



Modeling the relative importance of ecological factors in exotic invasion: The origin of competitors matters, but disturbance in the non-native range tips the balance



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ABSTRACT

Successful exotic plant invasions are likely to be caused by multiple, non-mutually exclusive mechanisms, and it is exceptionally difficult to weight the relative importance of these mechanisms identified in different experiments. To this end we used individual-based models to explore how integrating empirical results from experiments might help to elucidate the relative importance of seed origin, biogeographic differences in competitive outcomes, and disturbance in exotic plant invasion. We integrated results from (1) competition experiments between *Centaurea solstitialis* derived from populations in the non-native range (California), the native range (Spain), and co-occurring native species from both ranges, (2) seed production by *Centaurea* plants from the different ranges grown in a common-garden environment, and (3) responses to disturbance experiments with plants from different native and non-native ranges. Californian *C. solstitialis* reached slightly higher abundances than its Spanish counterparts in every scenario, mainly due to higher seed production of Californians than their Spanish conspecifics, indicating the potential importance of evolutionary changes in the non-native range. In the absence of disturbance, grass species native to Europe showed stronger competitive effects on *C. solstitialis* than grass species native to North America, suggesting that release from competition in the native range may have some explanatory power for successful *C. solstitialis* invasion. However, the intensity of competition depended on the disturbance regime used in models. When intense disturbance was incorporated into the model, *C. solstitialis* was favored, with plants from Californian seed sources reaching higher densities than plants from Spanish seed sources. Our results are consistent with the idea that disproportional positive responses to disturbance in California, relative to those in the invader's native range of Spain, may be an important factor in the dominance of *C. solstitialis* in its non-native ranges. It is not clear why disturbance would have more beneficial effects on the invader in its non-native range, but the powerful effects of disturbance appear to interact in subtle ways with biogeographic differences in evolutionary trends, competitive intensities, life histories, and reproductive rates.

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1. Introduction

Successful exotic plant invasions appear to be affected by a number of biogeographically explicit ecological processes,

including appropriate propagule pressure for establishment, spread, and occupation (Von Holle and Simberloff, 2005), competition with local residents (García-Serrana et al., 2007; Maron and Marler, 2008; Callaway et al., 2011), consumer pressure (Kulmatiski et al., 2008; Pearson et al., 2011; Schaffner et al., 2011), and responses to disturbance (Leishman and Thomson, 2005; Hierro et al., 2006). These ecological phenomena are likely to interact in complex ways, and this creates opportunities for ecologists to explore the combined or synergistic effects of complex mechanisms on invader abundance and impacts on native species (Lenz and Facelli, 2005; Besaw et al., 2011). However, ascertaining the

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relative importance of different ecological mechanisms is difficult for several reasons. First, it is hard to know whether mechanisms that are important at small scales, competition for example, are also important at the scale of invaded landscapes. Second, manipulating some combinations of mechanisms in biogeographically explicit field experiments, such as herbivory and competition, is problematic because of the risk of introducing additional non-native species or genotypes. Third, field experiments yield perspectives from the particular suite of conditions in which they are conducted, and it is difficult to extrapolate from one suite of conditions to others in order to derive more general hypotheses.

One approach to building and strengthening hypotheses for the relative importance and potential synergy of multiple interacting mechanisms in ecology is the use of empirical and individual-based modeling. These models can integrate experimental results that vary in intensity in order to assess potential conditionality in their relative importance and the generality of a mechanisms across a range of conditions. Individual-based models cannot replace multi-factorial field experiments, but they can provide a tool to develop hypotheses for causal links between individual-level interactions and ecological patterns at the population or community level (Grimm and Railsback, 2005). They are also suitable for investigating the characteristics and dynamics of complex systems, which are typical in ecological research, and in particular in the studies of communities (Chen et al., 2009; Xiao et al., 2009, 2010; Michalet et al., 2011).

A number of mechanisms appear to contribute to the invasiveness of *Centaurea solstitialis* L. (yellow starthistle) in California, including disturbance (Hierro et al., 2006), evolution of new trait responses in non-native ranges (Hierro et al., 2009; Dlugosch et al., 2015), weak density-dependent competitive resistance by native North American species in invaded grasslands (Munshaw and Lortie, 2010), escape from soil pathogens (Hierro et al., 2006; Andonian et al., 2011), competitive interactions (Graebner et al., 2012), and compensatory responses by individuals and populations to herbivory (Callaway et al., 2006; Garren and Strauss, 2009). However, for most if not all invasions, the relative importance of these and other mechanisms is unknown. Here, we use individual-based models to integrate several empirically derived datasets from different studies to develop hypotheses for the relative importance of disturbance, region-specific competitive intensities, and region-based differences in seed production in *C. solstitialis* invasion. For each mechanism, we incorporated biogeographic differences from experiments or measurements made for populations from the native and non-native ranges, allowing us to compare mechanisms in a biogeographical context after Hierro et al. (2006).

2. Methods

2.1. Overview

Centaurea solstitialis is a summer annual herb native of Eurasia and a highly aggressive invader in California, parts of South America, and Australia (Gerlach and Rice, 2003; Hierro et al., 2009). For our individual-based models, we integrated results from (1) an experiment comparing the intensity of competitive interactions (Relative Interaction Intensities; RII; Armas et al., 2004) between *C. solstitialis* from populations with North American and Spanish native grasses, to the competitive intensity of the same competitive interactions for *C. solstitialis* from Spain, (2) a common greenhouse experiment in which reproduction was compared for *C. solstitialis* plants from Spanish and Californian populations, and (3) results reported by Hierro et al. (2006) for the responses of *C. solstitialis* to experimental disturbance in California and another part of its native range, southwestern Turkey. We did not conduct a fully

factorial test of each of these processes, but applied biogeographic differences in reproductive rates and responses to disturbance to two different competitive scenarios; one created with *C. solstitialis* from California and grass species native to California, and one created with *C. solstitialis* from Spain and grasses native to Spain.

2.2. Assessment of competitive interactions

Centaurea solstitialis seeds were collected from ten individuals of each of eight populations across California and eight populations across Spain. Grasses native to Spain (*Aegilops geniculata*, *Avena barbata*, and *Brachypodium distachyon*) or California (*Bromus carinatus*, *Elymus glaucus*, *Hordeum brachyantherum*, and *Poa secunda*) were either collected from the wild in California or purchased (S&S Seeds, Carpinteria, CA, USA). Grasses represented species from a variety of common genera that overlap with the distribution of *Centaurea solstitialis* in its European and North American ranges. All species belong to Mediterranean habitats where germination occurs during the rainy season (i.e. winter). Spanish grasses have been introduced into California (plants.usda.gov), where they are widespread and commonly co-occur with *C. solstitialis*. Importantly, introduced European grass species were annuals, while Californian native grasses were perennial. Since our model incorporates a range of disturbance levels, the differences in life-history (annual invasive vs. perennial native grasses) could have an effect on our models, although such effect should be minimized at high disturbance rates, since on highly disturbed sites both annuals and perennials would be expected to perform as annuals.

For the competition contests we used five maternal lines from each of the eight *Centaurea* populations from each of the two regions (Spain or California). For each of these maternal lines, we sown in pots nine replicate *C. solstitialis* seeds, seven seeds in one-on-one competition with seeds of each of the seven grass species, and two controls. We also planted five replicates per population for one-on-one competition with another individual from the same *Centaurea* population, and five replicates for controls. Finally, we planted twenty replicates of each of the following: controls for each of the seven grass species, grass species in one-on-one competition with another individual of the same species, and one-on-one competition for each pair of grass species from the same region (i.e. within Spain or within California). Seeds were sown and germinated directly in pots and grown for 90 days in a greenhouse where temperatures were kept between 15 °C at night and 30 °C in the day, and natural light was supplemented with metal halide bulbs. Photosynthetic Active Radiation during the day peaked at $\approx 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ on cloudless days. We harvested plants 90 days after planting while they were in vegetative (non-reproductive) state. Each plant was dried for 72 h at 90 °C and weighed. Total mean masses for all controls and competition treatments are reported in Table 1.

From these pairwise competition contests we constructed an orthogonal matrix of RIIs depicting the intensity of each pair-wise interspecific interaction between *C. solstitialis* from either Spain or California, and three grass species native to Spain and four grass species native to California, all intraspecific RIIs, and RIIs among all Spanish grass species (with the exception of *Aegilops*) and among all Californian grass species (Appendix Tables A1–A4). This index has defined limits between -1 (competition) and $+1$ (facilitation), it is symmetrical around zero, and it is calculated as follows:

$$\text{RII} = \frac{(B_w - B_0)}{(B_w + B_0)},$$

in which B_0 represents the mass of control individuals and B_w the mass of individuals in competition.

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