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Abstract

Exotic species are sometimes phenologically distinct from native species in the invaded community, allowing them to be active when there may be reduced competition for resources. In Southern California, annual species are particularly problematic invaders, and prior work has shown that these species germinate earlier in the growing season, giving them a competitive advantage over later-germinating native species. This result begs the question, if being active earlier is advantageous, why haven't native species adapted earlier cues for germination? We hypothesized native species would benefit less from earlier germination than exotic species (potentially due to slower growth following germination), thus negating potential selection for early germination. Here we manipulated planting time for common native and exotic species, growing them in all possible species pairs, to evaluate how competitive outcomes were altered by the time of arrival and the origin of competing species. In contrast to our hypotheses, the exotic species often had lower biomass when planted first, potentially due to disturbance when the second species was planted,. In contrast, 3 out of our 4 native species benefited from earlier planting (a priority effect). Unlike the potential benefit of arriving early, we found no evidence that being planted one week later resulted in a competitive disadvantage, when compared to being planted simultaneously with a competitor. Further, we found that the magnitude and even direction of priority effects varied depending on the identity of the interacting species. Together these results suggest that a lack of directional selection may prevent adaptation towards earlier germination times of native species. Although this experiment was conducted with a limited suite of species, the results show that the role of seasonal priority effects varies among species, and

that native species could benefit from seasonal priority effects in restoration efforts even when in competition with fast-growing exotic annual species.

Introduction

Invasions by exotic species have long fascinated ecologists as natural experiments in community assembly (i.e. Elton 1958), and the widespread ecological and economic impacts of species invasions (Pimentel et al. 2005) make it critical to develop restoration and prevention strategies based on mechanistic understandings of the factors underlying invasions. For plant invasions, major progress has been made in quantifying niche-based mechanisms enabling invasion such as enemy release (Keane & Crawley 2002), plant strategies (i.e. trait syndromes) that vary between native and invasive species (van Kleunen et al. 2010, Leishman et al. 2007), and the role of native community structure in invasion resistance (Hooper and Dukes 2010, Funk et al. 2008). In addition to these more established hypotheses, exotic species may be successful because they exploit a vacant temporal niche (Godoy et al. 2009, Wolkovich and Cleland 2011). For instance in grasslands exotic species sometimes display earlier flowering phenology (e.g. Cleland et al. 2013, Wolkovich et al. 2013) and earlier or faster germination (e.g. Marushia et al. 2010, Wilsey et al. 2011, Chrobock et al. 2011, Wainwright & Cleland 2013, Wainwright et al. 2012) than native species.

Southern California is a region where early-germinating exotic annual species have become increasingly abundant, often lowering native species diversity over time (Gilbert and Levine 2013) and altering ecosystem functioning in invaded areas (Wolkovich et al. 2010). Restoration of the native community is difficult, if not impossible, to achieve once exotic annual species are dominant (Cox and Allen 2008), suggesting that native re-establishment may be hindered by exotic species priority effects (Grman and Suding 2010, Seabloom et al. 2003). Priority effects, whereby the relative abundance of species is influenced by the order of their arrival into a system, have long been a focus of theoretical and empirical study in ecology (e.g. Belyea and Lancaster 1999, Kokko et al. 2006) and can have strong influences on plant community composition (e.g. Kardol et al. 2013, Collinge and Ray 2009, Körner et al. 2008, Fukami et al. 2005). Exotic species germinating earlier in the growing season could pre-empt resources and subsequently suppress growth by later-active native species (Marushia et al. 2010, Wainwright et al. 2012), a type of priority effect acting on a seasonal timescale. Flexibility in germination cues has been suggested to be a key advantage for species establishing outside of their native range (Hierro et al. 2009), and even small differences in germination time have been shown to confer higher fitness on earlier active species (Ross & Harper 1972, Verdu & Traveset 2005). This suggests that while earlier phenology may be contributing to exotic species success, restoration efforts could also employ priority effects to facilitate native re-establishment (Marushia et al. 2010, Wainwright et al. 2012, Abraham et al. 2009, Young et al. 2005).

In addition to the ecological significance of earlier activity for community assembly, several studies have found evidence of recent evolutionary selection for earlier flowering phenology to keep pace with climate change (Munguía-Rosas et al. 2011, Anderson et al. 2012), and that exotic species have advanced their seasonal development more than native species over the same time period (Willis et al. 2010, Wolkovich et al. 2013). Together, these patterns beg the question: if being active earlier is so advantageous, why don't native species also become active earlier? One possibility is that exotic species benefit more from priority effects than native species, potentially because of other traits such as fast growth rates (van Kleunen et al. 2010, Leishman et al. 2007) Experiments manipulating seed arrival time of native versus exotic competitors have sometimes (Dickson et al. 2012, Stevens & Fehmi 2011) but not always (Grman & Suding 2010) found that exotic species benefit more than native species from arriving earlier, and the magnitude of the effects vary widely. It is possible that the strength of priority effects may vary depending on the identities of the earlier and later arriving species, resulting in weak selection for earlier activity. These prior experiments, however, have been limited in their ability to quantify variation in the strength of priority effects among multiple competitors and multiple focal species, because priority effects are often investigated in a limiting number of species pairs.

Here, we present an experiment designed to test the hypothesis that 1) the strength of priority effects vary depending on the identity of competing species, and 2) exotic species benefit more from priority effects as compared with native species, by factorially manipulating species origin, species identity and arrival order. Later-activity in native species could also be maintained if there is less of a disadvantage to native species of later activity as compared with exotic species, thus maintaining later-active individuals in the population. The symmetry of priority effects from early arrival versus the disadvantage of secondary arrival have been surprisingly untested. Hence, we additionally tested 3) the hypothesis that the priority advantage of early arrival is proportionally greater than the disadvantage of arriving later, as compared with individuals planted at the same time.

Methods

Experimental design

This experiment was conducted at the UC San Diego Biology Field Station. We planted 8 focal species which are common in Southern California (4 each of species native and exotic to California, see Table 1) in all possible 2 species combinations (28), and orders (first, second, or simultaneously so 28 x 3 = 84), with 8 replicates of every combination (total N = 672) comparing the biomass of each species in the competing pairs. One exotic species (*Lactuca serriola*) did not germinate under field conditions, hence species pairs involving this species were omitted from the analyses of priority effects; instead these pots were used to evaluate whether planting time influenced species biomass in the absence of competition.

Germination screens were performed for all species one month prior to the experiment by sowing 50 seeds into well watered potting soils and counting the resulting germinates after 3 weeks. The number of seeds planted was scaled by germination rate to achieve a target of 15 germinated individuals of each focal species per pot. On April 9^{th} 2013, seeds of the first focal species (for priority treatments) or both focal species (for the same-time planted treatments) were sown in 21 x 3.8 cm cylindrical cone-tainer pots (Stuewe & Sons SC10). This experiment utilized sieved topsoil from a local site dominated by native coastal sage scrub vegetation. After seeds were planted each pot received 50 mL water, and pots subsequently received ambient rainfall, supplemented by daily misting with an automated watering system (approximately 8 mL per pot per day).

Seeds for the later-planted focal species (in the priority treatments) were sown one week later, on April 15^{th}. This time between planting was chosen because it corresponded to the average difference in germination time between native and exotic species observed in a prior local experiment following the first large winter rain signaling the onset of the growing season (Wainwright et al. 2012). Seeds were mixed into the top 1 cm of soil regardless of planting time, so it should be noted that later-planting seeds in the priority treatments resulted in a potential disturbance to early-planted germinated seeds.

Pots were arrayed by block on a raised outdoor platform that prevented mammalian grazing, but plants were otherwise exposed to herbivores (although qualitative observations suggest there was little herbivory). All above-ground biomass (including senesced tissue) was harvested on June 4^{th}, corresponding to 8 or 7 weeks following planting, for the same time- and early-planted versus later-planted species respectively. By this time mosts plants had reached maximum vegetative biomass prior to flowering, and some had begun to senesce. Biomass was dried for 72 hours at 40 ºC before weighing.

Statistical analysis

All data analysis was performed in the R v. 3.0.2 statistical platform (R Core Development Team 2013). First, before evaluating our hypotheses, we evaluated whether there was an impact of planting time on species performance in the *absence of competition*. Biomass was fitted to a linear model where planting order (early or later), origin of each species (native or exotic), and species identity nested within origin were included individually and in all possible interactions (with the exception of interactions involving origin x species terms). Subsequent planned comparisons between early and later planting treatments were conducted as t-tests.

To evaluate our first hypothesis that priority effects would vary with the identity of interacting species, we fitted biomass for each focal species in a linear model where planting order, focal species identity and the identity of the competiting species were included as crossed fixed factors. To evaluate our second hypothesis that exotic species could benefit more from earlier planting as compared with native species when grown in competition, biomass of each focal species was fitted to a linear mixed model where planting order, origin of the focal species, and origin of the competing species were included as factorial fixed factors. Species identity in this model is thus nested in two different factors (origin of the focal species and origin of the competitor), hence species identities in this model are accounted for by including each unique species pair as a random factor. Individual analyses were also performed for each focal species where its biomass was fitted to a model including the time of planting and origin of the competition species, where the competing species identity was included as a random factor.

To evaluate whether there was symmetry in competitive interactions by planting time (hypothesis 3), we calculated both a priority effect (biomass of a focal species when planted first minus its average biomass when planted at the same time in a given species pair) and a secondary effect (calculated similarly but using the biomass of the focal species when planted second in a given species pair, again compared to when the focal species was planted at the same time). In two species pairs there was zero germination of one species in one treatment, , and hence those pairs were omitted from this analysis. The priority effects and secondary effects were predicted with linear mixed models where Order (priority versus secondary), Origin of the focal species and Origin of the competing species were included as factorial fixed effects, and the identifier for the specific species pair was included as a random effect.

Marginal (type II) tests were used throughout. For linear models F test statistics are presented. For linear mixed model analyses X2 test statistics are presented.

Results

In the absence of competition (Table 2, Figure1), species displayed significant variation in their performance depending on whether they were planted early or one-week later (Order

$F_{1,98}$ = 7.2, p=0.008, Species $F_{5, 98}$ = 26.4, p<<0.001, Order x Species $F_{5,98}$ = 19.4, p<<0.001), which was not predictable on the basis of species origin ($F_{1,98}$ = 2.78, p=0.10). Two exotic species achieved higher biomass when planted earlier (*B. hordeaceus* and *L. multiflorum*, both annual grasses), while one exotic species (*T. hirtum*, a legume) and one native species (*L. platygosa*, an annual forb) achieved higher biomass when planted a week later. There were no differences in ending biomass for the remaining three native species.

When planted in competition, both the identity of the focal species and the identity of the competition species interacted with planting order to influence the biomass of the focal species (Order x Origin x Competitor origin χ^2=2.3, p<<0.001, Table 3), in support of our first hypothesis that the strength of priority effects would vary with the identity of interacting species. The analysis that included origin of the focal and competiting species as model terms found that while exotic species had higher ending biomass than native species (χ^2=25.9, p<<0.001), there was no consistent effect of planting order or origin of the competing species (Table 4). When species were analyzed individually (following on the significant interactions between species and planting order in Table 3), there was substantial variation among focal species in the influence of planting order, and the identity of the competing species on their ending biomass (statistics in Table 5, Figure 2). *B. hordeaceus* achieved higher biomass when competing with native species than when competing with exotic species (Competitor origin χ^2=8.46, p=0.0036), and *L. multiflorum* achieved higher biomass when planted first in competition with other exotic species, but higher biomass when planted second in competition with native species (Order x Competitor origin χ^2=7.43, p=0.006). While planting order did not otherwise influence final biomass of any exotic species, *L. playgosa* (native annual forb) tended to achieve higher biomass when planted later, and the 3 other native species (*E. californica*, *L. purshianus*, and *S. pulchra*) all had significantly higher biomass when planted early (Table 5).

Consistent with the species-level analysis of planting order, the analysis of priority effects revealed that native species in our experiment had a larger benefit than exotic species when planted early as opposed to the same time as competitors, and in fact exotic species often achieved lower biomass when planted first (Order x Origin χ^2=5.5, p=0.018, Order x Comp. Origin χ^2=6.9, p=0.008, Figure 3A, Table 6). In contrast, there was little effect of being planted second as compared to being planted at the same time as competitiors (Figure 3B).

Discussion

The earlier seasonal phenology of problematic exotic annual invaders relative to herbaceous native species has been documented in multiple locations across California, and has often been hypothesized to enable invaders to establish during a time in the growing season when there is less competition from established native species (Cleland et al. 2013, Wainwright & Cleland 2013, Wainwright et al. 2012, Marushia et al. 2010, Abraham et al. 2009). Hence, we expected to find that exotic species would benefit more from seasonal priority effects than native species. Instead we found that when planted only one week earlier, native species had a proportionally greater advantage than exotic species, compared to when they were planted at the same time as a competitor. Across all species combinations, exotic species had lower final biomass when planted one week earlier than when planted at the same time as competitors, potentially due to a detrimental effect of disturbance on newly germinated seedlings. In contrast, there was little disadvantage to being planted one week later compared with being planted at the same time as a competitor for any species. This suggests that the role of phenology in competitive interactions may be asymmetrical, and that while arriving early can be a benefit, once competition is established there may be relatively little disadvantage to arriving a short time later. This may explain how later germinating individuals can be maintained in populations, even if earlier germinating individuals have higher fitness. For instance, in an old-field community Miller (1987) found greater growth of earlier emerging individuals across multiple species (but no impact on survival), and hypothesized that earlier emergence time was not correlated with selection pressure due to low trait heritability, insufficient time to observe evolution from selection, or selection on uncorrelated traits. Significant ramifications of later arrival could emerge later in the growing season with respect to reproduction and seed viability, via interactions with pollinators, late-season herbivores or seed predators (Brody 1997), but since we ended the experiment before flowering we could not evaluate these potential effects.

When planted in the absence of competition, two fast-growing exotic annual grasses species achieved higher biomass when planted earlier; in contrast, the exotic legume and a native annual forb achieved higher biomass when planted later. These species subsequently showed variation in whether they achieved greater biomass when planted earlier versus later in competition (compare Figures 1 and 2). Studies in animal systems have shown that competition can alter the optimal timing of species introductions, for instance Alford and Wilbur (1985) found tadpoles gained an advantage from arriving earlier if in competition, but fared better if arriving later without competition. They hypothesized this was caused by a greater accumulation of food reserves in ponds without anurans early in the growing season. In our experiment, plants may have experienced greater low temperature stress (Inouye 2008) or exposure to herbivory (Hanley 1998) when planted earlier, and both of these factors have been hypothesized to potentially play a role in stabilizing selection, preventing strong selection for earlier phenology (Anderson et al. 2012).

As with any experiment, the generality of these findings are limited by the focal species, abiotic context, and length of the experiment, all of which may alter the importance of priority effects for community assembly. For instance, in a similar experiment manipulating planting order, Kardol et al. (2013) found that priority effects exerted greater control over species composition at high soil resource availability, because early-establishing species grew and pre-empted light more quickly (but see Abraham 2009, where soil N did not alter the strength of priority effects). Abiotic context (water depth) also influenced the relative strength of priority effects among vernal pool plant communities in California (Collinge and Ray 2009), with the importance of priority effects for community assembly fading over time (potentially extinguished after 10 years). In contrast, Corbin and D'Antonio (2004) found that the strength of priority effect gained by already established perennial native bunchgrasses over annual exotic grasses increased in strength over time, highlighting how the growth strategies of interacting species can alter the temporal dynamics of priority effects. In Southern California annual species are often problematic invaders in perennial-dominated native communities; in our experiment all of our exotic species are annual while two of our native species are perennial. Thus live-history and origin are confounded in our experiment, introducing important caveats to our findings.

Variation in the length of time between earlier and later introductions may explain divergent results among prior experimental studies investigating the relative strength of priority effects for native versus exotic species. For instance, both Stevens and Fehmi (2011) and Dickson et al. (2012) found that exotic species achieved significantly greater biomass gains than native species when planted three weeks earlier, and they hypothesized this difference was caused by the faster growth rates of exotic species. In contrast, Grman and Suding (2010) found large priority effects of similar magnitude when either native or exotic species were established five weeks earlier, by which time the earlier established species exerted substantial size-asymmetric competitive suppression (Weiner 1990). This suggests that even slow-growing native species can gain a priority advantage if given sufficient time to establish dominance.

In this study, we used a much smaller difference between earlier and later plantings (one week) corresponding to the observed difference in timing of emergence between focal native and exotic species observed in the field following the onset of germinating rains (Wainwright et al. 2012), although we did not quantify how this translated into differences in emergence time due to difficulties in discerning the identification of seedlings. Still, even given this small advance in planting time we found a proportionally greater advantage for earlier arriving native species than exotic species when compared to individuals planted at the same time. While this allowed us to measure the realistic magnitude of seasonal priority effects in our system under controlled experimental conditions, overall biomass of exotic species was significantly higher than native species throughout our experiment. Restoration of native plant communities in Southern California can be difficult, due to large exotic seed banks and potential for re-invasion from surrounding areas (Cox and Allen 2008). Hence, while optimizing seasonal timing for plantings is only one among many strategies that could increase native species establishment during restoration, comparison between our results and other studies suggests that restoration efforts should aim to give native species a long “head start” over their exotic competitors in order to maximize a potential native priority effect (e.g. Martin & Wilsey 2012, Abraham et al. 2009, Stevens & Fehmi 2011).

One of the main conclusions to be drawn from this experiment is that there is significant variation among species in the strength of potential priority effects, which depends on the identity both of the earlier and later arriving species. Similar studies manipulating the emergence time of native versus exotic species have not systematically varied the identities of competing pairs of species, as done in this study, but similar aquatic mesocosm studies have documented complex impacts of priority effects on community assembly (Drake 1991) and resulting ecosystem functioning (Chase 2010) depending on the dual identities of early and later arriving species. Variation in species composition among sites has often been thought of as the result of stochastic, historical contingencies in the order of species arrival, in contrast to the deterministic, niche-based processes that result in predictable community assembly processes (Belyea and Lancaster 1999). Vanette and Fukami (2014) argue that this variation in the strength of priority effects may be predictable on the basis of niche overlap between earlier and later arriving species; greater priority effects are likely to be exerted when species overlap in their resource requirements or diverge in their impacts on ecosystem function. The variation in priority effects we observed in this study could have been due to variation among species in susceptibility to herbivory, climatic stressors or disturbance, or due to variation in rates of growth and resource pre-emption. Given our very limited species pool, we could not tease apart these potential drivers of variation in priority effects, and future work should build on these hypotheses to measure species traits and patterns of species resource uptake concurrent with the temporal trajectory of species interactions.

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Table 1: Focal species utilized in the experiment, including the abbreviation used in figures, their origin relative to California, functional group, and the quantity of seeds planted per pot.

Scientific name	Abbrevation	Origin	Functional group	# seeds
Bromus hordeaceus	BRHO	Exotic	annual grass	20
Lactuca serriola	LASE	Exotic	annual forb	20
Lolium multiflorum	LOMU	Exotic	annual grass	15
Trifolium hirtum	TRHI	Exotic	annual legume	20
Escholzia californica	ESCA	Native	perennial forb	25
Layia playgosa	LAPL	Native	annual forb	50
Lotus purshianus	LOPL	Native	annual legume	25
Stipa pulchra	STPA	Native	perennial grass	30

Table 2. Linear model analysis of species performance when planted early or later in the absence of competitors. Species identity is a fixed factor nested within Origin.

Model term:	Num df	F-value	p-value
Order	**1**	**7.26**	**0.008**
Origin	1	2.78	0.10
Species(Origin)	**5**	**26.4**	**<<0.001**
Order x Origin	1	1.23	0.27
Order x Species(Origin)	**5**	**19.4**	**<<0.001**

Table 3. Linear model analysis of species biomass when planted in competition early versus later (Order), where the identity of the focal species (Species) and the Competing species are included as factorial fixed effects.

Model term	F value	(df)	p-value
Order	0.03	(1,560)	0.8651772
Species	**57.0**	**(6,560)**	**< <0.0001**
Competing species	**10.8**	**(6,560)**	**< <0.0001**
Order x Species	**4.2**	**(6,560)**	**0.0004**
Order x Comp. species	**5.5**	**(6,560)**	**< <0.0001**
Species x Comp. species	**8.1**	**(27,560)**	**< <0.0001**
Order x Species x Comp. species	**2.9**	**(27,560)**	**< <0.0001**

Table 4. Overall linear mixed-model analysis of species biomass when planted in competition early versus later, across all focal species. Here the Origin of the focal species (Origin) as well as the Competitor origin are crossed factors. Species identity nested with each origin included by treating each unique species combination as a random effect. Significant effect in bold.

Model term:	χ^2	p-value
Order	0.018	0.89
Origin	**25.9**	**<<0.001**
Competitor origin	0.055	0.81
Order x Origin	1.21	0.27
Order x Competitor origin	1.86	0.17
Origin x Competitor origin	0.31	0.57
Order x Origin x Comp. origin	2.04	0.15

Table 5. Analyses of focal species biomass when planted in competition, significant terms are in bold. A separate analysis was performed for each focal species, with the identity of the competing species included as a random effect. Model terms are indicated with the double underline.

Focal exotic species	Order	Competitor origin	Order x Comp.origin
B. hordeaceus	χ^2= 0.31, p=0.58	χ^2=8.46, p=0.0036	χ^2=0.07, p=0.78
L. multiflorum	χ^2= 1.3, p=0.25	χ^2=0.00, p=0.96	**χ^2=7.43, p=0.006**
T. hirtum	χ^2=1.9, p=0.16	χ^2=0.01, p=0.91	χ^2=0.50, p=0.47
Focal native species			
E. californica	**χ^2=3.9, p=0.048**	χ^2=1.62, p=0.20	χ^2=0.50, p=0.48
L. platygosa	**χ^2=4.61, p=0.031**	χ^2=0.00, p=0.97	χ^2=0.11, p=0.73
L. purshianus	**χ^2=6.47, p=0.011**	χ^2=0.01, p=0.94	χ^2=3.01, p=0.083
S. pulchra	**χ^2=25.7, p<<0.001**	χ^2=0.65, p=0.41	**χ^2=17.9, p<<0.001**

Table 6. Analysis of differences in biomass for focal species planted earlier than a competitor versus at the same time (priority effect), and proportional difference in biomass when planted later than a competitor versus at the same time (secondary effect). In the model, Order represents the priority effect versus secondary effect for each unique species combination. Origin indicates the focal species biomass difference, and Competitor Origin represents the origin of the competing species. In this model species pair is included as a random effect. Model terms are indicated with the double underline, significant effect in bold.

Model term:	χ^2	p-value
Order	0.017	0.89
Origin	**4.24**	**0.039**
Competitor Origin	1.14	0.28
Order x Origin	**5.53**	**0.019**
Order x Comp. Origin	**6.88**	**0.009**
Origin x Comp. Origin	1.08	0.29
Order x Origin x Comp. Origin	2.30	0.13

Figure Legends:

Figure 1. The biomass of exotic focal species (A) and native focal species (B) when planted early or one week late in the absence of competition. Species names are abbreviated as in Table 1. (*) indicates that the mean biomass for a focal species was significantly different when planted early versus later. Error bars indicate +/-1 SE of the mean.

Figure 2. The biomass of each exotic (A-C) or native (D-G) focal species when planted early or one week later. The identity of the competing species is labeled on the horizontal access of each panel; exotic species are underlined. Species names are abbreviated as in Table 1.

Figure 3. Mean priority effects (A) and secondary effects (B) for exotic (white) and native (grey) focal species when grown with exotic versus native competitors, averaged across all species. Units are in grams biomass per pot. Priority effect is calculated as the difference in biomass of the focal species when planted one week earlier than the competitor versus at the same time. Secondary effect is calculated as the difference in biomass of the focal species when planted one week later than the competitor versus at the same time.

Figure 1.

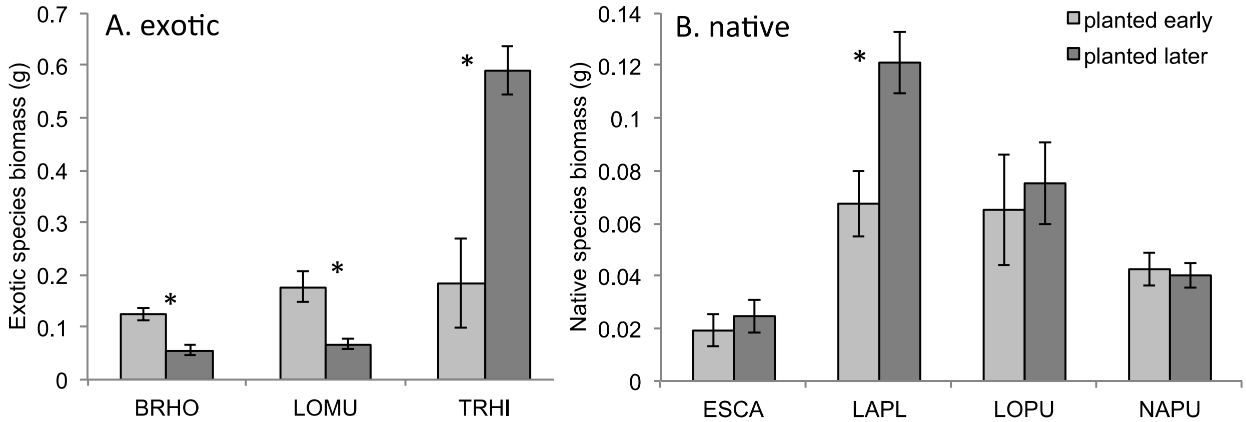
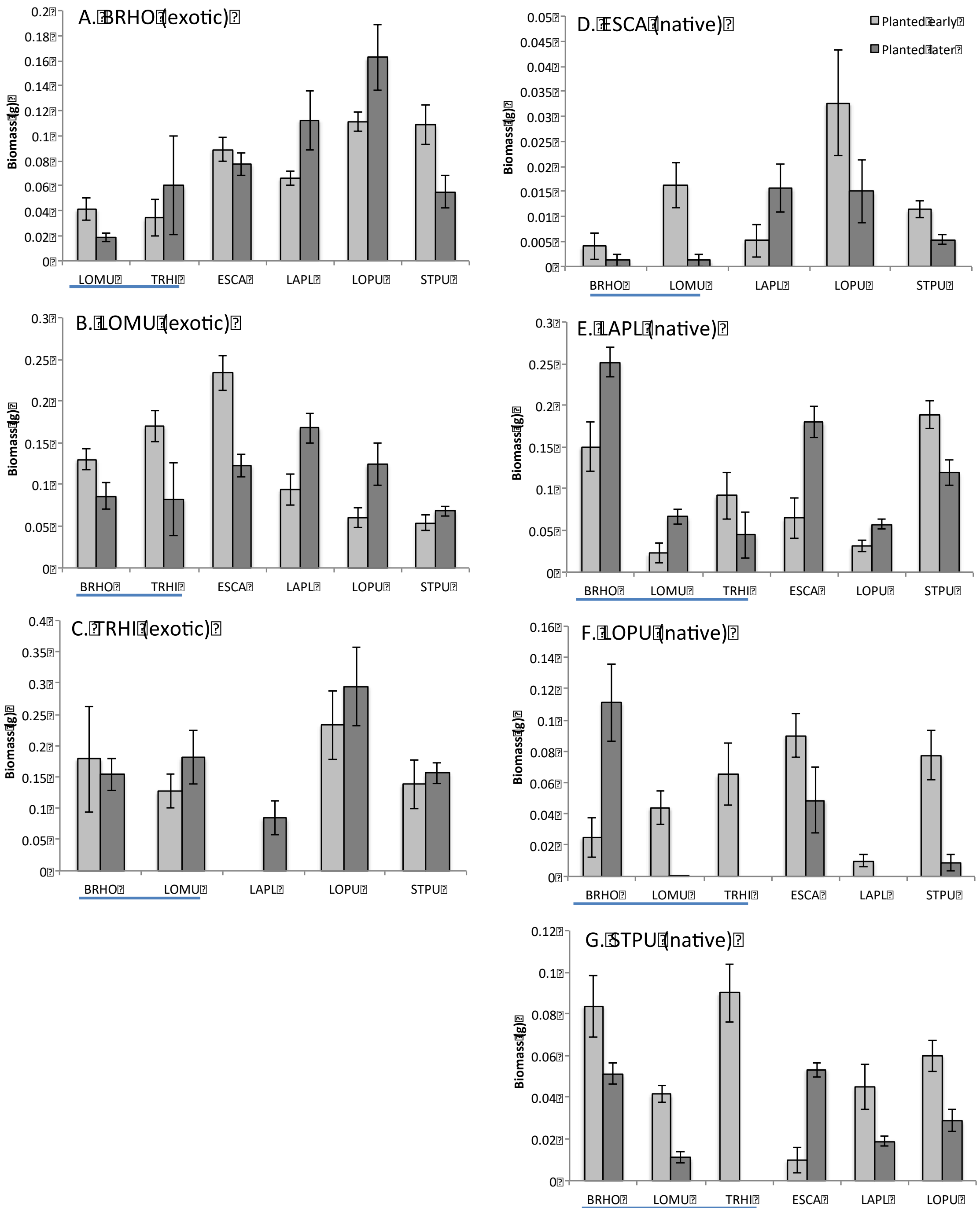

A. exotic
Exotic species biomass (g)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
*
*
*
BRHO
LOMU
TRHI
B. native
Native species biomass (g)
0
0.02
0.04
0.06
0.08
0.1
0.12
0.14
*
planted early
planted later
ESCA
LAPL
LOPU
NAPU

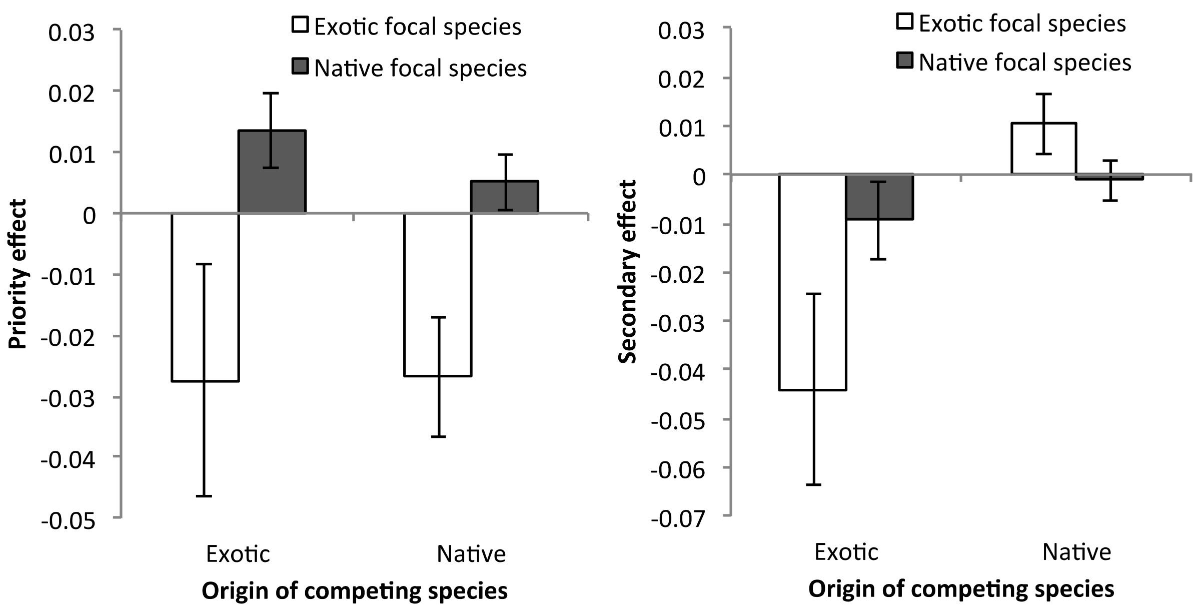
Figure 2.



A. BRHO (exotic)
B. LOMU (exotic)
C. TRHI (exotic)
D. ESCA (native)
E. LAPL (native)
F. LOPU (native)
G. STPU (native)
Planted early
Planted later
Biomass (g)
BRHO
LOMU
TRHI
ESCA
LAPL
LOPU
STPU

Figure 3.

A B



Exotic focal species
Native focal species
Priority effect
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
-0.04
-0.05
Exotic
Native
Origin of competing species
Exotic focal species
Native focal species
Secondary effect
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
-0.07
Exotic
Native
Origin of competing species