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Review

Impact of invasions by alien plants on soil seed bank communities: Emerging patterns

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ABSTRACT

Much of our current understanding of the impact of invasive species on plant communities is based on patterns occurring in the above-ground vegetation, while only few studies have examined changes in soil seed banks associated with plant invasions, despite their important role as determinants of vegetation dynamics. Here, we reviewed the literature on the impact of plant invasions on the seed bank and we provide a quantitative synthesis using a meta-analysis approach. Specifically, (1) we quantified the impact of 18 invasive alien plants on (i) species richness and (ii) density of the seed banks of invaded communities, based on 58 pair-wise invaded-uninvaded comparisons (cases); we identified (2) the invasive taxa that are responsible for the largest changes in the seed bank; and (3) the habitats where substantial changes occur. Our study showed three major findings: (1) species richness (68% of cases) and density (58% of cases) were significantly lower in native seed banks invaded by alien plants; (2) species richness and density of native and alien species were remarkably lower in seed banks invaded by large, perennial herbs compared to uninvaded sites; and (3) invaded seed banks were often associated with a larger richness and/or abundance of alien species. This study indicates a need for additional seed bank data in invasion ecology to characterize species-specific and habitat-specific impacts of plant invasions, and to determine whether changes in the seed banks of native and alien species are a symptom of environmental degradation prior to a plant invasion or whether they are its direct result. The findings of this study help improve our capacity to predict the long-term implications of plant invasions, including limitations in the recruitment of native species from the seed bank and the potential for secondary invasions by seeds of other alien species.

Contents

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Introduction

Invasions by alien plant species are known to exert significant impacts on plant diversity, community dynamics, and ecosystems processes (e.g. Gordon, 1998; Levine et al., 2003; Ehrenfeld, 2010; Vilà et al., 2011; Simberloff, 2011; Pyšek et al., 2012). To date, extensive research has been conducted to characterize and predict the effects of invasive plants on resident communities, ecosystem functioning, and, more recently, on ecosystem services (e.g. Charles and Dukes, 2007; see Eviner et al., 2012 and references therein). Ultimately, the long-term implications of plant invasions will depend upon (i) the persistence of an invader at a locality, (ii) the type, magnitude, and time scale of the impact, and (iii) the capacity of resident communities to buffer against the full or partial displacement of resident species (Vilà and Weiner, 2004; Gioria et al., 2011, 2012).

In many ecosystems, the above factors are strongly dependent upon changes in the soil seed banks (hereafter termed seed bank) of invaded communities. Seed banks are reservoirs of viable seeds, either in the soil or on its surface, produced in the most recent reproductive period or over previous years (Templeton and Levin, 1979; Roberts, 1981) and fulfil several ecological functions in the structuring of many plant community types (Major and Pyott, 1966; Fenner and Thompson, 2005). Their potential role in contributing to species invasiveness and affecting community invasibility has been recently highlighted (Gioria et al., 2012), particularly in the naturalization and invasion stages of an invasion process (Richardson et al., 2000; Richardson and Pyšek, 2012). First, they may affect the successful establishment and spread as well as the persistence of sexually-reproducing and apomictic alien species by acting as a source of propagules (Pyšek and Richardson, 2007; Gioria and Osborne, 2009a; Gioria et al., 2012), particularly where alien species are capable of forming large, long-term persistent seed banks (*sensu* Thompson et al., 1997). As reservoirs of genetic variability (Templeton and Levin, 1979; Venable and Brown, 1988; McCue and Holtsford, 1998; Levin, 1990; Mandák et al., 2012), the formation of a seed bank will affect the response of alien plants to novel conditions experienced in their non-native range. For native species, seed banks will affect the probability of successful recruitment of native species from the seed bank as well as their capacity to respond to those sets of novel conditions that may follow the introduction of an invasive species (Gioria et al., 2012). Native seed banks may also mitigate the effects of competitive interactions with invasive species and buffer against changes in the vegetation, allowing native species to persist in an invaded community even after being displaced from the above-ground vegetation, at least for a short period of time.

The impact of invasive species on seed banks may differ substantially from that on the above-ground vegetation (e.g. Vilà and Gimeno, 2007; Gioria and Osborne, 2009a,b, 2010; Gaertner et al., 2011; Abella et al., 2012, 2013), since seeds buried in the seed bank may tolerate and escape environmental conditions that are unfavourable to adults (Templeton and Levin, 1979; Fenner and Thompson, 2005). Moreover, seed banks include some species possessing different, and often, contrasting ecological strategies to those present in the above-ground vegetation (Pickett and McDonnell, 1989), also potentially contributing to a differential impact. Over the short term, plant invasions are likely to affect primarily the transient component of the seed bank (*sensu* Thompson et al., 1997), via alterations in the seed input associated with changes in the above-ground vegetation, while effects on the persistent component of the seed bank may not yet be evident (e.g. Marchante et al., 2011).

Since seed banks represent a source of propagules for both native and alien species (Gioria et al., 2012), knowledge of changes in the seed bank associated with plant invasions is essential to determining the persistence of an alien species at a locality and to developing cost-effective control and restoration measures (Holmes, 2002; Vilà and Gimeno, 2007; Richardson and Kluge, 2008; Abella et al., 2012). Any comprehensive characterization of the legacy of plant invasions on the resident vegetation should therefore include knowledge of changes in the seed bank of invaded communities. To date, however, our understanding of the effects of invasive species on plant communities is largely based on patterns occurring in the above-ground vegetation (e.g. Levine et al., 2003; Gaertner et al., 2009; Vilà et al., 2011; Pyšek et al., 2012), while comparatively few studies have examined directly the impact of plant invasions on the seed bank (see Gioria et al., 2012). Of those, some have reported significant differences in seed banks of invaded communities in various ecosystem types (e.g. Holmes and Cowling, 1997; Holmes, 2002; Gioria and Osborne, 2009a,b, 2010; French et al., 2011; Marchante et al., 2011; González-Muñoz et al., 2012), while others have failed to detect any significant impact (e.g. Wearne and Morgan, 2006; Vilà and Gimeno, 2007; Gaertner et al., 2011; Abella et al., 2012, 2013; see Gioria et al., 2012).

Here, we aim to review the literature on the impact of plant invasions on the seed bank and to provide a quantitative synthesis of those studies comparing species richness and density of seed banks in invaded and comparable uninvaded plant communities, in different habitat types, using a meta-analysis approach (Rosenberg et al., 2000). Specifically, we address three questions: (1) What is the impact of invasive alien plants on (i) species richness and (ii) density of the seed bank of invaded plant communities? (2) Which invasive species are responsible for the greatest changes in the seed bank? And (3) in which habitat types are these changes most pronounced? - Given that plant invasions often occur in disturbed areas, where other alien species may be present (e.g. Turner et al., 2008; Gaertner et al., 2011; Gioria et al., 2011, 2012; González-Muñoz et al., 2012), we examine the impact on the seed banks of all species, regardless of their native/alien status, that on native species only, and, indirectly, that on alien species. Finally, we discuss the significance of the results of this meta-analysis study, its limitations, and we offer future research directions.

Methods

Literature search and data extraction

The effects of plant invasions on the seed bank were examined by performing a search of the published literature, up to February 2014, in the Web of Science (ISI) electronic database and Google Scholar. To maximize the number of studies identified by the search, we used multiple combinations of the keywords 'invas*', 'exotic', 'alien' 'seed bank', 'species richness', 'diversity',