**Running head:** Plant invasions and intraspecific trait variation

**Provisional title:** Intraspecific trait variation increases the resistance of native species to plant invasions.

Another option: Intraspecific trait variation modifies competitive dynamics between invasive and native plant species

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**SUMMARY** (limit 350 words)

1. Ecologists recognise that intraspecific trait variation (ITV) can have important ecological and evolutionary effects on the population dynamics of competing species. However, whether ITV affects invasion success by altering species’ differences in niche and in competitive ability has not been explored yet.
2. We assessed the extent to which observed ITV in phenology, and height of an annual species native to California grasslands (*Lasthenia californica* DC. Ex Lindl.) determines coexistence or invasion resistance against two European invasive species with contrasted phenology (*Bromus madritensis* L.early phenology, and *Lactuca serriola* L. late phenology).
3. Our leading hypothesis is that *Lasthenia* will avoid competitive exclusion when ITV increases niche differences and/or equalise competitive imbalances with respect to the invaders.
4. Using recent advances in coexistence theory, we parameterised an annual plant model determining competitive outcomes with field information of species vital rates and variation in interaction coefficients coming from *Lasthenia’s* ITV.
5. We observed that *Lasthenia*’s ITVsignificantly varied depending on the invader identity. Against *Bromus* (the invader with similar phenology)*, Lasthenia* shifted its phenology to earlier phenotypes while showed a wider range of phenology and height when competing against *Lactuca* (the invader with different phenology).
6. From an ecological perspective, we found that ITV increases *Lasthenia* expected population density and delay the time to extinction thanks to the nonlinear effect that ITV has on per capita seed production via variation in competitive responses.
7. From an evolutionary perspective, we found that selecting taller and late season *Lasthenia* individuals tend to equalise competitive ability differences between the native and the invaders. Likewise, *Lasthenia* individuals with a larger phenologically offset with respect to the invaders enhanced their niche differences.
8. Although ITV substantially changed the determinants of competitive outcomes they were not enough to predict stable coexistence between the native and the two invaders.
9. Synthesis: Our work presents a novel framework to evaluate the effects of intraspecific trait variation on plant invasions using recent advances from coexistence theory.

**KEYWORDS:** biological invasions, coexistence theory, competitive ability, fitness differences, Jensen’s inequality, height, niche differences, plasticity, phenology, variance.

**INTRODUCTION**

It is common to observe in nature that individuals within species show variation in many traits. Such intraspecific trait variation (ITV) has gained renewed interest among ecologist for several reasons. Worldwide and regional studies have shown that the relative extent of ITV within ecological communities compared to interspecific trait variation is far from being considered negligible (Albert et al., 2010, Fajardo and Piper, 2011, Siefert et al., 2015). Moreover, ITV coming from genetic variability and/or phenotypic plasticity can have significant effects on species’ vital rates and interspecific competition (Ortego et al., 2007, Lankau, 2009), which affects community dynamics and ecosystem processes (Crutsinger et al., 2006, Violle et al., 2012) . It is clear that in the last decade significant progress has been made on disentangling the specific mechanisms by which ITV influences community dynamics (reviewed in Bolnick et al., (2011), yet applications of recent advances from coexistence theory (Chesson, 2000, Adler et al., 2007) are necessary to broaden our understanding of the role of ITV on ecological dynamics of competing species (Hart et al., 2016).

Perhaps one of the research questions that most needs to apply this progress is to clarify the role of ITV on invasion success. ITV is expected to influence invasion outcomes via potentially independent ecological and evolutionary pathways. The first pathway comes from the pure ecological effect that ITV has on the demographic rates at the population level and therefore on the average interaction strength between competitors (Bolnick et al., 2011). It is commonly observed that natural populations exhibit non-normal phenotypic distributions (Geiler-Samerotte et al., 2013, Li et al., 2015). These distributions can shape in turn a nonlinear relationship between ITV and plant fitness, which may result in increasing the average size of a population compare to a scenario with no phenotypic variation. This ecological property occurs when the nonlinear relationship between variation in competitive responses and per capita seed production is concave up (Hart et al., 2016). How this ecological pathway, known as Jensen’s inequality (Ruel and Ayres, 1999), determine invasion success remains unexplored despite the rich literature of ITV and plant invasion.

The second pathway by which ITV may determine invasion success is its evolutionary effect on selecting from an initial population those phenotypes with increased competitive ability and fitness related parameters (Baker, 1974, Barrett and Richardson, 1986, Sakai et al., 2001), which allows invaders to show higher fitness homeostasis than native counterparts across different environmental conditions (Rejmánek et al., 2013, Sharma et al., 2005, Richards et al., 2006). Although this evolutionary mechanism of invasion success has been subject of great debate, it has so far mixed support (Williams et al., 1995, Sexton et al., 2002, Funk, 2008, Davidson et al., 2011, Godoy et al., 2011, Lamarque et al., 2013, Lamarque et al., 2015), partly because researchers followed very different methodologies in single and multi-species comparison studies. To make expectations even more difficult to classify, other sources of research specifically dealing with population dynamics of competing species, which adopted a mixed eco-evolutionary approach, suggest that high ITV promotes coexistence between natives and exotic species rather than exotic dominance (Lankau, 2011, Lankau, 2012).

Discrepancies between expectations can be resolved by reframing these ecological and evolutionary expectations of the importance of ITV for plant invasions within a modern coexistence framework developed by Chesson (2000), by acknowledging that only some of the ITV will promote the species differences, termed ‘stabilising differences’, that favour coexistence, while others, termed ‘average fitness differences’ will favour competitive exclusion (Hart et al., 2016). Stabilising niche differences cause intraspecific competition to be greater than interspecific competition and favour coexistence by buffering species against extinction when they drop to low relative abundance (Adler et al., 2007). Average fitness differences drive competitive exclusion by favouring one competitor over other regardless of their commonness or rarity, and in the absence of niche differences, the fitness superior excludes all competitors. Differentiating between niche and fitness differences is crucial because if ITV primarily drives niche differences between competitors, then we can predict coexistence between invasive and native species. A completely different outcome occurs if ITV primarily drives fitness differences. In that case, either invasive species exclude the native community or the natives repel the invasion (MacDougall et al., 2009). Finally, two additional factors should be considered when establishing connections between ITV and niche and fitness differences. First, competitors may limit the phenotypic expression of a focal species (Violle et al., 2009), which may reduce the species’ ability to be differentiated in their niche and their fitness. Second, it is likely that not all observed ITV is directly linked to niche and/or fitness differences. For instance, ITV can also result on neutral or negative species’ fitness responses (Davidson et al., 2011, Godoy et al., 2012).

In a previous study, Godoy and Levine (2014) showed that average phenology differences promoted both niche and fitness differences between competing exotic and native annual plant species from California grasslands. However, fitness advantages obtained from being a later phenology species overwhelmed the resulting niche differences, making coexistence more difficult between phenologically offset competitors. This caused to an early phenology native community, containing mainly the native species *Lasthenia californica* L. (Asteraceae)(hereafter “*Lasthenia*”)*,* to be excluded against three invasive species of varying phenology. Here, we aim to determine whether *Lasthenia* ITV in two different functional traits (phenology and plant height)can potentially modify species dynamics from average trait differences. We address the importance of ITV for plant invasions from the side of a native species resisting against the invasion of exotic species. Nevertheless, the same approach can be applied to assess the role of ITV from the invader’s side. Specifically, for an inferior competitor as it is *Lasthenia* in our study, there are two different alternatives by which ITV can shift from a competitive exclusion into a coexistence scenario. These alternatives are either reducing fitness differences with the superior competitor and/or increasing their niche differences (Fig.1). In both cases, the resulting modifications need to reach the point of stabilising niche differences overcoming fitness differences (Chesson, 2000).

In this work, we first explore whether Lasthenia’s ITV depends on the identity of the two phenological contrasted competitors. Then, we focus on two questions representing both ends of the ecological and evolutionary effects of ITV on the dynamics of competing species: (1) How does the shape of *Lasthenia* ITV affects the ecological dynamics between the nativeand the invasive species? (2) Assuming a potential evolutionary scenario of directional selection towards a *Lasthenia* trait optimum, could some specific phenotypic ranges modify the outcome of competition to a coexistence scenario?

To address these questions, we examine the competitive mechanisms by which ITV determines changes in the competitive exclusion of *Lasthenia*. To theoretically predict competitive outcomes based on *Lasthenia* trait variation, we field-parameterized a model of competing annual plant species from which the stabilising niche differences and the relative fitness differences can be inferred with respect to their population dynamics. To do so, we quantified species’ vital rates (germination, seed viability, fecundity) and the variation in the interaction coefficients arising from the ITV observed in *Lasthenia*. Finally, we correlated *Lasthenia*‘s trait variability with the niche and fitness differences inferred from the parameterized models.

**MATERIAL AND METHODS**

*Quantifications of determinants of competitive outcomes.*

In 2010-2011, we conducted a field experiment with several native and invasive species in a grassland in Santa Barbara County, California, USA. The climate is Mediterranean with cool winters and dry summers (736 mm in the studied year). Among the species selected for the experiment, we focused here in one native and two invasive species. The native species is *Lasthenia californica* Dc. Ex Lindl. (Asteraceae), and the invasive species are *Bromus madritensis* L. (Poaceae), and *Lactuca serriola* L. (Asteraceae), both of which were introduced within the reserve at the end of the 19th century and afterwards largely spread by the cattle. Previous work done by Godoy and Levine (2014) have shown that *Lasthenia* is the inferior competitor in this system but none of the species

dominate the landscape at the site of the experimental plots. The competitive dynamics of a community of annual plant species can be modelled as follows:

(Equation 1)

where is the number of individuals of species *i* in year *t*, is the per individual seed production in the absence of neighbours, is the germination rate, and is the survival of seeds in the seed bank. The decline in population growth due to neighbours is described by the term in the denominator, where is the per capita effect of a germinant of species *j* on the seed production of a germinant of species *i* (the summation includes the intraspecific interaction as well).

For the model provided in eq. 1, Godoy and Levine (2014) following the approach of (Chesson, 2012) show that niche overlap between any pair of species, , is:   
 (Equation 2)

It reflects the average degree to which species limit individuals of their own species relative to a competitor. The stabilising niche difference is calculated as 1-ρ, and is 0 when species limits equally its own individuals and the individuals of the competitor (complete niche overlap) and 1 when species do not affect its competitor (complete niche differences). For instance, in case of no niche differentiation between competitors, ITV can increase niche differences when particular phenotypes start to diverge.

In contrast, the average fitness ratio between competitors is described as:   
 (Equation 3)

where is the annual seed production per seed lost from the seed bank due to death or germination (λ*jgj*) / 1−(1−*gi*)*si* and α*ji* and α*jj* are the per capita effects of a germinant of species *i* and species *j*, respectively, on the seed production of a germinant of species *j*. The species with higher value of eq. 3 (either or displaces the other in the absence of stabilising niche differences (Godoy and Levine, 2014).

With stabilising niche differences promoting coexistence and average fitness differences promoting competitive dominance, the condition necessary for species coexistence is (Godoy and Levine, 2014):

(Equation 4)

This condition permits both species to invade when rare. Therefore, invaders and native species can coexist when weak niche differences stabilize interactions between competitors with similar fitness differences, or the other extreme, when large niche differences overcome large fitness differences between competitors.

*Parameterizing the stabilising niche differences and fitness differences as a function of intraspecific trait variation.*

We set up a replacement series experiment, which consisted in 20 different plots in which we grew individuals of the native species against a varying proportion of viable seed mass of each invader, from 2%to 98%. These plots were combined with other 14 plots to parameterise our annual plant model for *Lasthenia* competing against each invader (see details below), obtaining estimates of species germination fraction (*gi*), per germinant fecundities in the absence of neighbours (), seed survival in the soil (*si*), and all pairwise competition coefficients (), including intraspecific competition (). Density sown was 10g of viable seed/m2, which approximates to the density usually observed at the study site. This design had a two-fold aim. First, it served to empirically determine niche (eq. 2) and fitness differences (eq. 3) between *Lasthenia* and the two invaders (*Bromus* and *Lactuca*). Second, the parameterisation of our theoretical model served in turn to investigate the ecological effects of ITV on plant invasions accounting simultaneously for all the trait variation found in *Lasthenia*.

To assess germination of viable seeds (*gi*), we placed toothpicks next to emerged individuals in repeated census of a subset of the subplots. These included plots with low (2%, 13%) and high (87%, 98%) *Lasthenia* relative abundance and 10 additional plots with no competition in which we sowed 100 viable seeds of each species. Seed bank survival (*si*) was measured by estimating seed viability before (November 2010) and after (September 2011) a growing season of burial in 10 nylon mesh bags per species (see Godoy and Levine, 2014 for details).

To assess the per germinants fecundities in the absence of neighbours () and the pairwise interactions coefficients (the ’s), which describes the per capita effects of each invaderon itself and on *Lasthenia*, we grew individuals of the invasive species in the absence of neighbours (10 plots of 0.5m2 as previously described) and with 1.2, 3.2, 7.6, 8.7, and 9.8 g/m2 of viable seed of the invader. These densities correspond to the high (76%, 87%, 98%) 10g/m2 density plots described in the previous section plus two additional plots of 2 and 4g/m2 with invader relative abundance of 80%. This combination of plots ensured a wide spread in the seeding rates of the competitor density. For the plots with no neighbours, we thinned these plots after germination to obtain individuals isolated from competition (>15 cm between individuals). For each of the five competition plots used to estimate intra- and inter-specific competitive effects, we ensured to select individuals that were either surrounded by only other individuals of the same species or by individuals of *Lasthenia*, respectively. This was accomplished by measuring the seed production (total seed mass/ average seed mass) corrected for viability in all target individuals (up to eight per plot per invasive species), and then averaging the seed production per species and plot to give an estimate of the per germinant fecundity (*Fi* ).

Afterwards, maximum likelihood methods in R version 3.3.1 (R Development Core Team 2016, function “optim”, method L-BFGS-B and log-normal error structure) were performed to fit both and (bounded to be positive) according to the function:

where had a common value independently of the competitor; was the value estimated in other plots and was the sown density of the competitor.

To assess the per capita effect of *Lasthenia* on itself and on each invader, we used the same overall approach. However, we estimated the pairwise interactions coefficients (the ’s) as a function of the intraspecific trait variation observed in *Lasthenia.* We focused on the study of two plant species traits: reproductive plant phenology, and height. From April to August 2010, we monitored bi-weekly the fruiting and the flowering of *Lasthenia.* We noted the flowering date of each individual when more than the 50% of the flowers were developing fruits. At the same time of recording flowering date, we measured the height of each individual. We measured a total of 1076 *Lasthenia* individuals. Despite measuring more than a thousand of *Lasthenia* individuals, we did not have enough replication to estimate by maximum likelihood the interaction coefficients for every value of the trait variation observed in this species.Hence*,* we pooled trait values into three ranges for each trait representing the most frequent phenotypes. The selected ranges were different depending on the identity of the competitor, as the most frequent phenotypes of *Lasthenia* whencompeting against each invader were also different. For *Lasthenia* competing against *Bromus*,phenology and height ranges were: 110-130, 140-150, and 165-175 ordinal days; and 4.0-5.9, 6.0-8.9, and 9.0-11.9 cm, respectively (Fig. 2). For *Lasthenia* competing against *Lactuca*,phenology and height ranges were: 120-130, 145-160, and 165-175 ordinal days; and 5.0-6.9, 7.0-8.9, and 9.0-10.9 cm, respectively (Fig. 2). Average *Bromus* phenology peak occurred between days 140-160 (mid May) and average *Lactuca* phenology peak occurred between days 240-260 (late August).

*Ecological effects of intraspecific trait variation on plant invasion*

We estimated how the effect of trait variation in *Lasthenia*’sresponses to intra and interspecific competition affect the dynamics of competing species compared to a scenario of average traits determining average interaction coefficients. This allow investigating the overall ecological effects of *Lasthenia* ITV on competitive outcomes against *Bromus* and *Lactuca*. For that, we separated the effects of variation in plant height from the effects in phenology.

Hart et al. (2016) shows that variation in intra and interspecific competition can be included into the annual plant model (eq.1) as follows:

(Equation 5)

where describes the joint distribution of individual variation in the intra and interspecific interaction coefficients.

To conduct these analyses, we first used eq. 5 to estimate population size of *Lasthenia* at a single-species equilibrium, as would be expected given our phenotypic measurements of all individuals across the entire experiment (excluding phenotypic classes for which we were unable to estimate alphas) (Hart et al., 2016). At this equilibrium, *Lasthenia* is considered the resident species, and hence, experiences only intraspecific competition. Second, we evaluated the ability of *Lasthenia* to maintain a positive population size during 20 generations against the invasion of each exotic species from low density. Finally, we repeated the same procedure without considering the observed variation in intra and interspecific *Lasthenia* competitive responses. The comparison of both scenarios (with and without variation in the interaction coefficients, the ’s) allows evaluating the effect of ITV on competitive outcomes. In all cases, we assumed that the population size of each of the invaders at low density was large enough to avoid stochastic processes.

*Evolutionary effects of intraspecific trait variation on plant invasion*

To explore the potential evolutionary rescue of *Lasthenia*’s ITV from competitive exclusion against the two invaders, we theoretically predicted the outcome of competitive interactions separating between each trait range and invader. This exploration assumes that *Lasthenia* trait ranges are completely heritable, and the initial population size and the strength of the directional selection is enough to stabilize ITV towards an optimum trait range. Indeed, this is a rather speculative exercise that needs further exploration, but it presents the substrate of how evolutionary studies dealing with ITV can benefit from recent advances in coexistence theory.

We used the estimates of vital rates and interaction coefficients to calculate niche differences (eq. 2), fitness differences and its two components (eq. 3), and predicted outcomes of competition between each pair of species (eq. 4). Eq. 4 summarise the criterion that two species can coexist by mutual invasibility by showing positive population growth rates when they become rare. If not, the species with higher fitness wins. Importantly, we do not present errors for the estimates of niche differences, fitness differences, and per capita population growth rate when rare because their component vital rates and interaction coefficients were estimated in different spatial locations, obscuring the meaning of their propagated error.

**RESULTS**

*Lasthenia* showed a wide non-normal intraspecific variability in plant phenology and height (Shapiro-Wilk normality test, *p*<0.001), which interestingly was associated with the invader’s identity (Kolmogorov-Smirnov test, phenology comparison D=0.2231, *p* =3.03e-11; height comparison D=0.1738, *p* =5.43e-7). Specifically, *Lasthenia* shifted its phenology to earlier phenotypes when competing against *Bromus* (the invader with similar phenology) while showed a wider spectrum of phenology and height when competing against *Lactuca* (the invader with much later phenology) (Fig. 2). These results suggest that *Lasthenia* was able to respond plastically to the two different competitive environments.

We expected that considering together the whole range of *Lasthenia’* ITV, would have ecological consequences for the dynamics of competing species. Accordingly, we found that variation in *Lasthenia* substantially increased expected single-species equilibrium population densities. These effects were large for variation in height and phenology against *Bromus* (Fig. 3 a and b), and for variation in phenology against *Lactuca* (Fig. 3 d). Effects were though negligible when individuals vary in height against *Lactuca* (Fig. 3 c). These increases in equilibrium densities were driven by Jensen’s inequality. Specifically, they occurred because population growth depends nonlinearly (convex shape) on the variation of the interaction coefficients estimated. The mathematical underlying cause is the positive averaging effect (positive second derivative) of the non-linear relationship observed, which increased the average per capita seed production. However, the benefits of individual variation for *Lasthenia* were not sufficient to reverse competitive outcomes with either invasive species. The best that ITV accomplished was to delay competitive exclusion for a few generations (Fig. 3).

Considering each range separately for a hypothetical evolutionary scenario, we observed that intra and interspecific competitive effectswere lower when *Lasthenia* individuals were taller and later in the season (Table 1). However, the change of magnitude of the effects differed again depending on the invasive species. Variation in the interspecific competitive effects of *Bromus* on *Lasthenia* was from three to twelve times higher compared to the effect of *Lactuca* on Lasthenia, and of *Lasthenia* on itself (Table 1), which in turn resulted in significant differences in how ITV modified niche and fitness differences between competitors. A significant reduction in the interspecific competitive effect of *Bromus* on *Lasthenia* increased niche differences between both speciesamong those *Lasthenia* phenotypes that were taller or increased their phenology offset with respect to *Bromus* by advancing their phenology (Table 1 and Fig. 4a). In contrast, variation in plant phenology and height barely modified niche differences between *Lasthenia* and *Lactuca*, and remained constant to almost complete niche differentiation; intraspecific effects in both *Lasthenia* and *Lactuca* were greater than interspecific effects. The effects of ITV on reducing intra and interspecific competition modified fitness differences as we expected. We observed that those individuals of *Lasthenia* that were taller and late in the season increased their competitive response ratio and therefore reduced their fitness differences with respect to both invaders (eqs. 3 and 4). This effect was especially pronounced when *Lasthenia* varied its height competing against *Bromus* (Fig. 4b).

In sum, studiedphenotypic ranges modified niche and fitness differences according to the two pathways by which *Lasthenia* could increase its likelihood of coexistence with the two invasive species (Fig. 1). Nevertheless, neither the increase in niche differentiation nor the decrease in competitive imbalance was enough to promote stable coexistence between *Lasthenia* and the two invaders for any of the trait ranges considered. Using the coexistence criterion (eq. 4, we did not find in any case that the observed niche differences were equal or higher than the theoretical niche differences needed for coexistence according to the observed fitness differences (Fig. 4).

**DISCUSSION**

Ecologists have gained renewed interest in evaluating the importance of intraspecific trait variation (ITV) for species dynamics and community assembly (Bolnick et al., 2011, Siefert et al., 2015, Hart et al., 2016) including its relevance within the context of biological invasions (Lankau, 2009, Lamarque et al., 2015). However, most of the empirical studies have not been able to frame field and experimental observations within recent advances of coexistence theory, and those able to rigorously address that link have used numerical simulations (Hart et al., 2016). Here, by combining theory with experimentation, we show that trait variation within individuals changes niche and fitness differences between competitors at the species-level and therefore modifies competitive dynamics between invasive and native species.

*Ecological effect of ITV on competitive dynamics*

From an ecological perspective, our results highlight the importance of evaluating whether exist nonlinear relationship between ITV and species responses to competition. We consistently find that variation either in phenology or in height promoted changes in *Lasthenia* responses to intra and interspecific competition, increasing the potential population densities of *Lasthenia* at single-species equilibriumand delaying its time to extinction against both invasive species, in comparison to a scenario of no ITV (Fig. 3). Yet, our results also show that not all trait variation equally promotes the ability of *Lasthenia* to reduce its competitive imbalance with respect to the exotics. Variation in phenology was most effective when *Lasthenia* was competing against *Bromus* (the invader with similar phenology), whereas variation in height was most effective when competing against *Lactuca* (the invader with bigger size) (compare Fig. 3a and b, and Fig.3 c and d), suggesting that ITV has adaptive value only depending on the competitive environment created by the presence of the specific invader. Although the literature of plant invasion and plant competition in general focuses mostly on average trait differences between species (e.g. Richards et al., 2006, Keller and Taylor, 2008, Alexander and Edwards, 2010, Matesanz and Sultan, 2013, Kraft et al., 2015), we present here evidences suggesting that future works need to include the effect of ITV on demographic rates, as Jensen’s inequality can strongly modify competitive dynamics between species.

*Effects of particular phenotypes on changing niche and fitness differences between species*

When we considered three phenotypic ranges for each trait instead of all the observed ITV, our results clearly showed that variation at the individual level has the capacity to modify average niche and fitness differences between competitors at the species level. But at the same time, the magnitude of these modifications was not equal across all ITV observed (Fig. 4), reinforcing the idea that these effects depend on the interaction between the trait and the competitor’s identity. Specifically, those individuals of *Lasthenia* taller and with later phenology increased their ability to respond to competition and therefore reduced their fitness differences. For instance, we found that a change in height of 5 cm produced the strongest effect in the reduction of fitness differences between *Lasthenia* and each of the invaders(5 times reduction against *Bromus* and 3 times reduction against *Lactuca*). These results are consistent with the fact that plant vigour is well correlated with species fitness, and plays an important role in the dynamics of plant invasions either facilitating invasion success or promoting invasion resistance (Callaway and Maron, 2006, Funk et al., 2008, Van Kleunen et al., 2010). Moreover, intraspecific variation in phenology promoted niche differences between the native species and each of the invaders, though the pattern was more evident for those early *Lasthenia* phenotypes competing against *Bromus* (Fig. 4). Early phenology individuals of *Lasthenia* reduced on average one-third their niche overlap with *Bromus* compared to late phenology individuals. These results are consistent with the idea that phenological offsets can promote invaders establishment by the use of resources unused in the native community, but this differentiation in resources depletion tends to limit the impact that the invader can have on the native community (Fargione and Tilman, 2005, Hooper and Dukes, 2010, Wolkovich and Cleland, 2010).

*Different pathways of Lasthenia exclusion*

Despite *Lasthenia* ITV modified the drivers of competitive interactions, we did not predict stable coexistence between species (Fig. 3 and 4). One important consideration is that the pathways of *Lasthenia* exclusion greatly differed between both invaders.Against *Bromus,* individuals taller in the season greatly reduced their fitness differencesbut also drove their niche differences to zero, making coexistence impossible. Similarly, *Lasthenia* individuals with delayed phenology increased their niche differences with *Bromus* but more importantly increased their competitor inferiority up to a point of making coexistence impossible again. Against *Lactuca*, *Lasthenia* maintained a high niche differentiation regardless of the trait variability displayed and its exclusion was a clear case of the impossibility of reducing fitness differences enough with respect to the invader to allow stable coexistence.

A remaining open question is whether potential changes in *Lasthenia* trait variation, producing phenotypes different to those observed would modify the general outcome of competitive exclusion in our system. A speculative exercise of extrapolation requires a separation of the ecological effects caused via Jensen’s inequality from the effects of selecting a specific trait range. For Jensen’s inequality effects, *Lasthenia* individuals could sharp the shape of the concave up relationship between variation in competitive responses and per capita seed production via an increase in ITV. For specific trait ranges, *Lasthenia* individuals of 12 cm high would stably coexist with *Bromus* by making fitness differences favourable to the native species (Fig. 4b). Even *Lasthenia* individuals with a peak of reproductive phenology at 187 ordinal days could exclude *Bromus*,assuming that niche differences after 175 days are kept constant to zero (Fig. 4a). Of course, whether these scenarios occur ultimately depends on other important factors not considered here, such as the degree of trait heritability, the size of the initial population sampled, the occurrence of stochastic events, and the directional strength of trait selection (Bell and Gonzalez, 2009). We therefore view our study as an example showing the ecological and potential evolutionary consequences of ITV in the competing dynamics between invasive and native species.

*Limitations*

This work evaluates for the first time the role of ITV on invasion dynamics from the perspective of the inferior competitor using a modern framework of coexistence theory. However, the considerable field effort needed to parameterize these models (we measured over a thousand of *Lasthenia* individuals) limited the possibility of assessing the additional effect of ITV of invasive species on the native. In principle, these effects would be similar to those observed in our native species. Invaders can benefit from ITV by increasing their population size and their competitive ability via Jensen’s inequality. Invasive dominance can additionally occur through the effect of particular phenotypes on the determinants of competitive outcomes (i.e. reducing niche differences and increasing fitness differences with respect to the native species) (Fig. 1). Undoubtedly, a more deep knowledge of the role of ITV in ecological dynamics of competing species and their link with evolutionary dynamics would require to measure the effect of ITV on both the native and the invasive species (Vasseur et al., 2011).

Another limitation of our study comes from the lack of consideration of the spatial and temporal variation in key resources for plants, mainly nutrient and water, which is characteristic of Mediterranean ecosystems (Aschmann, 1973, Cowling et al., 1996). The inclusion of drier years or locations with low nutrient availability can change the extent of ITV observed during the climatic conditions in which our experiment was conducted. For instance, a drier climate could reduce the overall ITV of *Lasthenia*, also potentially reducing the competitive advantage gained via Jensen’s inequality. Whether this is an undesirable environmental effect is unclear as the reduction in rainfall could also more strongly reduce the competitive ability of the invasive species, mainly of those species with later phenology such as *Lactuca* that are more sensitive to water shortage during summer.

Finally, a third limitation is that our study only considers competitive interactions between pairs of species, and natural communities are composed by multiple species. Currently, there are no studies addressing how trait variation within multiple native species determines resistance to plant invasions, and efforts on this regard are urgent to better understand the mechanisms of invasion success or resistance in heterogeneous environments.

*Conclusions*

There is a growing body of literature recognising that intraspecific trait variation (ITV) have important effects on the population dynamics of competing species. Our work adds critical information showing that these effects occur because ITV modifies niche and fitness differences between species. These results may prevent researchers focused on biological invasions from only considering relevant interspecific trait differences. Nevertheless, our work shows that to fully account for the effect of ITV on biological invasions we need to consider two distinct and complementary pathways: 1) the traditional evolutionary view which studies which specific phenotypic range of native or invasive species is better competitor; and 2) the much less explored the Jensen’s inequality effect, occurring when all ITV is considered together. Further studies addressing the role of ITV coming from multiple traits on invasion success in diverse communities are needed.

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**AUTHORSHIP**

OG and JML designed the study. OG and NGM conducted field work. OG, NGM and SH analysed the data. OG and NGM wrote the first draft of the manuscript with substantial contribution from SH and JML.

**DATA ACCESSIBILITY**

Data of species’ vital rates and competitive interactions as a function of *Lasthenia* intraspecific trait variation will be stored in an online repository such as Dryad upon acceptance.

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**TABLES**

**Table 1.** Intraspecific trait variation of *Lasthenia californica* in plant phenology and heightcaused different competitive effects of the native species against itself ( and of each of the two invasive species on *Lasthenia* (. Competitive effects of *Lasthenia* on *Bromus* and *Bromus* against itself were respectively 9.58 and 0.122 whereas competitive effects of *Lasthenia* on *Lactuca* and *Lactuca* against itself were respectively 0.021 and 0.049.

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| *Lasthenia* trait  ranges | Against  *Bromus* |  | x10-3 | Against  *Lactuca* |  | x10-3 |
| Phenology  (Ordinal days) | 110-130 | 3.48 | 17.56 | 120-130 | 2.32 | 2.12 |
| 140-150 | 1.99 | 6.88 | 145-160 | 0.95 | 1.94 |
| 165-175 | 0.75 | 23.75 | 165-175 | 0.75 | 7.31 |
| Height (cm) | 4.0-5.9 | 4.71 | 54.50 | 5.0-6.9 | 2.93 | 4.56 |
| 6.0-8.9 | 2.60 | 29.09 | 7.0-8.9 | 3.08 | 3.18 |
| 9.0-11.9 | 0.98 | 9.82 | 9.0-10.9 | 2.01 | 1.00 |

**FIGURE LEGENDS**

**Figure 1.** In a two-species system, an invasive and a native species can coexist if both have positive per capita population growth rates when they are at low relative abundance (rare) in a community. The native species (dashed line) cannot coexist with the invasive species (solid line) because only the invasive species show positive growth rates when rare (scenario a). There are two non-exclusive pathways by which intraspecific trait variation of a native species can change this competitive exclusion to a coexistence scenario. First, it can increase the degree of the negative slope that result from increasing stabilising processes (niche differences) (scenario b). Second, it can reduce fitness differences with respect to the invasive species in such manner to show positive growth rates when drops to low relative abundance (scenario c). Niche differences occur when intraspecific competition exceeds interspecific competition. Niche differences properties limit dominance in a system by self-limiting species at high relative frequency but prevent exclusion when they drop to low relative abundance. The stepper the negative slope, the higher the niche differences between competitors. Figure adapted from Adler et al. (2007).

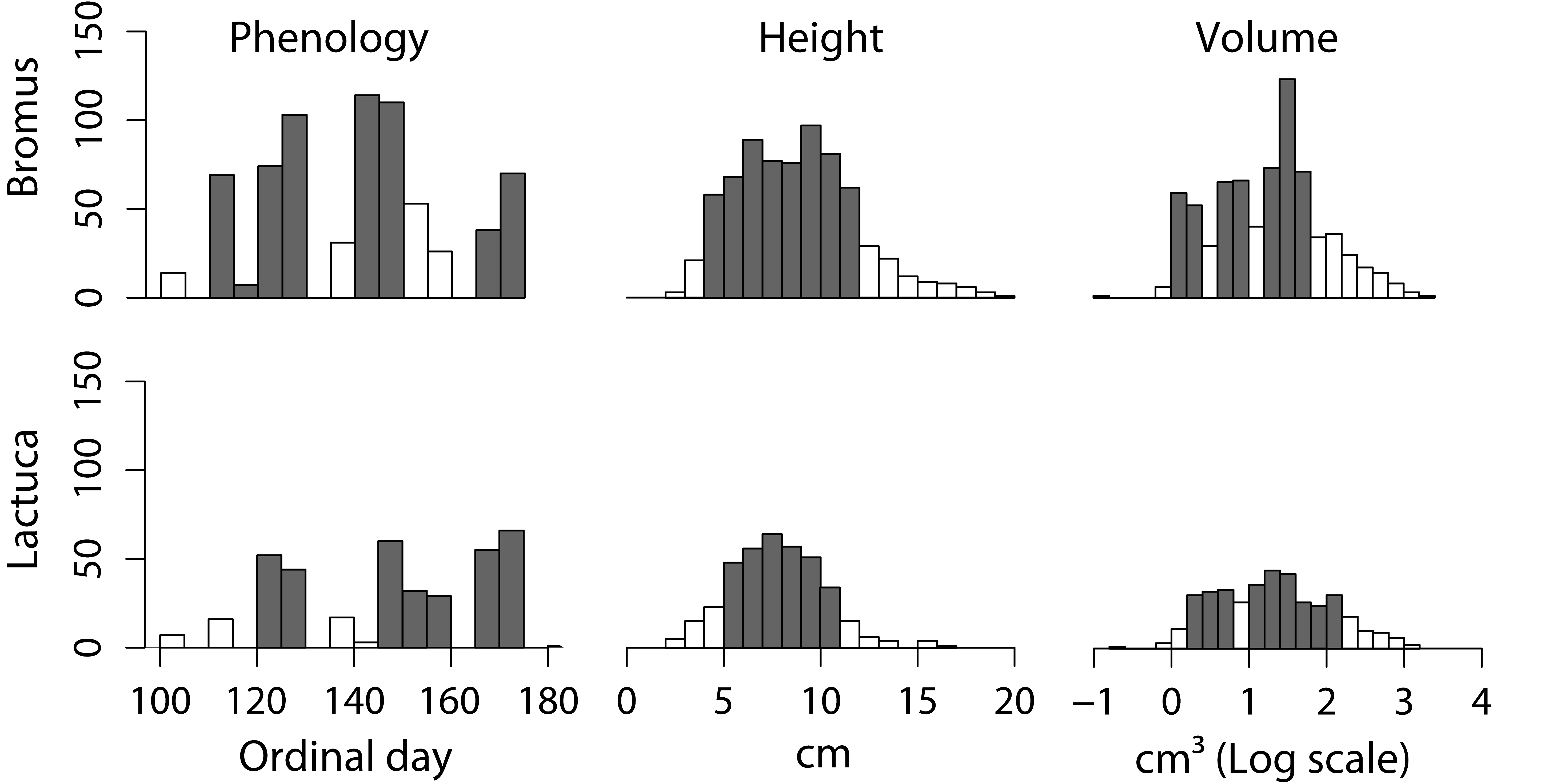
**Figure 2.** Intraspecific trait variation observed in *Lasthenia* when competing against *Bromus madritensis* (the invasive species with similar phenology to *Lasthenia*) and *Lactuca serriola* (the invasive species with much later phenology than *Lasthenia*). Grey columns indicate those phenotypic ranges selected to assess interaction effects between competitors.

**Figure 3.** Numerical simulations of population size dynamics over 20 generations with (solid lines) and without (dashed lines) considering the intraspecific trait variation showed in *Lasthenia* when competing against *Bromus* (panels a and b), and *Lactuca* (panels c and d). ITV effects were separated between phenology effects (panels a and c) and plant height effects (panels b and d). Blue lines represent *Lasthenia*’s population size. Grey lines represent invader’s population size.

**Figure 4.** Average fitness and stabilising differences for each pair of species (denoted by a single point) in the experiment. The red line separates the coexistence from the competitive exclusion region according to the coexistence criterion of eq. 4. The black and white points correspond to the three phenotypic ranges of *Lasthenia* competing against *Bromus* and *Lactuca* respectively for (a) phenology and (b) height. Note that any phenotypic range observed was enough to promote stable coexistence between *Lasthenia* and the invasive species.



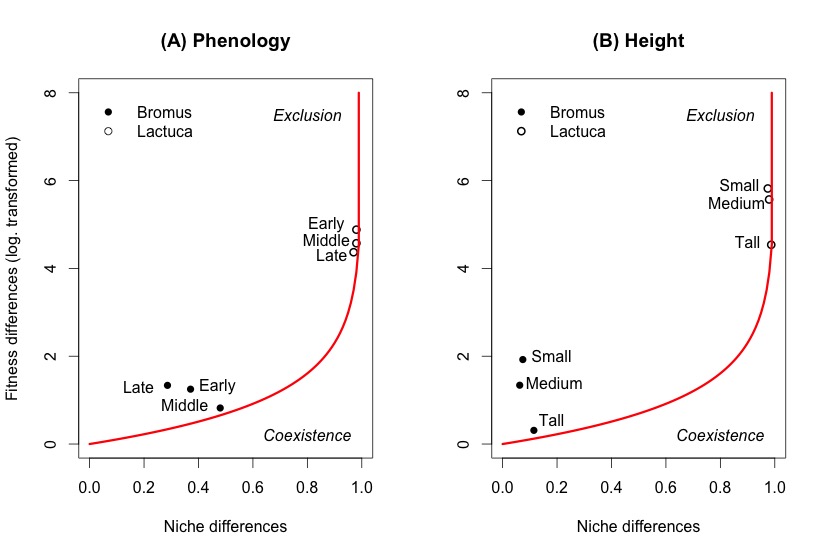
**Figure 1**



**Figure 2**



**Figure 3**



**Figure 4**