

# The relative importance of latitude matching and propagule pressure in the colonization success of an invasive forb

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Factors that influence the early stages of invasion can be critical to invasion success, yet are seldom studied. In particular, broad pre-adaptation to recipient climate may importantly influence early colonization success, yet few studies have explicitly examined this. I performed an experiment to determine how similarity between seed source and transplant site latitude, as a general indicator of pre-adaptation to climate, interacts with propagule pressure (100, 200 and 400 seeds/pot) to influence early colonization success of the widespread North American weed, St. John's wort *Hypericum perforatum*. Seeds originating from seven native European source populations were sown in pots buried in the ground in a field in western Montana. Seed source populations were either similar or divergent in latitude to the recipient transplant site. Across seed density treatments, the match between seed source and recipient latitude did not affect the proportion of pots colonized or the number of individual colonists per pot. In contrast, propagule pressure had a significant and positive effect on colonization. These results suggest that propagules from many climatically divergent source populations can be viable invaders.

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Successful invasions by exotic species are the culmination of a multi-step process. Individuals must be transported to a new range, they must successfully colonize areas within recipient communities, and they must reproduce and spread from these initial areas of introduction (Richardson et al. 2000). Because each of these steps acts as a filter that can reduce the probability of successful invasion, only a small fraction of exotic species successfully invades new areas (Williamson 1996).

A growing literature suggests that intrinsic attributes of recipient communities, such as disturbance (Elton 1958, Burke and Grime 1996, Lonsdale 1999, D'Antonio et al. 1999, Mack et al. 2000), nutrient availability (Burke and Grime 1996, Wedin and Tilman 1996, Leishman and Thomson 2005), native plant diversity (reviewed by Levine et al. 2003), and native enemy pressure (Darwin

1859, Williams 1954, Elton 1958, DeWalt et al. 2004) can greatly affect the probability that an exotic plant will successfully colonize in recipient environments. External factors, such as the number and frequency of exotic seeds introduced to areas can also influence the probability of successful colonization by exotics (Williamson 1996, Lonsdale 1999, Mack et al. 2000, Rouget and Richardson 2003, Lockwood et al. 2005). Although the relationship between factors internal or external to particular recipient communities and invasion success has received increasing attention, we know less about how characteristics of particular exotic genotypes (as opposed to species-level characteristics) influence their colonization success. In particular, it is often unclear how important the “match” between a genotype's source and recipient environment is to its colonization success.

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At a very coarse level, climate clearly controls plant distribution globally (Salisbury 1926, Woodward 1987) and therefore dictates where particular species establish as exotics. The fact that exotics are likely to be more successful in recipient communities experiencing similar abiotic conditions as possessed by their home environment is the basis for the use of climate envelope models to assess how vulnerable particular areas might be to future invasion by particular species (Pearson and Dawson 2003, Rouget et al. 2004). Furthermore, abiotic conditions likely account for why both native and exotic diversity tend to peak in similar locations (Stohlgren et al. 2005). Yet, while colonizing individuals must have some minimal preadaptation to broad-scale abiotic conditions in the recipient community, it is unclear how tightly preadapted organisms must be. Plants with general purpose phenotypes (*sensu* Baker 1974) may be able to invade a wide range of environments, some of which may be quite different from their home sites.

Many exotics have extremely broad native distributions that encompass diverse abiotic conditions. For example, a multitude of successful plant invaders in North America are native across a wide latitudinal distribution in Europe (Whitson 2002). Plants from southern European populations may be adapted to more benign Mediterranean climates whereas those from northern or northeastern Europe may be adapted to harsher northern conditions. For species such as these, we do not know how strongly latitude matching between region of origin and region of introduction predicts successful colonization. Within a species, do genotypes from southern latitudes in Europe arriving in northern sites in North America have a lower probability of establishment than do genotypes from northern Europe? How might the relative importance of latitudinal matching between source and recipient environment change depending on other factors, such as propagule pressure? For example, is tight coupling between source and recipient environment more important at low versus high propagule pressure? Because of both the ethical and logistical difficulties of adding exotic seeds from multiple source populations to a recipient environment that may not contain that species, it is often unclear how propagule pressure interacts with other factors to influence the initial stages of invasion (Lockwood et al. 2005).

In this paper, I evaluate the relative importance of matching between source and recipient latitude and propagule pressure (i.e. the number of seeds arriving at a site) in affecting colonization success of *Hypericum perforatum* (St. John's wort). *Hypericum perforatum* is a widespread, successful and damaging invader in North America that has a very broad native distribution, where it occurs across Europe, North Africa and Asia. In previous work, it has been shown that native popula-

tions of *H. perforatum* exhibit latitudinal clines in physiological traits and fitness when placed in common gardens in both southern and northern European and North American sites (Maron et al. 2004, Maron et al. unpubl.). These latitudinal clines suggest that native European populations of *H. perforatum* have adapted to broad scale climatic conditions that vary with latitude across Europe. In this previous work, latitude of origin was a better predictor of variation among populations in a variety of traits related to fitness in common gardens than were composite parameters that summarized climate conditions of source populations (Maron unpubl.).

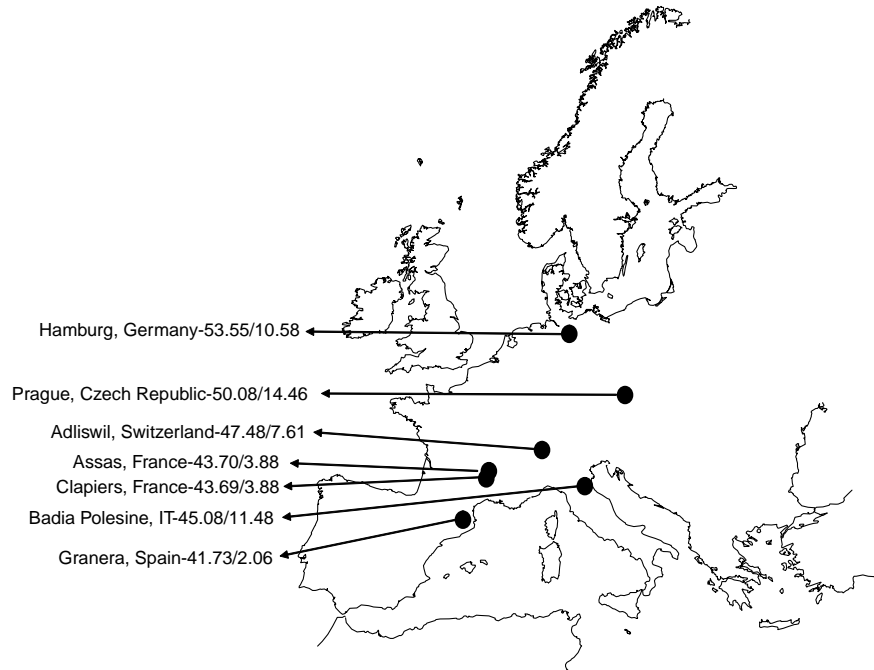
Here I use the "match" between home and recipient latitude as a rough surrogate for degree of broad-scale preadaptation to the recipient environment. Latitude correlates with many climatic variables that might influence plant establishment, including evapotranspiration potential, precipitation, mean annual temperature, solar radiation, etc. While other factors besides latitude can certainly influence a plant's level of preadaptation to the recipient environment, at a coarse scale, and in lieu of detailed knowledge about how specific climate variables (perhaps in combination) might influence St. John's wort germination and subsequent survival, similarity in latitude between regions should indicate some broad level of convergence in climatic conditions. I also explore how propagule pressure influences colonization and quantify how the importance of climate matching changes depending on propagule pressure.

## Methods

In May 2003, I initiated a fully randomized factorial experiment where propagule pressure and seed source populations were fully crossed. I buried large plastic pots, (23 cm diameter  $\times$  22 cm deep) in a plowed field at Fort Missoula, Missoula, Montana. There were no St. John's wort plants growing within the vicinity (i.e. several kilometers) of this site (Maron unpubl.). Pots were arranged in a 7  $\times$  35 grid, with ca 35 cm between pots. Pots were buried so that the top 3 cm of each pot extended above ground level. Pots were filled with native soil to ground level.

On 1 September 2003, ca 3.5 months after pots were placed in the ground, I removed all plants that had colonized pots through spring and summer and added 100, 200 or 400 *H. perforatum* seeds to each pot. After sowing seeds, I watered pots to ensure that there was good contact between seeds and the soil surface. Seeds were added in autumn, to mimic the time when seeds are naturally dispersed off of St. John's wort. Pots received seeds from one of seven seed source populations (Fig. 1), which differed to varying extents in latitude and climate

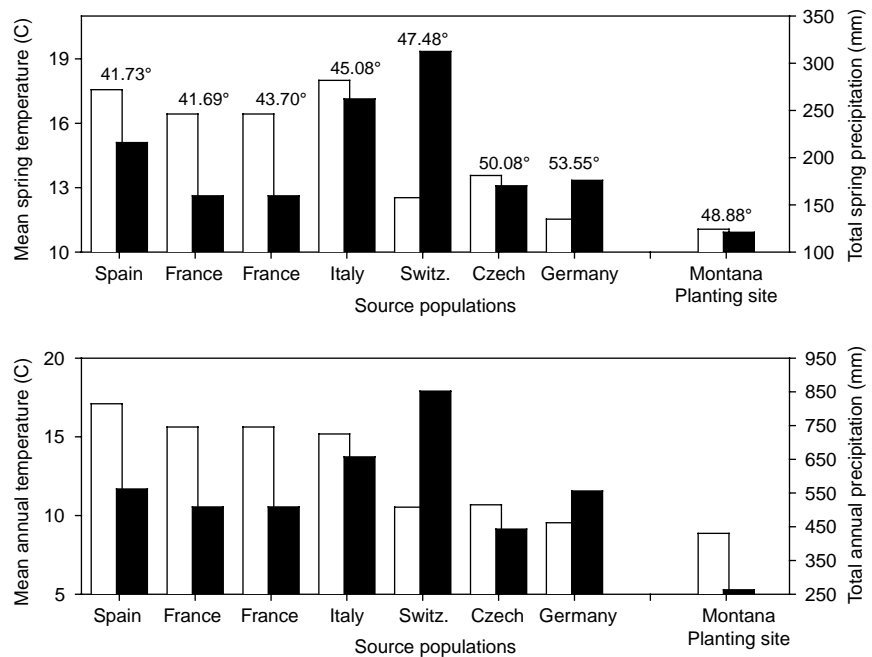
Fig. 1. Map of Europe showing the city, country, and latitude/longitude of each seed source population.



from the recipient experimental site (Fig. 2), which was located at latitude  $46.88^\circ$  and  $113.94^\circ$  longitude. Since my goal was to examine how adaptation to climatic conditions associated with latitude in Europe might affect a plant's colonization success in Montana, St. John's wort seeds were collected at European sites below 1000 m, and from populations that grew in sunny sites in broadly similar habitat. This reduced the chance that latitudinal effects on the climate would be subsumed by

local rain shadow or elevational effects (Stohlgren et al. 2005). Treatment combinations (seed number and source population) were randomly assigned to pots across the experimental grid and each treatment combination was replicated between 7 and 9 times. Uninvaded pots were not included in the experimental design since there were no *H. perforatum* populations within at least several kilometers of the experimental site and thus no chance that *H. perforatum* seeds could have been present in a

Fig. 2. Top panel: mean spring (April–June) temperature (white bars) and total spring precipitation (black bars) for seed source locations in Europe and experimental planting site in Montana. Bottom panel: mean annual temperature and total annual precipitation for the same sites. Mean temperatures and total precipitation calculated as the average (temperature) or sum (precipitation) of mean monthly values. Values above bars on top panel are latitude of source population and planting site.



pre-existing seedbank. Seed capsules were collected from natural populations across Europe (Fig. 1) in late summer/autumn 1998 and 1999. Seeds were subsequently extracted from their capsules and stored in envelopes in the laboratory. Seeds from each source population were a pooled sample of propagules collected from 10 maternal plants. There were no significant differences between source populations in seed weight (Maron unpubl.).

We tested the viability of seeds used in the field experiment by sowing between 15 and 20 seeds from each population into each of 5 plastic pots filled with a mix of sand and potting soil. Pots were placed at random locations on benches in a heated greenhouse and watered daily for 1.5 months. The number of seedlings in each pot was recorded on a bi-weekly basis. For each pot I calculated the average number of seeds that germinated. The average germination rate per population was 15%.

From April–September 2004 and 2005, I monitored each pot for germination every 2–3 weeks, scoring the number of *H. perforatum* germinants in each pot and following the fate of each germinant. I removed species other than *H. perforatum* that colonized pots to ensure that pots were free of interspecific competitors. I also removed weeds that came up immediately around each pot so that *H. perforatum* colonizing pots would not be shaded. At the end of the experiment, I harvested the above-ground portion of *H. perforatum* plants from each pot and placed plants from different pots in individually labeled paper bags. Plants were subsequently dried to constant weight at 60°C and then weighed.

## Analysis

Colonization success can be quantified in two ways: 1) the probability that there is at least some successful colonization at a site and 2) the size of the colonizing population. To assess how propagule pressure and seed source origin influenced the first component of colonization success, I calculated the proportion of pots that experienced any *H. perforatum* recruitment. I then performed an ANCOVA on these proportions (arcsin square-root transformed), with source population as a discrete (random) factor and propagule pressure as a covariate. While this analysis, in isolation, does not directly test for the importance of latitudinal matching in colonization success, it is the first step in such a test, as it asks for a given propagule pressure whether identity of source population (regardless of its exact location) has any significant influence on successful colonization. As a further test, I performed a multiple logistic regression, where propagule pressure and the difference in latitude between source and

transplant environment were regressed on the binary variable of whether or not pots contained at least one successfully established *H. perforatum* individual at the end of the experiment.

To determine how propagule pressure and seed source population influenced the size of the colonizing population that established in each pot, I performed a two-way ANOVA, with these factors (and their interaction) as main effects and number of individuals per pot and total per pot plant biomass as response variables.

To examine in greater detail how latitude and specific climate conditions that vary with latitude between seed source and recipient site might have influenced the number of plants that established in the pots, I ran separate ANCOVAs testing how propagule pressure (covariate) and: 1) the absolute value of the difference in latitude between seed source and Missoula, 2) difference in average 24 h spring temperatures (averaged across April–May) or 3) difference in average monthly precipitation (averaged across April and May) between seed source and recipient site influenced the number of seedling that established per pot. I used weather statistics for spring time (April/May) because these are the months that *H. perforatum* germinates in Montana. For examining the impact of latitudinal difference on seedling numbers I performed separate regressions for each propagule pressure treatment since preliminary ANCOVA revealed that the slope of this relationship varied among propagule pressure treatments. Weather statistics were extracted from the website WorldClimate (<<http://www.worldclimate.com>>). If climate data were not available for the exact location from which seeds were collected, I obtained data from the closest location from which data were available.

## Results

In the first year of the experiment (summer 2004) there was no germination of St. John's wort seeds in any pots. Seeds that were added the previous autumn remained dormant in the soil. In 2005, however, 39% (63 of 162) of all pots had at least some St. John's wort recruitment. Of the pots where recruitment occurred, 70% (44 of 63) contained at least one St. John's wort individual that survived until the end of the experiment, in August 2005.

Propagule pressure positively affected the proportion of pots that had any St. John's recruitment (Fig. 3; two-way ANCOVA,  $F_{1,13}=20.4$ ,  $p<0.0007$ ). As well, population identity influenced the proportion of pots that experienced St. John's wort recruitment (two-way ANCOVA;  $F_{6,13}=4.4$ ,  $p<0.02$ ). However, only two populations (Italy and Switzerland; Fig. 1) significantly

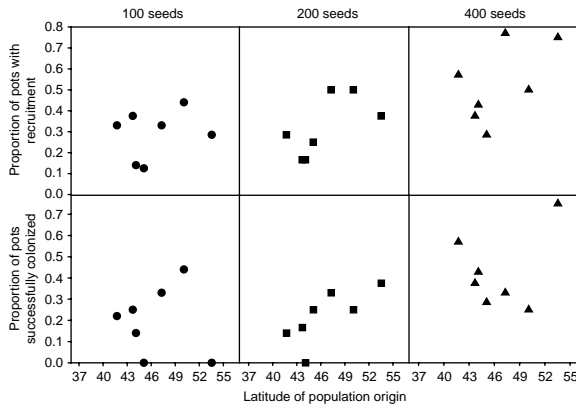


Fig. 3. Effect of seed source latitude in Europe on St. John's wort seedling germination. Top panels: the proportion of pots with any St. John's wort recruitment during the course of the experiment. Bottom panels: the proportion of pots with at least one established St. John's wort plant at the end of the experiment. Panels from left to right compare results at an initial propagule pressure of 100, 200 and 400 seeds per pot.

differed from each other in recruitment probability (Bonferroni post-hoc test,  $p=0.05$ ).

In a multiple logistic regression propagule pressure significantly affected whether or not individual pots contained at least one St. John's wort plant at the end of the season (Fig. 4;  $t$ -ratio = 2.1,  $p < 0.04$ ). However, latitudinal difference between source and recipient sites had no significant effect (Fig. 4;  $t$ -ratio = 0.17,  $p = 0.86$ ).

The average number of established plants per pot increased with propagule pressure (Fig. 5;  $F_{1,152} = 4.2$ ,  $p < 0.05$ ), from an average of 0.28 plants per pot at a propagule pressure of 100 seeds per pot to 0.32 and 0.72 plants per pot at propagule pressures of 200 and

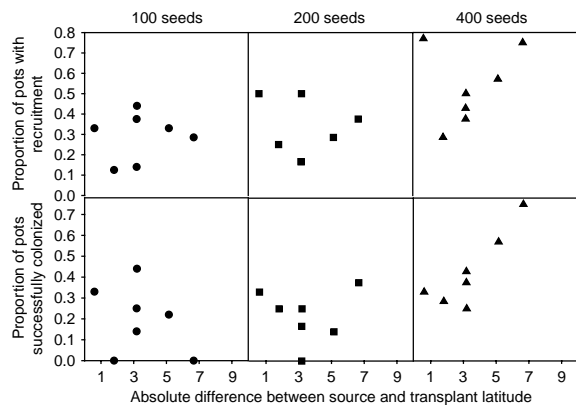


Fig. 4. Effect of difference in latitude between seed source in Europe and experimental site in Missoula, Montana. Top panels: St. John's wort germination, measured as by the proportion of pots that produced any St. John's wort seedlings during the course of the experiment. Bottom panels: the proportion of pots containing at least one established St. John's wort plant at the end of the experiment. Panels from left to right compare results at an initial propagule pressure of 100, 200 and 400 seeds per pot.

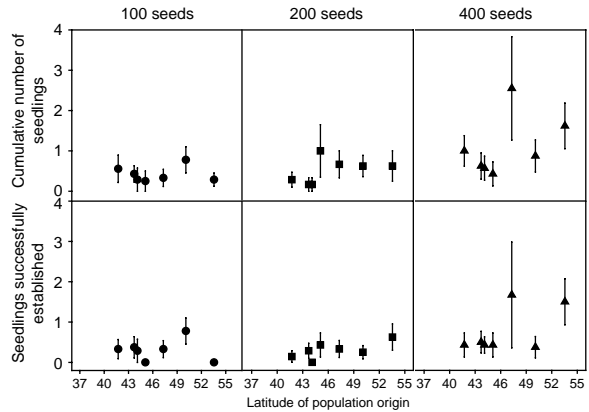


Fig. 5. Effect of seed source latitude in Europe on St. John's wort abundance. Top panels: the mean ( $\pm$ SE) cumulative seedling recruitment per pot. Bottom panels: the mean ( $\pm$ SE) number of established plants per pot at the end of the experiment. Panels from left to right compare results at an initial propagule pressure of 100, 200 and 400 seeds per pot.

400, respectively. Seed source identity had no significant influence on final abundance of plants in pots (ANOVA  $F_{6,152} = 0.79$ ,  $p = 0.58$ ) nor on the total biomass of plants per pot (ANOVA  $F_{6,28} = 1.8$ ,  $p = 0.12$ ).

The number of colonists per pot was unrelated to the difference in latitude between source and recipient location (Fig. 6; 100 seeds:  $F_{1,52} = 0.24$ ; 200 seeds:  $F_{1,48} = 0.98$ , 400 seeds:  $F_{1,54} = 0.004$ ,  $p > 0.05$  for each propagule pressure, respectively). As well, neither the difference between Missoula and seed source populations in spring temperature ( $F_{1,156} = 3.4$ ,  $p = 0.07$ ) nor spring rainfall ( $F_{1,156} = 2.1$ ,  $p = 0.14$ ) significantly influenced colonization success.

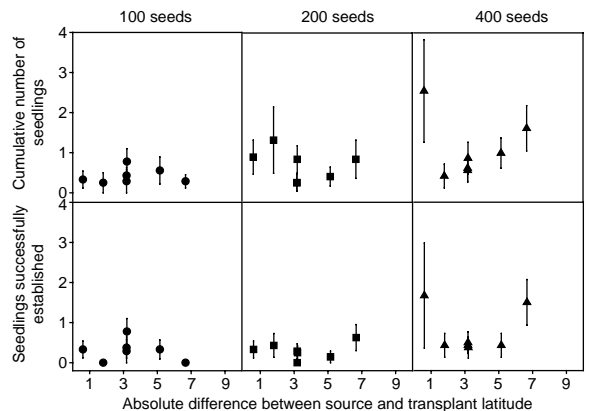


Fig. 6. Effect of difference in latitude between seed source in Europe and experimental site in Missoula, Montana on St. John's wort abundance. Top panels: the mean ( $\pm$ SE) cumulative seedling recruitment per pot. Bottom panels: the mean ( $\pm$ SE) number of established plants per pot at the end of the experiment. Panels from left to right compare results at an initial propagule pressure of 100, 200 and 400 seeds per pot.

## Discussion

Many widely distributed exotic weeds inhabit large geographic ranges where native. Several authors have speculated that this may not be a coincidence; species that grow under diverse environmental conditions in their native range may be pre-disposed to exploit a wide range of conditions where introduced (Crawley 1987, Williamson and Fitter 1996).

Results reported here support these suggestions. Propagules from divergent geographic locations across western Europe were all capable of colonizing pots in western Montana, regardless of the extent of mis-match between source and recipient latitude. Here successful colonization was the product of two processes: germination and the subsequent survival of emerged seedlings through the hot and dry summer season. In general, neither of these processes appeared substantially influenced by the identity or latitude of seed source populations. Thus, for invaders with broad native distributions such as St. John's wort, individuals from many portions of the native range are potentially viable colonists.

There are two non-mutually exclusive hypotheses for why plants with wide native distributions may be capable of colonizing diverse recipient environments. First, widespread native species may harbor extensive genetic variation partitioned between many locally adapted populations. Multiple introductions from this genetically diverse source pool may ultimately produce a good match between the set of conditions a genotype is adapted to and the conditions it experiences where introduced. Alternatively, widely distributed species may be particularly plastic in their phenotype, allowing them to colonize large, environmentally diverse areas in both their native and introduced ranges. If this scenario is generally true, small genetically depauperate founding populations may establish and spread simply because individuals in those populations are phenotypically plastic.

In previous work, *H. perforatum* from diverse native source populations across Europe exhibited latitudinal clines in fitness-related traits when grown in common gardens (Maron et al. 2004). These latitudinal clines suggest that on a coarse scale, native *H. perforatum* are adapted to abiotic conditions that vary with latitude across their native range. Yet, in this study I found no evidence that this regional-scale adaptation to climate translated to significant differences among populations in colonization success. Rather, it appears that *H. perforatum* genotypes possess sufficient plasticity in their germination and growth responses that they can perform adequately even if in an environment substantially different from that to which they are adapted.

These results bolster prior conclusions regarding the invasion history of *H. perforatum* into North America.

Based on AFLP markers, we found evidence suggesting that: 1) there had been multiple introductions of *H. perforatum* into North America, and 2) plants introduced into southern or northern locales in North America did not exclusively originate from matching latitudes in Europe (Maron et al. 2004). The current study strengthens this conclusion because it shows that even plants from the most southern populations that were sampled in Europe (i.e. Spain) can be as successful at colonizing pots in the relatively northern latitude location of Montana, as can propagules from northern European populations. Previous research has shown that there is very low post-establishment mortality of plants in common gardens, even for plants from populations that differ greatly in latitude from common garden sites (Maron et al. 2004).

Although propagule pressure is commonly discussed as an important factor influencing invasions, the relative importance of propagule pressure versus other potentially important factors such as community diversity, disturbance, or source of invading propagules is seldom explored (Lockwood et al. 2005). Where propagule pressure and other factors have been manipulated in the same study, propagule pressure often has the greatest relative effect on exotic establishment. For example, Levine (2000) found that propagule pressure overwhelmed the effects of native species richness in affecting the invasion of tussock clumps along a river. Results from this study similarly suggest a key role for propagule pressure in colonization success. As propagule pressure rose from 100 to 400 seeds per pot, the proportion of pots that were successfully colonized doubled, from 0.2 to 0.41. Interesting, however, the proportion of pots successfully colonized at 200 seeds per pot was virtually the same (0.21) as what was the case at a propagule pressure of 100. Thus, the relationship between propagule pressure and the probability of successful establishment may not be linear. This suggests a potentially fruitful avenue of future work.

Although results clearly suggest that propagule pressure is more important than latitudinal "matching" in the colonization success of *H. perforatum*, these conclusions must be tempered by several limitations of this study. First, for logistical reasons I could only use a limited number of source populations. It may be that with a greater number of source populations, there would be greater power to detect meaningful effects of latitude, or differences in climate between source and recipient sites, on colonization success. Nonetheless, this study suggests that seeds arriving to disturbed sites from source populations that are both different in latitude, and in the degree to which climate is coastally versus continentally-influenced compared to the recipient environment (i.e. in this study, populations from Spain, Germany and the Czech Republic) can be successful colonists under field conditions. Second, I did not

determine the overwinter mortality of experimental plants. However, in our previous work, overwinter mortality of first-year plants in multiple common gardens was very low, regardless of their latitude of origin (Maron et al. 2004, unpubl.). Moreover, in the current experiment there were no significant difference in final biomass between plants from different home latitudes, reducing the likelihood of consistent differences in overwinter mortality between plants from different populations based on their size. Third, since only an average of between 0.2 and 0.4% of *H. perforatum* seeds germinated and emerged (depending on propagule pressure), and since *H. perforatum* seeds are capable of remaining viable for up to 20 yr in a seedbank (Tisdale et al. 1959), there may have been viable seeds that remained in the soil at the end of the experiment. Thus, it is unclear how results might vary if this experiment were conducted for more than two years. Such long-term seed addition experiments would be valuable, although they are logistically difficult to perform on exotics, since they require constant and careful vigilance to ensure that no experimental plants reproduce and thereby spread new genotypes into recipient assemblages. Finally, with a greater pool of available seeds, it would have been advantageous to have had a greater number and range of seed density treatments. For studies on propagule pressure, where one wants to mimic conditions at the early stages of an invasion where seeds are arriving from outside the system, it is unclear what a typical propagule pressure might be. Once an area is successfully invaded, propagule pressure could be quite high. For example, one large *H. perforatum* can potentially produce 30 000 seeds, which even on a per unit area basis is likely a higher seed density than I used in this experiment. However, it may be that typical numbers of propagules arriving for the first time at sites may be fairly low.

In sum, results from this work indicate that *H. perforatum* propagules from wide-ranging populations across Europe are capable of successfully founding experimental populations at a particular location in North America. This suggests that *H. perforatum* and perhaps other weeds like it, have great amplitude to invade, regardless of differences between source and recipient environments. Whether these species have greater plasticity than others with more narrow native distributions remains an open question, and one ripe for future research. As result show, however, regardless of location of source population, establishment probability is greatly increased with enhanced propagule supply.

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