Tognetti et al., 2010). Additionally, if a particular invasive species occurs in both old-field and forest ecosystems (Belote et al., 2003; Cole and Weltzin, 2005; Souza et al., 2010) and if these species persist in secondary forest understories they could negatively affect colonization by forest herbs (McLane et al., 2012; Meiners, 2007; Myster and Pickett, 1992). Second, old field to forest succession can be measured as the change in woody:herbaceous ratios through time (i.e., increasing proportion of woody plants as old fields age; Wright and Fridley, 2010). If the presence of invasive plants is associated with differences in herbaceous:woody cover ratios, this could indicate that invaders might alter the rate at which fields transition to forests.

Though the impacts of individual invaders in old-field ecosystems have been intensively studied (Brandon et al., 2004; Dickson et al., 2010; Emery and Gross, 2006; Knapp, 1996), studies on the effects of multiple invasive species on the co-occurrence patterns of old-field species are less common (Powell et al., 2013). Here, we use a multifaceted approach to explore how invasive species might affect the trajectories of old-field communities as they transition into forests. First, we examine the patterns of occurrence of invasive plants in old-field ecosystems by asking (1) What abiotic and biotic factors shape the abundance of non-native invasive species and invasive and native functional groups? Predictive models, such as these, could assist managers in targeting areas that have a higher likelihood of invasion by multiple species. Next, to understand how nonnative invasive species affect assembly patterns and successional dynamics in old-field communities we address the following two questions: (2) How do multiple invasive species alter co-occurrence patterns of native and non-native invasive species? and (3) How do multiple invasive species alter successional trajectories (herbaceous:woody foliar cover ratios) in old fields?

2. Materials and methods

2.1. Study site and plant surveys

In the summer of 2006, we located 17 fields across the Three Bend Scenic and Wildlife Management Refuge, which is part of the Oak Ridge National Environmental Research Park near Oak Ridge, TN (35–58′N, 84–17′W). Old-field communities were agricultural fields until ca. 1943 following abandonment and are maintained by periodic mowing for early-successional wildlife species. Management regimes among fields varied in mowing frequency: monthly mowing, annual mowing, biannual mowing (half of the field in the spring and other half of the field in the fall), or biennial mowing. Soils at the sites are characterized as Typic Hapludult with a silty clay loam texture (Phillips et al., 2001). Mean monthly temperatures range from approximately 3 °C in the winter to 31 °C in the summer and mean annual rainfall is 1322 mm.

We chose fields based on the presence of well-defined boundaries such as forests or roads. Within each field, we randomly placed two to six 50-m transects (depending on field area, which ranged from ca. 2000 m^2 to 50,000 m^2). We placed five 1-m^2 plots 10 m apart starting 10 m from the origin of each transect. In each 1-m^2 plot, we identified and estimated percent foliar cover of all native and non-native vascular plant species during the peak of the growing season. We estimated species-specific foliar cover using a modified Braun-Blanquet cover class scale (Braun-Blanquet, 1932). The modified Braun-Blanquet scale included six categories: 1 = <1%, 2 = 1–5%, 3 = 5–25%, 4 = 25–50%, 5 = 50–75%, 6 = 75–100%.

For the purpose of our study, we considered a species to be non-native if humans transported it across fundamental geographic barriers (Richardson et al., 2011). We also distinguish between "naturalized" non-native species (hereinafter, non-native)—those that are remnants of old-field agricultural but do not spread far from the source of introduction—and "invasive" non-native species (hereinafter, invasive)—those that have spread far from their original source of introduction and therefore are considered rank one invasive species (for a full list of species see Supplementary Information Table 1). We consider this to be an important distinction because while non-native and native species tend to follow similar successional patterns from old field to forest (i.e., decrease in herbaceous cover and increase woody cover) invasive plants do