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Original article

Propagule pressure governs establishment of an invasive herb

Satu Ramula [a, b, *], Miia Jauni [b], Tapio van Ooik [b]

[a] Aronia Coastal Zone Research Team, Åbo Akademi University and Novia University of Applied Sciences, Raseborgsvägen 9, 10600 Ekenäs, Finland
[b] Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland

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ABSTRACT

The success of plant invasions may be limited by the availability of propagules and/or of suitable microsites, with microsite availability being affected by, for example, disturbance and interspecific competition. A mechanistic understanding of the contributions of propagule pressure and microsite limitation to plant invasions is therefore required to minimise future invasions. Here, we investigated the relative roles of propagule pressure, the availability of microsites, and their interaction on the establishment of an invasive herb, *Lupinus polyphyllus*, in two geographic regions representing different climate and growth conditions in Finland (a more productive southern region and a harsher central region). We carried out a field experiment in 14 *L. polyphyllus* populations, in which we manipulated both propagule pressure and disturbance. In a complementary greenhouse experiment, we manipulated propagule pressure and interspecific competition. Seedling establishment of *L. polyphyllus* was higher in the more productive southern region than in the harsher central region. The number of *L. polyphyllus* seedlings increased with increasing propagule pressure regardless of disturbance or interspecific competition. However, the number of *L. polyphyllus* seedlings per sown seed (relative establishment) tended to decrease with increasing propagule pressure, indicating that the positive effect of propagule pressure on early invasion is partially counteracted by density-dependent mortality at high seed densities. Our results highlight the dominant role of propagule pressure over disturbance and interspecific competition in the establishment of *L. polyphyllus*, suggesting that the early stage of invasion is limited by the availability of propagules rather than the availability of suitable microsites.

1. Introduction

The success of plant invasions may be restricted by several factors, such as the availability of propagules or of suitable microsites. The former, also known as propagule pressure, has frequently been found to be positively associated with successful plant invasions (reviewed by Colautti et al., 2006). The availability of suitable microsites may, in turn, be determined by disturbance, co-occurring plant species, or geographic location (as a proxy for different growth conditions and productivity levels). For example, disturbance may increase both the amount of resources available per individual plant and the number of accessible microsites, thus increasing the probability of plant recruitment and, consequently, community invasibility (Davis et al., 2000). On the other hand, strong interspecific competition may reduce community invasibility (Crawley, 1986) because fewer microsites and resources are available per individual plant. Efforts to minimise future invasions, therefore, require a mechanistic understanding of the relative contributions of propagule pressure and microsite limitation to plant invasions.

The significant role of disturbance in plant invasions was supported by a recent meta-analysis that revealed that non-native plant species are more abundant and diverse at disturbed sites than at undisturbed sites (Jauni et al., 2015). However, previous studies have also questioned the importance of disturbance in plant invasions. For example, a global, empirical study reported that disturbance is a poor predictor of plant invasions in general, although it tends to slightly increase the richness and cover of non-native plant species (Moles et al., 2012). Moreover, Buckley et al. (2007) showed theoretically that disturbance has a negligible effect on plant invasions when the level of disturbance is equal between invader occupied and unoccupied sites because in such a situation invasibility depends on propagule pressure only. These somewhat contrasting findings about the importance of

* Corresponding author. Section of Ecology, Department of Biology, University of Turku, 20014 Turku, Finland.
E-mail address: satu.ramula@utu.fi (S. Ramula).

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disturbance in plant invasions may be because of interactive effects between disturbance and other factors that contribute to plant invasions. In other words, the importance of disturbance to plant invasions may vary depending on community properties, such as propagule pressure and productivity. Both theoretical and empirical studies indeed suggest that interactive effects between propagule pressure and disturbance (or other factors that affect microsite availability) should not be ignored (e.g., Huston, 2004; Buckley et al., 2007; Eschtruth and Battles, 2009). In general, one might expect microsite availability to play a more prominent role in determining community invasibility under conditions of high, rather than low, propagule pressure because of stronger intraspecific competition for resources (Lockwood et al., 2005). In order to make such generalisations, though, and to determine the relative roles of propagule pressure and the availability microsites in plant invasions, it is necessary to carry out experimental studies that explicitly manipulate these two factors under different conditions at multiple sites. So far, such large-scale studies conducted in the invaded range are rare.

Here, we investigated the relative roles of propagule pressure, microsite limitation, and their interaction in the establishment of an invasive herb, *Lupinus polyphyllus* Lindl. We carried out an experiment in 14 *L. polyphyllus* populations, in which we manipulated propagule pressure and disturbance in two geographic regions of Finland, a more productive southern region and a harsher central region. In a complementary greenhouse experiment, we manipulated propagule pressure and interspecific competition. We hypothesised that propagule pressure and disturbance would increase the establishment of *L. polyphyllus*, while interspecific competition would decrease it. We also hypothesised that seedling establishment would increase with high propagule pressure and disturbance, and with high propagule pressure and less interspecific competition (i.e. we predicted an interaction between propagule pressure and disturbance, and between propagule pressure and interspecific competition). Moreover, we predicted that community susceptibility to invasion would be greater at disturbed sites in the southern region than at disturbed sites in the central region because of more favourable growth conditions (i.e. better resource availability).

2. Materials and methods

2.1. Study species

L. polyphyllus (Fabaceae) is a perennial herb which originates from North America and stands 50–100 cm high. In its invaded range, *L. polyphyllus* often inhabits frequently disturbed habitats, such as road verges and wastelands (Fremstad, 2010), suggesting that disturbance is essential for its persistence. The species primarily reproduces from seed (Fremstad, 2010; S. Ramula, personal observation), although clonal reproduction is also possible at least in the invaded range (Rapp, 2009). An individual *L. polyphyllus* plant can produce hundreds of seeds which are dispersed ballistically up to a few metres from the parent plant.

2.2. Propagule pressure and disturbance

We examined the role of propagule pressure in the establishment of *L. polyphyllus* in the presence and absence of disturbance in 14 populations. Seven of the populations were located in southwestern Finland (hereafter, “southern region”) and seven were located about 500 km to the north, in central Finland (hereafter, “central region”). Generally, the southern region can be considered more productive than the central region, as indicated by the longer growing season (Tuhkanen, 1980; Grytnes et al., 1999) and about 40% greater seed production (per plant) of *L. polyphyllus* in southern Finland (Ramula, 2014). Most study populations (11 out of 14) inhabited road verges or wastelands, while the rest inhabited forest understories close to roads. All study sites were characterised by light, sandy soils. In each *L. polyphyllus* population, we established 14 plots of 1 m^2 which we further divided into four subplots of 0.5 × 0.5 m. The plots were at least 0.5 m apart in each study population. In half of the plots, we simulated mechanical disturbance by breaking the soil surface of the whole plot with a hoe (about 20–30 hits per plot), whereas the rest of the plots were left undisturbed. The purpose of this treatment was to simulate small-scale natural disturbances that are caused by, for example, trampling and grazing. The mechanical disturbance did not remove the existing vegetation but created small openings of bare soil (about a 29% increase in the amount of bare soil), thus increasing the number of litter-free microsites available. The disturbance treatment had also the potential to damage the aboveground and belowground parts of the existing plants, possibly reducing their competitive ability. To minimise differences in vegetation and underlying abiotic conditions, disturbed and undisturbed plots were paired, and each pair was located only a few metres from the nearest *L. polyphyllus* individual (i.e. the plots were in locations that were suitable for the study species). *L. polyphyllus* seeds were sown in the study plots in late July 2011. Within each plot, four sowing densities (7, 15, 30, and 60 seeds) were randomly allocated to the subplots. Seeds were collected, cleaned, and sown on the same day in the field, ensuring that all sown seeds at a given site were from the same *L. polyphyllus* population, and that only fully developed seeds were sown. Fully developed seeds of *L. polyphyllus* tend to have viability close to 100% with little variation among populations (mean ± SD = 97.7% ± 2.1%, n = 21 populations; unpublished data). We revisited the study plots at the end of May 2012 and recorded the number of *L. polyphyllus* seedlings per subplot (hereafter, “absolute establishment”). We also calculated relative establishment as the number of *L. polyphyllus* seedlings in May divided by the number of seeds sown per subplot. To control for potential background germination from the soil seed bank, we observed seedling establishment from three unsown control plots (0.5 × 0.5 m) per population in 2012, but no seedlings were detected in these plots during the experiment. Unfortunately, one population in the southern region was lost due to vandalism and was therefore excluded from the analyses (leaving 13 populations; 6 in the southern region and 7 in the central region).

2.3. Propagule pressure and interspecific competition

To examine the role of propagule pressure in the establishment of *L. polyphyllus* in the presence of a competing species, we conducted a greenhouse experiment in which we manipulated propagule pressure and interspecific competition. We used two different competitors: the perennial grass *Elymus repens* (L.) Gould (Poaceae) and the perennial herb *Trifolium pratense* L. (Fabaceae), which both co-occur with *L. polyphyllus* in Finland. *E. repens* is a common native weed, while *T. pratense* is a common native species that belongs to the same family as *L. polyphyllus*. For both competitors, we used commercial seed material, while for *L. polyphyllus*, we collected seeds from the 14 study populations in July 2011. First, to assess the effect of propagule pressure in the absence of interspecific competition, we sowed the *L. polyphyllus* seeds into 8 × 8-cm pots at five different densities (2, 4, 8, 16, and 32 seeds per pot) in February 2012. Then, to explore how interspecific competition affects seedling establishment under different degrees of propagule pressure, the seeds of *L. polyphyllus* and one competitor were sown in the following density combinations: 1) 2 *L. polyphyllus* and 32 competitor seeds, 2) 4 *L. polyphyllus* and 16 competitor seeds, 3) 8