Ecological Modelling 335 (2016) 39–47

Contents lists available at ScienceDirect

Ecological Modelling

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

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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ARTICLE INFO

Article history:
Received 10 December 2015
Received in revised form 6 May 2016
Accepted 8 May 2016

Keywords:
Biogeography
Competition
Disturbance
Individual-based model
Modeling
Centaurea solstitialis

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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http://dx.doi.org/10.1016/j.ecolmodel.2016.05.005
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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 multifactorial 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 were 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 ≈1500 μmol m^{-2} 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:

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

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

Table 1
Mean dry biomass (mg, mean ± SD) for plants from Europe or North America, in control groups, or in competition with either European or North American plants, in the absence of disturbance.

	European *C. solstitialis*	North American *C. solstitialis*	European grasses	North American grasses
Control	137 ± 48	186 ± 36	305 ± 35	301 ± 34
Competition with Europe	39 ± 25	59 ± 34	337 ± 129	206 ± 95
Competition with North America	62 ± 41	92 ± 53	290 ± 99	199 ± 103

2.3. Assessment of reproductive rates

We measured the reproductive rates of *C. solstitialis* from California and Spain in another greenhouse experiment in which pollinators were excluded (see Montesinos et al., 2012 for detailed methodology). For each of the 10 mother plants from each of the 16 populations, we sowed one seed in a 2 L pot and grew them under common greenhouse conditions. We grew *C. solstitialis* until the plants flowered and manually pollinated all capitula (from now on named flower-heads) within populations to obtain seed-set. *Centaurea solstitialis* plants from Spain and California produced a similar number of flowers (mean ± SD = 27 ± 3 flowers per individual; D. Montesinos, *unpublished data*); consequently, reproductive rates for an individual were calculated as the mean number of seeds produced per capitulum (8.24 for Spain, and 9.33 for California) multiplied by the mean germination rate (37% for Spain, and 60% for California), which equaled 5.6 germinated seeds per flower-head for Californian populations and 3.0 germinated seeds per flower-head for Spanish populations. Since we did not have measurements of the reproductive rates for grass species, we assigned a single reproductive rate to all grasses in the models that equal the mean value of Californian and Spanish *C. solstitialis* reproductive rates: 4.3, which did not favor model outcomes in either biogeographic scenario. Additionally, we conducted a sensitivity analysis by including native reproductive values from 2.16 to 8.64, to assess the robustness of our models. We assumed annual reproduction for all species.

2.4. Assessment of the effect of disturbance

Hierro et al. (2006) investigated the effects of disturbance on the success of *C. solstitialis* in California and in its native Turkey by simulating different field disturbances and adding locally collected *C. solstitialis* seeds. They found that disturbance increased *C. solstitialis* density and relative performance far more in non-native ranges than in the native range. We used results from Hierro et al. (2006) to model biogeographic responses to disturbance in the context of the other factors studied here. We used post-disturbance *C. solstitialis* densities from native and non-native ranges to calculate a constant "*c*". We divided post-disturbance density in the native range by post-disturbance density on the non-native range. Therefore "*c*" values lower than one would indicate that native *C. solstitialis* populations are more negatively affected by disturbance than non-native populations, and values higher than one would indicate that non-native populations were more negatively affected by disturbance than native populations. Therefore, the obtained value of $c = 0.403$ indicates a more negative impact of disturbance on *C. solstitialis* populations in the native range than populations in the non-native range.

2.5. Model design

We used the RII matrix described above to build an individual-based spatially explicit dual-lattice model (Travis et al., 2005, 2006; Michalet et al., 2011) with *C. solstitialis* and all native species occupying one two-dimensional lattice (100 × 100 cells) for California and Spain, respectively. Each individual of each *C. solstitialis* and each native species occupied one cell in the lattice. When reproduction occurred (annually), individuals produced propagules that were identical to their parents. The total number of these propagules equalled the reproductive rate r_C of the *C. solstitialis* plant and the reproductive rate r_N of the native species. r_C was 5.598 in California and 3.045 in Spain, and r_N was the same for all native species populations, which equaled 4.321. All propagules of *C. solstitialis* and native species were dispersed sequentially to one of the patches that were randomly selected within the lattice. The propagules were only allowed to establish in empty cells and the propagule arriving first occupied the cell. We used a "wraparound" (torus) approach to avoid edge effects (Yamamura et al., 2004).

We assumed that both intra- and inter-specific competition decrease the survival rate of the species, and that this negative effect increases linearly with the increase of the RII value. Individuals competed only with other individuals within a neighborhood, and the neighborhood was defined as the Moore neighborhood in our model, including eight immediate neighbors of a given cell: north, northeast, east, southeast, south, southwest, west and northwest (Ifti et al., 2004).

Therefore, the survival rate of species *i* was:

$$S_i = S_{\max} - \sum_{j=1}^{n} \left(\frac{\mathrm{RII}_{j\ \mathrm{on}\ \mathrm{i}}}{8} \right)$$

where S_{max} was the maximum survival rate of the species without competition, and we assumed that it was the same for all species, with a value equal to 0.8. However, we conducted a sensitivity analysis with S_{max} values equalling to 0.4, 0.6 and 1.0, to confirm the robustness of our models. $\mathrm{RII}_{j\ \mathrm{on}\ i}$ indicates the competitive RII values of neighboring species *j* on species *i*. *n* is the total number of neighboring plants of one individual of species *i*.

To account for the impact of disturbance, we defined *d* as the intensity of disturbance in both the native and non-native ranges, ranging from 0 to 1. In our models, *d* was set to 0 (no disturbance), 0.1 (low disturbance), 0.4 (moderate disturbance) and 0.7 (high disturbance). We assumed that the impact of disturbance also decreased the survival rate of species and that this impact increased linearly with the increase of the *d* value. Therefore, the survival rate of species *i* experiencing disturbance was:

$$S_i = S_{\max}(1 - c * d) - \sum_{j=1}^{n} \left(\frac{\mathrm{RII}_{j\ \mathrm{on}\ \mathrm{i}}}{8} \right)$$

As described above, *c* equals 0.403 for Californian *C. solstitialis*, and 1 for Spanish *C. solstitialis*, and 1 for all native species both from North America and Europe. We used asynchronous updating in the model that worked in the following way. First a single individual of species was selected at random. Second, we determined whether the individual survived at a certain survival rate S_i. If the individual survived it reproduced and dispersed propagules. Each time step was made up of *N* of such updates, where *N* referred to the number of all individuals within the community. Since the initial population sizes of invaders are likely to be relatively small at the beginning of invasions, all simulations were initiated with only 100 individuals of Californian *C. solstitialis*. Initial conditions started with saturated communities of native species with each having the same number

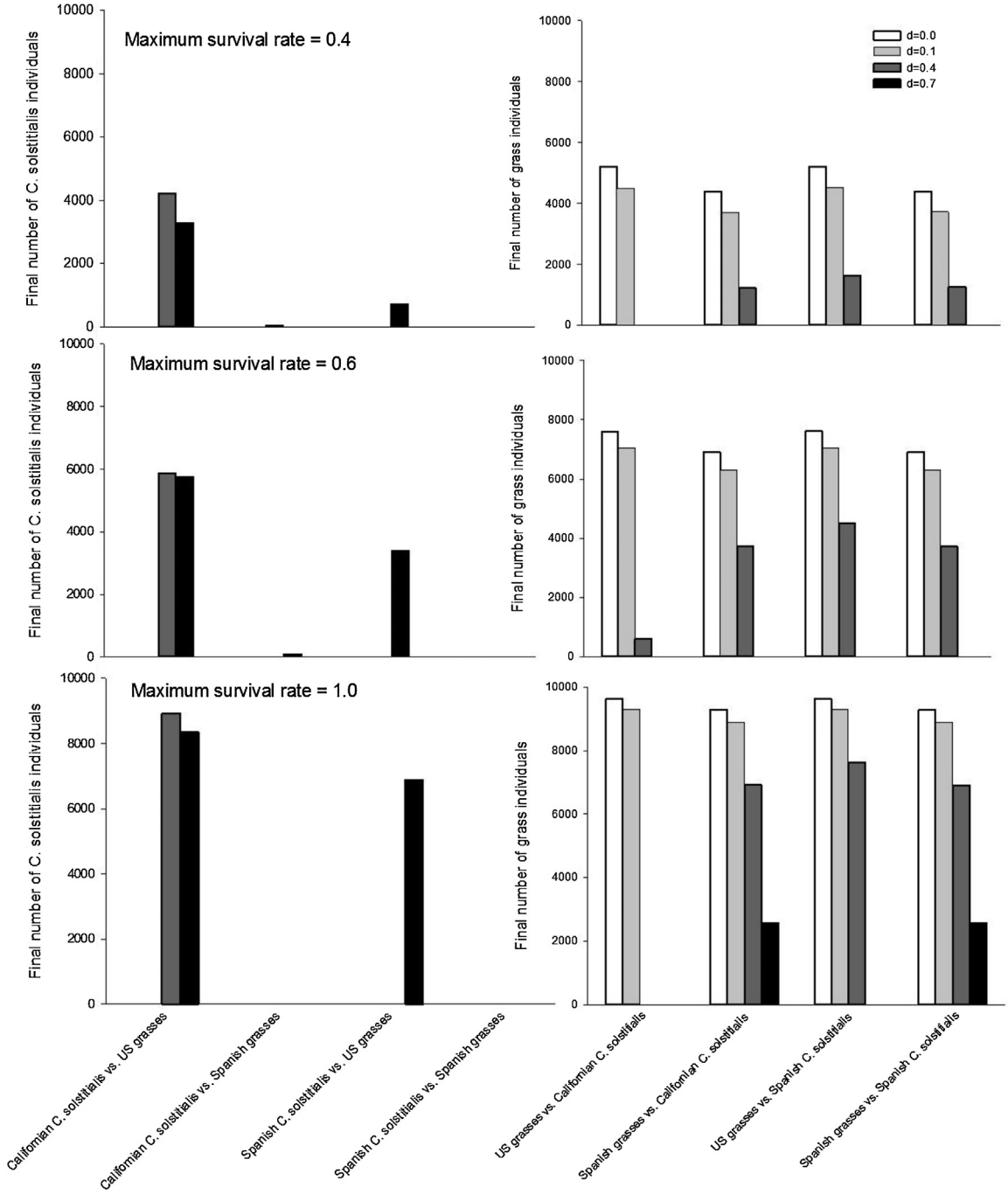

Fig. 1. Final plant densities for *C. solstitialis* (left), and *B. hordeaceus* (right) considering three different maximum survival rates, experiencing four different disturbance levels (d).

of individuals. All individuals of species were randomly dispersed across the lattice.

All simulations were run for 10,000 time steps in order to allow the system to reach a steady state. However, note that all simulations reached stable proportional of species before 100 generations. *Centaurea solstitialis* was introduced to California roughly 200 years ago, thus even assuming a time lag from the first introduction until high densities were reached our simulations generally correspond with the timeframe of *C. solstitialis* invasion. All measurements were determined as the mean values of 100 independent replicate runs for each time step. Simulations were performed in NetLogo (Wilensky, 1999, http://ccl.northwestern.edu/netlogo/), a powerful multi-agent modeling language particularly well suited for modeling complex systems that develop over time. Both the ODD protocol (Grimm et al., 2010) and the NetLogo code for the model used can be found as Supplementary Information 1 and 2, respectively.

3. Results

3.1. *Response of* Centaurea solstitialis

In the absence of disturbance, the modeled abundance of *C. solstitialis* decreased rapidly in all scenarios but one, and was

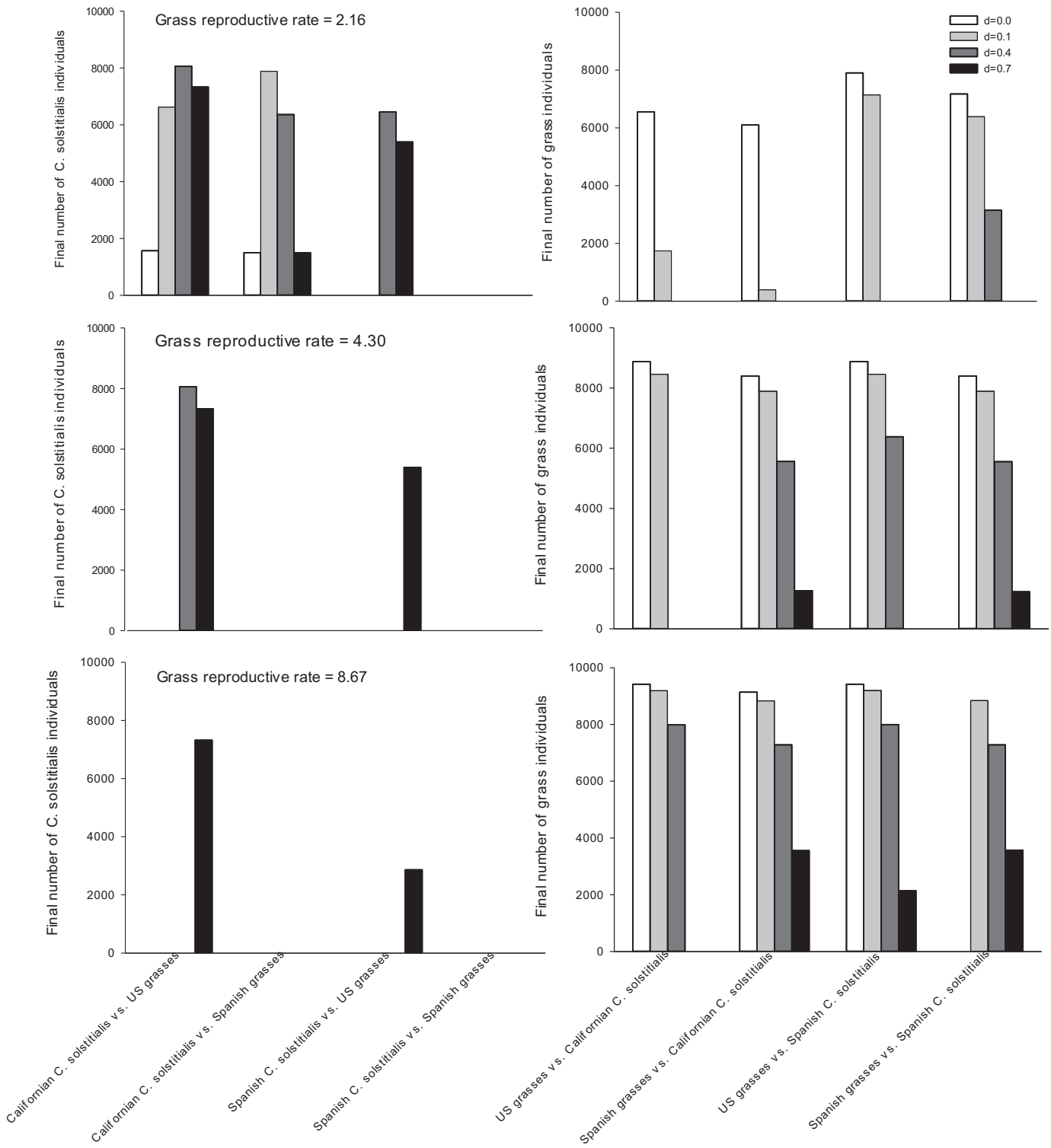

Fig. 2. Final plant densities of *C. solstitialis* (left), or *B. hordeaceus* (right) considering three different levels of grass reproductive rates, experiencing four different disturbance levels (d).

eliminated in less than 50 time steps (Figs. 1 and 2). In one case, utilizing a very low grass reproductive rate, a Californian *C. solstitialis* population was able to persist (Fig. 2). In all scenarios, the final abundance of *C. solstitialis* was slightly higher, and *C. solstitialis* survived for a short time longer, when competing with native North American grasses than when competing with native European grasses. Nevertheless, the final abundance of *C. solstitialis* was consistently much higher when moderate or high levels disturbance occurred across all survival and reproductive rates.

At the lowest level of disturbance, *C. solstitialis* abundances were higher than without disturbance, but decreased rapidly, and *C. solstitialis* was eliminated from the models with native European grasses in approximately 10 time steps. The models with native North American grasses required roughly 50 time steps for the

extirpation of *C. solstitialis*. At moderate disturbance levels, *C. solstitialis* became dominant only when in competition with native North American grasses. *Centaurea solstitialis* from both ranges were rapidly eliminated from the model when in competition with native European grasses. Similar results occurred at high disturbance levels, with *C. solstitialis* becoming highly abundant in competition with Californian grasses but not when in competition with Spanish grasses.

The sensitivity analysis for grass reproductive rates showed that increasing grass reproductive rates decreased the final densities of *C. solstitialis*. However, even at the highest grass reproductive rate, *C. solstitialis* populations were able to establish, with higher final abundances for populations of Californian origin. Thus the sensitivity analyses showed that our modeled outcomes were robust regardless of grass reproductive rates.

3.2. Responses of North American and European grasses

Modeled dynamics of the abundances of grass species native to North America versus those native to Europe, with all species in each region combined, reflected those for the abundance of *C. solstitialis*. Without disturbance and at low disturbance levels native grasses from both regions rapidly became dominant, reflecting differences between the regions in competitive outcomes and matching the rapid decline in *C. solstitialis* abundance.

In moderate disturbance levels modeled outcomes were strikingly different than without disturbance. There were substantial decreases in the abundance of native grasses in both ranges, but stronger decreases for North American grasses. At the moderate disturbance level, North American grasses abundances decreased sharply and were ultimately eliminated from the model.

At the highest disturbance level, the abundance of native grasses decreased substantially for plants from both ranges, but native grass species remained in the system and reached stable levels when in competition with Spanish *C. solstitialis*. At this high disturbance rate, all native grasses were extirpated within 10 time steps when in competition with Californian *C. solstitialis*. Results from sensitivity analyses, with S_{max} values equalling 0.4, 0.6 and 1.0 were qualitatively the same as those reported above, again indicating that the general patterns in our models were robust. Sensitivity analyses using different reproductive rates for different grass species were qualitatively similar, although higher reproductive levels for grasses resulted in slightly lower final densities of *C. solstitialis*.

4. Discussion

Our models supported the fundamental importance of disturbance for invasion by *Centaurea solstitialis*. Differences in competitive interactions and reproductive rates may contribute to higher relative abundances of *C. solstitialis* in its non-native range than in its native range, but biogeographic differences in competitive outcomes were not manifest without disturbance. To best illustrate the interaction between disturbance and biogeographically based competition, even at moderate or high disturbance rates, *C. solstitialis* reached dominance (i.e. the most abundant species in the community) in competition with Spanish grasses only when survival rates were set to be lower than one, or when grasses' reproductive rates were set to the lowest point. However, *C. solstitialis* became dominant in high disturbance rates in competition with Californian native grasses regardless of biogeographic differences in reproductive rates or survival rates.

We do not have data for grass reproductive rates, but our models suggest that abundant native seed availability might be crucial for controlling *C. solstitialis* invasion. Furthermore, the modeled effect of disturbance on survival rates was important, since only in the models in which survival responses to disturbance were moderate or low were systems dominated by *C. solstitialis*, regardless of the origin of the grass species.

Our models incorporated *relative* biogeographical differences in greenhouse-based competitive outcomes and reproductive rates with *relative* biogeographical differences in the abundance of *C. solstitialis* and native species in field experiments with disturbance, the outcome of which was also affected by competition and reproductive rates. Therefore, we have not tested each mechanism in a factorial manner, and thus our models only suggest potential directions in which to focus more intensely in order to better understand *C. solstitialis* invasion. These models suggest that biogeographical differences in response to disturbance might be crucial. Disturbance is associated with nearly 70% of all plant invasions (Lozon and MacIsaac, 1997), and it commonly increases the abundance of exotic plants (Gray, 1879; Elton, 1958; D'Antonio et al., 1999). Changes in resource availability (Davis et al., 2000) and disturbance (MacDougall and Turkington, 2005) have been considered more determinant of invasive success than particular species traits (Bennett et al., 2012). Experimental data consistently shows a high benefit of disturbance to *C. solstitialis* performance (Hierro et al., 2013; Gerlach and Rice, 2003). However, we know little about how disturbance affects exotics in their native ranges. For disturbance to explain biogeographic differences in the abundance of exotic invaders we must know whether disturbance triggers the same extraordinary response in the abundance of some invaders where they are natives as observed where they are exotics (Hierro et al., 2005). In our case, the competitive advantage *C. solstitialis* has against Californian grasses may be a key link to understanding why disturbance has a stronger effect in California than in the native range of the invader.

The vast majority of California grasslands have been invaded by European grasses, which are common competitors of *C. solstitialis* in California. Our results indicate that *C. solstitialis* dominates grass communities at high disturbance rates regardless of the origin of the grass community, but European grasses survive with *C. solstitialis* although at much lower densities. This suggest that ruderalization of native plant communities in California greatly facilitates invasive processes by ruderal species like *C. solstitialis*. One other potential biogeographical mechanism that might explain the stronger positive effects of disturbance in the non-native ranges of *C. solstitialis*, is soil biota. For example, Hierro et al. (2006) found that soil from the native range suppressed the growth of *C. solstitialis*, whereas soil biota from two non-native ranges did not. However, other biogeographical comparisons of soil biota are not as clear. Andonian et al. (2012) found that soil biota from both native and non-native ranges of *C. solstitialis* had negative effects on plants, but these negative effects were significantly weaker in soils from non-native ranges in Chile and California than in those from the non-native range in Argentina and the native range in Eurasia, patterns that did not correspond completely with the strength of invasion in non-native ranges. In another study, Andonian et al. (2011) found that *C. solstitialis* generated strong negative feedbacks in regions where it is the most invasive but neutral plant-soil feedbacks where it is non-invasive.

A leading hypothesis for invasive success is escape from natural enemies, and therefore a major gap in our study is that we did not incorporate effects of herbivores. However, *C. solstitialis* may actually experience greater attack by biological control agents in its introduced range in California than it does in its native range. In California, biological control weevils can be found in

over 50% of *C. solstitialis* inflorescences and on over 90% of plants (Gutierrez et al., 2005; Swope and Parker, 2010a,b), but in native regions in Eurasia no more than 18% of plants in a population have been found to be infested (Uygur et al., 2004). And Wallace et al. (2008) found that livestock herbivory early in the growth of *C. solstitialis* in its non-native range stimulated overcompensation in reproduction. Similarly, Garren and Strauss (2009) found that two biocontrol agents strongly reduced seed production but that several compensatory processes prevented effective population control. Self-thinning, apparently caused by intraspecific competition, reduced the numbers of seedlings to the point where the effects of biocontrol agents were not detected. Swope and Parker (2010a,b) found a similar pattern for *C. solstitialis*, in which initial high plant density resulted in lower final *C. solstitialis* density, but having no overall effect on fitness due to compensatory reproductive responses of surviving adults. Other studies have shown that biocontrol agents can decrease seed production by 40–100% per head (Pitcairn and DiTomaso, 2000), and yet others suggest that this effect may not significantly reduce yellow starthistle populations (Turner and Fornasari, 1992; Sun and Ritland, 1998; DiTomaso and Gerlach, 2000). The incorporation of any biogeographic differences in herbivore effects would have improved our models, but a number of studies suggest that specialist and generalist herbivores do not have unusually strong effects in the non-native range of *C. solstitialis*.

A second weakness of our model is that we did not incorporate variation in the reproductive rates of the Californian and European grasses. Instead, we simply set these reproductive rates at an arbitrary but identical background against which the consequences of experimentally measured variation in the reproductive rates of *C. solstitialis* could be estimated. Thus, it is important to note that the outcome of biological interest in this context is the effect of the *relative* difference in measured reproductive rate of plants from Californian and Spanish populations of *C. solstitialis*. Regardless, our results are likely to be representative only for similar annual herbs presenting strict sexual reproduction in disturbed ruderal habitats.

We do not know the mechanism for why *C. solstitialis* had stronger competitive effects on North American native grasses than on European grasses, but common explanations for such differences, such as novel allelopathic effects (Callaway and Ridenour, 2004; Inderjit et al., 2011; Svensson et al., 2013) are unlikely to apply. Qin et al. (2007) found that experiments with activated carbon, crude root exudates, and chloroform-extracted root exudates from *C. solstitialis* did not demonstrate evidence for allelopathic inhibition of native North American species. Furthermore, field experiments testing the effects of competition in two non-native ranges, California and Argentina, competition from annual grasses and perennial grasses reduced *C. solstitialis* performance similarly in both ranges (Hierro et al., 2011). In contrast, Munshaw and Lortie (2010) added *C. solstitialis* seed into existing vegetation and found no evidence for regulation of the invader via intra or interspecific competition in the non-native range.

Our measurements of greater reproductive rates for Californian populations than Spanish populations support the possibility that evolution has occurred in the non-native range. Recent studies point to changes in the reproductive system, which is establishing reproductive barriers between populations in the native and non-native ranges of the species (Montesinos et al., 2012). Other studies have found differences between *C. solstitialis* derived from its native and non-native ranges in germination, relative growth rates, competitive resistance, seed and seedling mass, resistance to disturbance, and resource use (Hierro et al., 2006, 2009, 2013; Graebner et al., 2012; Dlugosch et al., 2015). These changes might be partially responsible for the results observed in our simulations. Regardless, our models primarily point to biogeographical differences in the effects of disturbance, with other factors appearing to be secondary. Our simulations indicate that an important aspect of biotic resistance to *C. solstitialis* in the non-native ranges is the competitive effects of native grass species, which is consistent with empirical studies (Gerlach and Rice, 2003; Hierro et al., 2011, 2013). Disturbance has negative effects on native grass species in the Californian scenarios, which of course reduces their ability to competitively resist *C. solstitialis*. Disturbance also had a direct negative effect on *C. solstitialis*, but the impact of disturbance was lower for *C. solstitialis* than for grass species, particularly for grass species native to North America. Our results also suggest that the ruderalization of native Californial grasslands could be key to facilitating invasive processes by exotic species pre-adapted to high disturbance regimes.

5. Conclusions

The most important contribution of our work is to provide a suggestion for how ecologists might link small-scale mechanistic results to ecological patterns at the population or community level (Grimm and Railsback, 2005), and through this linkage to estimate the relative importance of different smaller scale results. In our case, our models point most strongly to the need to explore biogeographic differences in disturbance as a key driver for invasion by *C. solstitialis*. But our results also indicate that escape from stronger competitive environments and evolution toward greater reproductive capacity in non-native ranges may also contribute to larger scale patterns of the invader's distribution and abundance.

Acknowledgements

RMC thanks the NSF EPSCoR Track-1 EPS-1101342 (INSTEP 3) for support. DM was funded by the Spanish Micinn (2008-0662), by the Portuguese FCT (PCT/BIA-PLA/3389/2012 and IF-00066-2013), and by the European Commission (FP7-PEOPLE-MC-CIG-321909); FCT is partially funded by the EU via QREN, COMPETE and FEDER. SX thanks the State Key Program of the National Natural Science of China (31230014, 41430749), the Program for New Century Excellent Talents in University (NCET-13-0265), the Central University Special Fund (lzujbky-2014-k09, lzujbky-2014-200), the National Key Technology R&D Program (No. 2014BAC05B02), and the National Natural Science Foundation of China (31470492).

Appendix A.

See Tables A1–A4.

Table A1
RII values for competition between Californian *C. solstitialis* and North American native species. Each RII value represents the competitive effects of the species from each column on the species in each row.

	Species causing the competitive response				
Species	*Centaurea*	*Poa*	*Bromus*	*Elymus*	*Hordeum*
Centaurea	−0.238	−0.152	−0.226	−0.194	0.085
Poa	−0.107	−0.244	0.028	−0.145	−0.071
Bromus	−0.387	−0.492	−0.142	−0.321	−0.348
Elymus	−0.378	−0.421	−0.248	−0.301	−0.343
Hordeum	−0.491	−0.461	−0.151	−0.251	−0.215

Table A2
RII values for competitive effects between Spanish *C. solstitialis* and North American native species. Each RII value represents the competitive effects of the species from each column on the species in each row.

Species causing the competitive response					
Species	*Centaurea*	*Poa*	*Bromus*	*Elymus*	*Hordeum*
Centaurea	−0.298	−0.059	−0.202	−0.175	0.075
Poa	−0.092	−0.244	0.028	−0.145	−0.071
Bromus	−0.452	−0.492	−0.142	−0.321	−0.348
Elymus	−0.444	−0.421	−0.248	−0.301	−0.343
Hordeum	−0.527	−0.461	−0.151	−0.251	−0.215

Table A3
RII values of competitive effects among Californian *C. solstitialis* and European native species. Each RII value represents competitive effects of the species from each column on the species in each row. We did not conduct pair-wise competition trials between *Aegilops* and the other grass species or intra-specific competition trials for *Aegilops*. Therefore we used the mean of RII values for the inter-specific and intra-specific competitions of *Avena* and *Brachypodium* as substitutes for the corresponding RII values of *Aegilops*.

Species causing the competitive response				
Species	*Centaurea*	*Avena*	*Brachypodium*	*Aegilops*
Centaurea	−0.238	−0.063	−0.026	0.026
Avena	−0.485	−0.250	−0.341	−0.341
Brachypodium	−0.526	−0.293	−0.231	−0.293
Aegilops	−0.546	−0.293	−0.341	−0.240

Table A4
RII values of competitive effects among Spanish *C. solstitialis* and European native species. Each RII value represents the competitive effect of the species from each column on the species in each row. We did not conduct pair-wise competition trials between *Aegilops* and the other grass species or the intra-specific competition trials for *Aegilops*. Therefore we used the mean of RII values for the inter-specific and intra-specific competitions of *Avena* and *Brachypodium* as substitutes for the corresponding RII values of *Aegilops*.

Species causing the competitive response				
Species	*Centaurea*	*Avena*	*Brachypodium*	*Aegilops*
Centaurea	−0.298	0.044	−0.035	0.108
Avena	−0.494	−0.250	−0.341	−0.341
Brachypodium	−0.556	−0.293	−0.231	−0.293
Aegilops	−0.609	−0.293	−0.341	−0.240

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.05.005.

Appendix C. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.05.005.

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Supplementary Information 1

Model description in the ODD protocol

The model description follows the ODD (overview, design concepts and details) protocol for describing individual- and agent-based models (Jovani and Grimm 2008; Grimm et al. 2010). The model is implemented in NetLogo (Wilensky, 1999. http://ccl.northwestern.edu/netlogo/) and available in the electronic supplementary material (basic model).

1. *Purpose.* The purpose of the model is 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.
2. *State variables and scales.* We used an RII matrix to build an individual-based spatially-explicit dual-lattice model (Travis et al. 2005, 2006, Michalet et al. 2011) with *C. solstitialis* and all native species occupying one two-dimensional lattice (100 × 100 cells) for California and Spain, respectively. r_C was the reproductive rate of *C. solstitialis* plant and r_N was the reproductive rate of the native species. S_i was the survival rate of the species. To account for the impact of disturbance, we defined d as the intensity of disturbance in both the native and non-native ranges, ranging from 0 to 1. We used a "wraparound" (torus) approach to avoid edge effects (Yamamura et al. 2004). All simulations were run for 10,000 time

steps in order to allow the system to reach a steady state. However, note that all simulations reached stable proportional of species before 100 generations. *Centaurea solstitialis* was introduced to California roughly 200 years ago, thus even assuming a time lag from the first introduction until high densities were reached our simulations generally correspond with the timeframe of *C. solstitialis* invasion.

3. *Process overview and scheduling.* Each individual of each *C. solstitialis* and each native species occupied one cell in the lattice. The propagules were only allowed to establish in empty cells and the propagule arriving first occupied the cell. When reproduction occurred (annually), individuals produced propagules that were identical to their parents. All propagules of *C. solstitialis* and native species were dispersed sequentially to one of the patches that were randomly selected within the lattice. We used asynchronous updating in the model that worked in the following way. First a single individual of species was selected at random. Second, we determined whether the individual survived at a certain survival rate S_i. If the individual survived it reproduced and dispersed propagules. Each time step was made up of N of such updates, where N referred to the number of all individuals within the community.

4. *Design concepts.* We assumed that both intra- and inter-specific competition decrease the survival rate of the species, and that this negative effect increases linearly with the increase of the RII value. We also assumed that the impact of disturbance also decreased the survival rate of species and that this impact

increased linearly with the increase of the *d* value. Individuals competed only with other individuals within a neighborhood, and the neighborhood was defined as the Moore neighborhood in our model, including eight immediate neighbors of a given cell: north, northeast, east, southeast, south, southwest, west and northwest (Ifti et al. 2004). All measurements were determined as the mean values of 100 independent replicate runs for each time step.

5. *Initialization.* Since the initial population sizes of invaders are likely to be relatively small at the beginning of invasions, all simulations were initiated with only 100 individuals of California *C. solstitialis*. Initial conditions started with saturated communities of native species with each having the same number of individuals. All individuals of species were randomly dispersed across the lattice.

6. *Input.* The total number of these propagules equalled the reproductive rate r_C of the *C. solstitialis* plant and the reproductive rate r_N of the native species. r_C was 5.598 in California and 3.045 in Spain, and r_N was the same for all native species populations, which equaled 4.321. As described above, *c* equals 0.403 for Californian *C. solstitialis*, and 1 for Spanish *C. solstitialis*, and 1 for all native species both from North America and Europe.

7. *Submodels*. The survival rate of species *i* experiencing disturbance was:

$$S_i = S_{max}(1 - c * d) - \sum_{j=1}^{n}(RII_{j\,\mathrm{on\,i}} / 8),$$

where S_{max} was the maximum survival rate of the species without competition, and we assumed that it was the same for all species, with a value equal to 0.8. However, we conducted a sensitivity analysis with S_{max} values equalling to 0.4,

0.6 and 1.0, to confirm the robustness of our models. $RII_{j\,\mathrm{on\,i}}$ indicates the competitive RII values of neighboring species *j* on species *i*. *n* is the total number of neighboring plants of one individual of species *i*. 1. *d* was set to 0 (no disturbance), 0.1 (low disturbance), 0.4 (moderate disturbance) and 0.7 (high disturbance).

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Supplementary Information 2

```
globals [rn is Su rinv trinv1 trinv2 trinv3 trn1 trn2 trn3]
patches-own [s]

to setup
  clear-all
  crt (totaltime + 1)
  if Invader = "California_C_solstitialis" and Place = "America"
    [set is [[0.238263325    0.152122642   0.225548902    0.193588676   -
0.084776013]
             [0.106690778    0.243571763  -0.028222555    0.145407112
0.07119255 ]
             [0.387230827    0.491867639   0.142315504    0.321400285
0.347694633]
             [0.378378378    0.420940171   0.247928994    0.301404056
0.343379167]
             [0.490864799    0.460735859   0.150572831    0.250862198
0.21540559 ]]
     if Reproductive_difference = "With"
       [set rinv 5.598]
     if Reproductive_difference = "Without"
       [set rinv 4.32134]
     ask patches
       [set s 5]
     ask n-of 100 patches
       [set s 0]
     ask turtles with [who < 5 and who > 0]
       [let temp who
        ask n-of ((count patches - 100) / 4) patches with [s = 5]
          [set s temp]]]
  if Invader = "Spanish_C_solstitialis" and Place = "America"
    [set is [[0.297709924    0.058504875   0.201565558    0.175240828   -
0.075202885]
             [0.092244898    0.243571763  -0.028222555    0.145407112
0.07119255 ]
             [0.451980467    0.491867639   0.142315504    0.321400285
0.347694633]
             [0.44414463     0.420940171   0.247928994    0.301404056
0.343379167]
             [0.52739726     0.460735859   0.150572831    0.250862198
0.21540559 ]]
     if Reproductive_difference = "With"
       [set rinv 3.04468]
     if Reproductive_difference = "Without"
       [set rinv 4.32134]
     ask patches
       [set s 5]
     ask n-of 100 patches
       [set s 0]
     ask turtles with [who < 5 and who > 0]
       [let temp who
        ask n-of ((count patches - 100) / 4) patches with [s = 5]
```

```
          [set s temp]]]
  if Invader = "California_C_solstitialis" and Place = "Europe"
    [set is [[0.238263325    0.063145809   0.026478056   -0.025957973]
             [0.485436893    0.24980349    0.340967356    0.340967356]
             [0.526184539    0.292682927   0.23055207     0.292682927]
             [0.546105263    0.292682927   0.340967356    0.24017778 ]]
     if Reproductive_difference = "With"
       [set rinv 5.598]
     if Reproductive_difference = "Without"
       [set rinv 4.32134]
     ask patches
       [set s 4]
     ask n-of 100 patches
       [set s 0]
     ask turtles with [who < 4 and who > 0]
       [let temp who
        ask n-of ((count patches - 100) / 3) patches with [s = 4]
          [set s temp]]]
  if Invader = "Spanish_C_solstitialis" and Place = "Europe"
    [set is [[0.297709924   -0.044375645   0.035302725   -0.108373146]
             [0.494137353    0.24980349    0.340967356    0.340967356]
             [0.555813953    0.292682927   0.23055207     0.292682927]
             [0.609140108    0.292682927   0.340967356    0.24017778 ]]
     if Reproductive_difference = "With"
       [set rinv 3.04468]
     if Reproductive_difference = "Without"
       [set rinv 4.32134]
     ask patches
       [set s 4]
     ask n-of 100 patches
       [set s 0]
     ask turtles with [who < 4 and who > 0]
       [let temp who
        ask n-of ((count patches - 100) / 3) patches with [s = 4]
          [set s temp]]]
  set rn 4.32134
  set trinv1 rinv - (int rinv)
  set trinv2 (int rinv) + 1
  set trinv3 int rinv
  set trn1 rn - (int rn)
  set trn2 (int rn) + 1
  set trn3 int rn
  reset-ticks
end

to go
    if Place = "America"
    [ask patches with [s != 5]
      [set Su 0
       ask neighbors with [s != 5]
         [set Su Su + item ([s] of myself) (item s is)]
       ifelse s = 0
         [set Su Smax * (1 - 0.402589635 * d) - (Su / 8)]
         [set Su Smax * (1 - d) - (Su / 8)]
```

```
      ifelse random-float 1 > Su
        [set s 5]
        [ifelse s = 0
          [ifelse trinv1 > random-float 1
            [repeat trinv2
              [ask one-of patches
                [if s = 5
                  [set s 0]]]]
            [repeat trinv3
              [ask one-of patches
                [if s = 5
                  [set s 0]]]]]
          [ifelse trn1 > random-float 1
            [repeat trn2
              [ask one-of patches
                [if s = 5
                  [set s [s] of myself]]]]
            [repeat trn3
              [ask one-of patches
                [if s = 5
                  [set s [s] of myself]]]]]]]
  if Place = "Europe"
    [ask patches with [s != 4]
      [set Su 0
       ask neighbors with [s != 4]
        [set Su Su + item ([s] of myself) (item s is)]
       set Su Smax * (1 - d) - (Su / 8)
       ifelse random-float 1 > Su
        [set s 4]
        [ifelse s = 0
          [ifelse trinv1 > random-float 1
            [repeat trinv2
              [ask one-of patches
                [if s = 4
                  [set s 0]]]]
            [repeat trinv3
              [ask one-of patches
                [if s = 4
                  [set s 0]]]]]
          [ifelse trn1 > random-float 1
            [repeat trn2
              [ask one-of patches
                [if s = 4
                  [set s [s] of myself]]]]
            [repeat trn3
              [ask one-of patches
                [if s = 4
                  [set s [s] of myself]]]]]]]
  tick
  if ticks = totaltime
    [stop]
end
@#$#@#$#@
GRAPHICS-WINDOW
```

282
12
1322
1073
-1
-1
10.3
1
10
1
1
1
0
1
1
1
0
99
0
99
1
1
1
ticks
30.0

BUTTON
10
10
94
44
NIL
setup
NIL
1
T
OBSERVER
NIL
NIL
NIL
NIL
1

BUTTON
108
10
172
44
NIL
go
T
1
T
OBSERVER

```
NIL
NIL
NIL
NIL
1

SLIDER
0
194
174
227
Smax
Smax
0
1
0.8
0.1
1
NIL
HORIZONTAL

SLIDER
0
268
175
301
totaltime
totaltime
0
10000
10000
100
1
NIL
HORIZONTAL

CHOOSER
-1
50
178
95
Invader
Invader
"California_C_solstitialis" "Spanish_C_solstitialis"
1

SLIDER
0
231
172
264
d
d
0
```

1
0.7
0.1
1
NIL
HORIZONTAL

CHOOSER
-1
98
91
143
Place
Place
"America" "Europe"
1

CHOOSER
-1
146
147
191
Reproductive_difference
Reproductive_difference
"With" "Without"
1

@#$#@#$#@
WHAT IS IT?

This section could give a general understanding of what the model is trying to show or explain.

HOW IT WORKS

This section could explain what rules the agents use to create the overall behavior of the model.

HOW TO USE IT

This section could explain how to use the model, including a description of each of the items in the interface tab.

THINGS TO NOTICE

This section could give some ideas of things for the user to notice while running the model.

THINGS TO TRY

This section could give some ideas of things for the user to try to do (move sliders, switches, etc.) with the model.

EXTENDING THE MODEL

This section could give some ideas of things to add or change in the procedures tab to make the model more complicated, detailed, accurate, etc.

NETLOGO FEATURES

This section could point out any especially interesting or unusual features of NetLogo that the model makes use of, particularly in the Procedures tab. It might also point out places where workarounds were needed because of missing features.

RELATED MODELS

This section could give the names of models in the NetLogo Models Library or elsewhere which are of related interest.

CREDITS AND REFERENCES

This section could contain a reference to the model's URL on the web if it has one, as well as any other necessary credits or references.

@#$#@#$#@
default
true
0
Polygon -7500403 true true 150 5 40 250 150 205 260 250

airplane
true
0
Polygon -7500403 true true 150 0 135 15 120 60 120 105 15 165 15 195 120 180 135 240 105 270 120 285 150 270 180 285 210 270 165 240 180 180 285 195 285 165 180 105 180 60 165 15

arrow
true
0
Polygon -7500403 true true 150 0 0 150 105 150 105 293 195 293 195 150 300 150

box
false
0
Polygon -7500403 true true 150 285 285 225 285 75 150 135
Polygon -7500403 true true 150 135 15 75 150 15 285 75
Polygon -7500403 true true 15 75 15 225 150 285 150 135
Line -16777216 false 150 285 150 135
Line -16777216 false 150 135 15 75
Line -16777216 false 150 135 285 75

bug
true
0
Circle -7500403 true true 96 182 108

```
Circle -7500403 true true 110 127 80
Circle -7500403 true true 110 75 80
Line -7500403 true 150 100 80 30
Line -7500403 true 150 100 220 30

butterfly
true
0
Polygon -7500403 true true 150 165 209 199 225 225 225 255 195 270 165
255 150 240
Polygon -7500403 true true 150 165 89 198 75 225 75 255 105 270 135 255
150 240
Polygon -7500403 true true 139 148 100 105 55 90 25 90 10 105 10 135 25
180 40 195 85 194 139 163
Polygon -7500403 true true 162 150 200 105 245 90 275 90 290 105 290 135
275 180 260 195 215 195 162 165
Polygon -16777216 true false 150 255 135 225 120 150 135 120 150 105 165
120 180 150 165 225
Circle -16777216 true false 135 90 30
Line -16777216 false 150 105 195 60
Line -16777216 false 150 105 105 60

car
false
0
Polygon -7500403 true true 300 180 279 164 261 144 240 135 226 132 213
106 203 84 185 63 159 50 135 50 75 60 0 150 0 165 0 225 300 225 300 180
Circle -16777216 true false 180 180 90
Circle -16777216 true false 30 180 90
Polygon -16777216 true false 162 80 132 78 134 135 209 135 194 105 189 96
180 89
Circle -7500403 true true 47 195 58
Circle -7500403 true true 195 195 58

circle
false
0
Circle -7500403 true true 0 0 300

circle 2
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240

cow
false
0
Polygon -7500403 true true 200 193 197 249 179 249 177 196 166 187 140
189 93 191 78 179 72 211 49 209 48 181 37 149 25 120 25 89 45 72 103 84
179 75 198 76 252 64 272 81 293 103 285 121 255 121 242 118 224 167
Polygon -7500403 true true 73 210 86 251 62 249 48 208
Polygon -7500403 true true 25 114 16 195 9 204 23 213 25 200 39 123
```

```
cylinder
false
0
Circle -7500403 true true 0 0 300

dot
false
0
Circle -7500403 true true 90 90 120

face happy
false
0
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 255 90 239 62 213 47 191 67 179 90 203
109 218 150 225 192 218 210 203 227 181 251 194 236 217 212 240

face neutral
false
0
Circle -7500403 true true 8 7 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Rectangle -16777216 true false 60 195 240 225

face sad
false
0
Circle -7500403 true true 8 8 285
Circle -16777216 true false 60 75 60
Circle -16777216 true false 180 75 60
Polygon -16777216 true false 150 168 90 184 62 210 47 232 67 244 90 220
109 205 150 198 192 205 210 220 227 242 251 229 236 206 212 183

fish
false
0
Polygon -1 true false 44 131 21 87 15 86 0 120 15 150 0 180 13 214 20 212
45 166
Polygon -1 true false 135 195 119 235 95 218 76 210 46 204 60 165
Polygon -1 true false 75 45 83 77 71 103 86 114 166 78 135 60
Polygon -7500403 true true 30 136 151 77 226 81 280 119 292 146 292 160
287 170 270 195 195 210 151 212 30 166
Circle -16777216 true false 215 106 30

flag
false
0
Rectangle -7500403 true true 60 15 75 300
Polygon -7500403 true true 90 150 270 90 90 30
Line -7500403 true 75 135 90 135
Line -7500403 true 75 45 90 45
```

```
flower
false
0
Polygon -10899396 true false 135 120 165 165 180 210 180 240 150 300 165
300 195 240 195 195 165 135
Circle -7500403 true true 85 132 38
Circle -7500403 true true 130 147 38
Circle -7500403 true true 192 85 38
Circle -7500403 true true 85 40 38
Circle -7500403 true true 177 40 38
Circle -7500403 true true 177 132 38
Circle -7500403 true true 70 85 38
Circle -7500403 true true 130 25 38
Circle -7500403 true true 96 51 108
Circle -16777216 true false 113 68 74
Polygon -10899396 true false 189 233 219 188 249 173 279 188 234 218
Polygon -10899396 true false 180 255 150 210 105 210 75 240 135 240

house
false
0
Rectangle -7500403 true true 45 120 255 285
Rectangle -16777216 true false 120 210 180 285
Polygon -7500403 true true 15 120 150 15 285 120
Line -16777216 false 30 120 270 120

leaf
false
0
Polygon -7500403 true true 150 210 135 195 120 210 60 210 30 195 60 180
60 165 15 135 30 120 15 105 40 104 45 90 60 90 90 105 105 120 120 120 105
60 120 60 135 30 150 15 165 30 180 60 195 60 180 120 195 120 210 105 240
90 255 90 263 104 285 105 270 120 285 135 240 165 240 180 270 195 240 210
180 210 165 195
Polygon -7500403 true true 135 195 135 240 120 255 105 255 105 285 135
285 165 240 165 195

line
true
0
Line -7500403 true 150 0 150 300

line half
true
0
Line -7500403 true 150 0 150 150

pentagon
false
0
Polygon -7500403 true true 150 15 15 120 60 285 240 285 285 120

person
```

```
false
0
Circle -7500403 true true 110 5 80
Polygon -7500403 true true 105 90 120 195 90 285 105 300 135 300 150 225
165 300 195 300 210 285 180 195 195 90
Rectangle -7500403 true true 127 79 172 94
Polygon -7500403 true true 195 90 240 150 225 180 165 105
Polygon -7500403 true true 105 90 60 150 75 180 135 105

plant
false
0
Rectangle -7500403 true true 135 90 165 300
Polygon -7500403 true true 135 255 90 210 45 195 75 255 135 285
Polygon -7500403 true true 165 255 210 210 255 195 225 255 165 285
Polygon -7500403 true true 135 180 90 135 45 120 75 180 135 210
Polygon -7500403 true true 165 180 165 210 225 180 255 120 210 135
Polygon -7500403 true true 135 105 90 60 45 45 75 105 135 135
Polygon -7500403 true true 165 105 165 135 225 105 255 45 210 60
Polygon -7500403 true true 135 90 120 45 150 15 180 45 165 90

square
false
0
Rectangle -7500403 true true 30 30 270 270

square 2
false
0
Rectangle -7500403 true true 30 30 270 270
Rectangle -16777216 true false 60 60 240 240

star
false
0
Polygon -7500403 true true 151 1 185 108 298 108 207 175 242 282 151 216
59 282 94 175 3 108 116 108

target
false
0
Circle -7500403 true true 0 0 300
Circle -16777216 true false 30 30 240
Circle -7500403 true true 60 60 180
Circle -16777216 true false 90 90 120
Circle -7500403 true true 120 120 60

tree
false
0
Circle -7500403 true true 118 3 94
Rectangle -6459832 true false 120 195 180 300
Circle -7500403 true true 65 21 108
Circle -7500403 true true 116 41 127
```

```
Circle -7500403 true true 45 90 120
Circle -7500403 true true 104 74 152

triangle
false
0
Polygon -7500403 true true 150 30 15 255 285 255

triangle 2
false
0
Polygon -7500403 true true 150 30 15 255 285 255
Polygon -16777216 true false 151 99 225 223 75 224

truck
false
0
Rectangle -7500403 true true 4 45 195 187
Polygon -7500403 true true 296 193 296 150 259 134 244 104 208 104 207
194
Rectangle -1 true false 195 60 195 105
Polygon -16777216 true false 238 112 252 141 219 141 218 112
Circle -16777216 true false 234 174 42
Rectangle -7500403 true true 181 185 214 194
Circle -16777216 true false 144 174 42
Circle -16777216 true false 24 174 42
Circle -7500403 false true 24 174 42
Circle -7500403 false true 144 174 42
Circle -7500403 false true 234 174 42

turtle
true
0
Polygon -10899396 true false 215 204 240 233 246 254 228 266 215 252 193
210
Polygon -10899396 true false 195 90 225 75 245 75 260 89 269 108 261 124
240 105 225 105 210 105
Polygon -10899396 true false 105 90 75 75 55 75 40 89 31 108 39 124 60
105 75 105 90 105
Polygon -10899396 true false 132 85 134 64 107 51 108 17 150 2 192 18 192
52 169 65 172 87
Polygon -10899396 true false 85 204 60 233 54 254 72 266 85 252 107 210
Polygon -7500403 true true 119 75 179 75 209 101 224 135 220 225 175 261
128 261 81 224 74 135 88 99

wheel
false
0
Circle -7500403 true true 3 3 294
Circle -16777216 true false 30 30 240
Line -7500403 true 150 285 150 15
Line -7500403 true 15 150 285 150
Circle -7500403 true true 120 120 60
Line -7500403 true 216 40 79 269
```

Line -7500403 true 40 84 269 221
Line -7500403 true 40 216 269 79
Line -7500403 true 84 40 221 269

x
false
0
Polygon -7500403 true true 270 75 225 30 30 225 75 270
Polygon -7500403 true true 30 75 75 30 270 225 225 270

@#$#@#$#@
NetLogo 5.3.1
@#$#@#$#@
@#$#@#$#@
@#$#@#$#@
@#$#@#$#@
@#$#@#$#@
default
0.0
-0.2 0 0.0 1.0
0.0 1 1.0 0.0
0.2 0 0.0 1.0
link direction
true
0
Line -7500403 true 150 150 90 180
Line -7500403 true 150 150 210 180

@#$#@#$#@
0
@#$#@#$#@