

# Priority effects: natives, but not exotics, pay to arrive late

Katharine L. Stuble<sup>1,2\*</sup> and Lara Souza<sup>2</sup>

<sup>1</sup>Department of Plant Sciences, University of California, Davis, CA 95616, USA; and <sup>2</sup>Oklahoma Biological Survey & Department of Microbiology and Plant Biology, University of Oklahoma, Norman, OK 73019, USA

## Summary

**1.** Assembly history can determine ecosystem structure and function by influencing the relative abundances of species. Priority effects (impacts associated with early arrival) likely promote the success of exotic invaders, which often arrive at larger propagule sizes and germinate earlier than native species and tend to grow more quickly. However, the potential for exotic species to tolerate late arrival is unknown.

**2.** Using a suite of native and exotic old-field plant species, we established a mesocosm experiment varying the order of species arrival to address the following question: Does plant origin influence a species' response to priority effects?

**3.** We found that, while all plant groups benefited from arriving early to a similar extent, arriving late came at a lower cost for exotic species.

**4. *Synthesis.*** We suggest that, when exploring assembly mechanisms in community ecology, the costs associated with late arrival may be as important as the benefits of arriving early. These priority effects may ultimately play a role in promoting the local success and overall distribution of exotic invaders.

**Key-words:** assembly, dominant, exotic, invasion ecology, invasive, priority effects, subordinate

## Introduction

The order in which species arrive into a community can strongly influence community composition and ultimately ecosystem structure and function by regulating access to resources (Connell & Slayter 1977; Cole 1983; Chase 2003). In particular, early arrival can benefit species by both controlling size-asymmetric competition (Ejrnæs, Bruun & Graae 2006; Körner *et al.* 2008; Grman & Suding 2010) and plant-soil feedbacks (Grman & Suding 2010; van de Voorde, van der Putten & Bezemer 2011). These priority effects are typically thought of in terms of the benefits received by those species arriving early. However, it is also possible that some species may be adept at acquiring resources even in the presence of an already established community. Thus, the ability to proliferate despite later arrival into a community may be an important driver of the strength of priority effects. We can think about the costs incurred by late-arriving species as the other half of the priority effects equation, working in tandem with the benefits associated with the success of early-arriving species to drive community composition. In fact, the strength of priority effects is determined by the extent to which a

species alters the environment, but also by overlap in resource use among species and the ability of a species to tolerate environmental changes (Tan *et al.* 2012; Vannette & Fukami 2014). These latter two mechanisms have the potential to alter how species tolerate late arrival.

Priority effects have been suggested to influence the success of exotic species (Kardol, Souza & Classen 2013; Young *et al.* 2015). In addition to arriving early, germinating quickly and possessing a generally advanced phenology (Wilsey, Daneshgar & Polley 2011; Wainwright, Wolkovich & Cleland 2012), exotic species may benefit from priority effects more strongly than do native species (Dickson, Hopwood & Wilsey 2012; Wilsey, Barber & Martin 2015), potentially amplifying the spatial-temporal distribution and ecological impacts of exotic species across the landscape. However, exotic species may also be particularly capable of successfully establishing in existing communities. Specifically, traits that tend to be common among exotic species, such as strong competitive abilities and quick growth rates (Rejmanek & Richardson 1996; Levine *et al.* 2003; Van Kleunen, Weber & Fischer 2010), may ultimately limit the consequences exotic species experience as a result of late arrival. Similarly, exotic species may be more tolerant of resource-limited environments relative to natives, also lowering the cost of late arrival (Daehler 2003).

\*Correspondence author. E-mail: klstuble@gmail.com

Priority effects can ultimately influence community trajectories, having long-lasting impacts on community composition (Chase 2003; Porensky, Vaughn & Young 2012; Vaughn & Young 2015). These dynamics are important as resident native and exotic species typically differ in regard to their impacts on community dynamics and ecosystem function (Vilá *et al.* 2011). Exotic species lack a co-evolutionary history with co-occurring native species, potentially allowing introduced exotics to have larger impacts on community dynamics and ecosystem processes than do invading native species (Pyšek *et al.* 2012; Simberloff *et al.* 2012; Ricciardi *et al.* 2013). Therefore, it is important to understand the interplay between priority effects and plant species origin to fully understand species coexistence and the extent to which these factors may drive community dynamics and ultimately determine ecosystem structure and function.

Here, we used a glasshouse mesocosm study to examine the relative benefits of arriving early and the costs of arriving late across a suite of exotic and native old-field plant species representing one of two dominance categories (dominant or subdominant) and four common functional groups (C<sub>3</sub> graminoids, C<sub>4</sub> graminoids, forbs and nitrogen-fixers). We predicted that exotic species would be better able to cope with late arrival than would native species, exhibiting the least loss in biomass as a result of late arrival.

## Materials and methods

### STUDY SYSTEM

We selected the 16 plant species used in this glasshouse study based on their co-occurrence across several old-field plant communities at the Three Bend Scenic Wildlife Management Refuge Area as part of the Oak Ridge National Environmental Research Park near Oak Ridge, TN (35–58' N, 84–17' W) (Souza *et al.* 2011). We purposefully selected equal numbers of locally dominant and subdominant species from both native and exotic classifications. According to previous plant surveys, old-field communities at our site consisted of 142 plant species, with 106 species being native and 36 exotic. Plant species were classified into four groups based on their reported per cent foliar cover and invasion status: native dominant, native subdominant, exotic dominant and exotic subdominant (Table 1). We used the USDA Plant Database to determine plant origin (e.g. native and exotic) and foliar cover to determine local dominance status (dominant vs. subdominant across local field sites) (e.g. Rabinowitz & Rapp 1981; Mariotte 2014). Subdominant species were common (occurring across sites), but at low abundances within these sites. Each of these four groups was composed of four species, with one

species from each of the following functional groups typical of old-field communities: C<sub>3</sub> grass, C<sub>4</sub> graminoid, forb and nitrogen fixer (N-fixer) (Table 1, see Table 2 for exact planting combinations). All species were perennials. Using the glasshouse for this experiment placed all of the study species under novel conditions, but the non-native species still lack an evolutionary history with the natives. This logic has frequently been used for conducting such studies of non-native species in the glasshouse (e.g. Körner *et al.* 2008; Dickson, Hopwood & Wilsey 2012; Kuebbing *et al.* 2015).

### EXPERIMENTAL DESIGN

We started plants from seed (purchased from American Meadows, Williston, VT, USA; Ernst Seed, Meadville, PA, USA; Everwilde Farms, Bloomer, WI, USA; Prairie Moon Nursery, Winona, MN, USA; and Roundstone Native Seed, Upton, KY, USA) on potting mix (Sun Gro Metro-Mix 366-P; SunGro Horticulture, Agawam, MA, USA) in the glasshouse in early June 2014. These seedlings were assembled into mesocosm-based communities contained in 18.5 cm (height) × 25 cm (diameter) pots on potting soil in one of two basic planting treatments. In 'ordered' treatments, we planted a single 4-week-old seedling of each of four species (a mix of exotics and natives) (early arrival) and then added a single 6.5-week-old seedling of each of the remaining twelve species eighteen days later (late arrival) to create mesocosms that ultimately contained all 16 of the study species (one individual of each). In the control treatment, we added a single seedling of all 16 species to the mesocosm at the time of the early planting. We selected species for early planting such that each group of four species contained a dominant native, a dominant exotic, a subdominant native and a subdominant exotic (but a random combination of functional groups). Each group combination was unique (i.e. there were no replicates with the exact same four species in the early cohort), and each species appeared in six early cohorts. We had 24 communities assembled by the ordered treatment, and six control communities in which all species were added at the same time (Table 2). We kept these mesocosms under glasshouse conditions (the temperature of the glasshouse fluctuated between 21 and 31 °C during night and day, respectively, and the relative humidity was maintained at approximately 55%) and watered them to the point of saturation once daily for 2 months after the early planting. At the end of the experiment, we harvested, sorted by species and weighed above-ground biomass for each species after drying 48 h at 65 °C in a forced-air oven.

It is fairly common to use seedlings in experiments testing priority effects, as we do here (e.g. Maron & Marler 2008; Kardol, Souza & Classen 2013). We made the decision to establish our communities using seedlings as opposed to seeds in order to tightly control the difference in arrival time. Using seeds, variability in germination time would have confounded our results by conflating our imposed arrival treatment (in which both native and exotic species were planted

**Table 1.** Plant species classifications

	Dominant native	Dominant exotic	Subdominant native	Subdominant exotic
C3 forb	<i>Solidago canadensis</i> L.	<i>Plantago lanceolata</i> L.	<i>Ludwigia alternifolia</i> L.	<i>Chrysanthemum leucanthemum</i> Lam.
C3 graminoid	<i>Carex frankii</i> Kunth	<i>Dactylis glomerata</i> L.	<i>Elymus virginicus</i> L.	<i>Phleum pratense</i> L.
C4 graminoid	<i>Panicum clandestinum</i> (L.) Gould	<i>Festuca pratensis</i> (Huds.) P. Beauv.	<i>Tridens flavus</i> (L.) Hitchc.	<i>Cynodon dactylon</i> (L.) Pers.
N fixer	<i>Desmodium rotundifolium</i> DC.	<i>Lespedeza cuneata</i> (Dum. Cours.) G. Don	<i>Desmanthus illinoensis</i> (Michx.) MacMill.	<i>Trifolium repens</i> L.



2 weeks early) with germination times, as exotic species tend to germinate earlier and more prolifically (Wilsey, Barber & Martin 2015).

#### STATISTICAL ANALYSIS

To understand the benefit each species received from arriving in the early group and the cost to each species associated with arriving in the late group, we examined effect sizes calculated as log response ratios (Hedges, Gurevitch & Curtis 1999). We calculated the benefit of arriving early as  $\ln(\text{mass with early arrival/mass in control group})$  and the cost of arriving late as  $\ln(\text{mass with late arrival/mass in control group})$ . We conducted 2–3-way ANOVAs and Tukey's HSD to examine the variation in the benefit associated with (i) arriving early (log response ratio) and (ii) the cost associated with arriving late, across dominance (high abundance or low abundance), origin (native or exotic) and functional groups ( $C_3$  graminoid,  $C_4$  graminoid, forb, N-fixer). This was a balanced design, with equal numbers of dominant and subordinate/exotic and native species. ANOVAs were run based on type III sums of squares using the car package in R (Fox & Weisberg 2011). None of the interaction terms were significant and so were removed from the model. Additionally, we treated species as independent units, even though they co-occurred with one another in pots, thus experiencing the same environmental conditions. This is a common limitation to community-level studies (e.g. Hoelzle, Jonas & Paschke 2012; Kardol, Souza & Classen 2013), though we have tried to mitigate this limitation by replicating the experiment using unique combinations of early-arriving species.

#### Results

Plant species were  $2 \times$  larger when arriving early and  $9 \times$  smaller when arriving late relative to the control group, irrespective of functional group, origin or dominance. However, when we examined the magnitude of the benefit conferred by arriving as a part of the early group as compared to the control group ( $\ln(\text{early arrival/control})$ ), we found no significant differences among functional groups, invasion status or dominance (Table 3a) (Fig. S1 in Supporting Information). However, the cost associated with arriving late ( $\ln(\text{late arrival/control})$ ) was unequal across species (Fig. 1). Specifically, the cost of arriving late was much higher (i.e. more negative) for native species relative to exotic species (Table 3b; Fig. 2a). There was also a marginally significant difference in the response to late arrival across functional groups, with  $C_3$  graminoids experiencing the highest cost associated with late arrival, while  $C_4$  grasses and N-fixers experienced less cost associated with late arrival (Fig. 2b). Dominant and subordinate species did not differ significantly in the strength of their response to late arrival (Fig. 2c).

#### Discussion

We found strong negative effects of late arrival on plant growth, and the magnitude of these effects varied across plant species. Specifically, the growth of exotic species was damped to a lesser degree as a result of late arrival than was the growth of native species. We also found, perhaps unsurprisingly, that all species grew larger when arriving early. Contrary to expectations, however, the magnitude of the

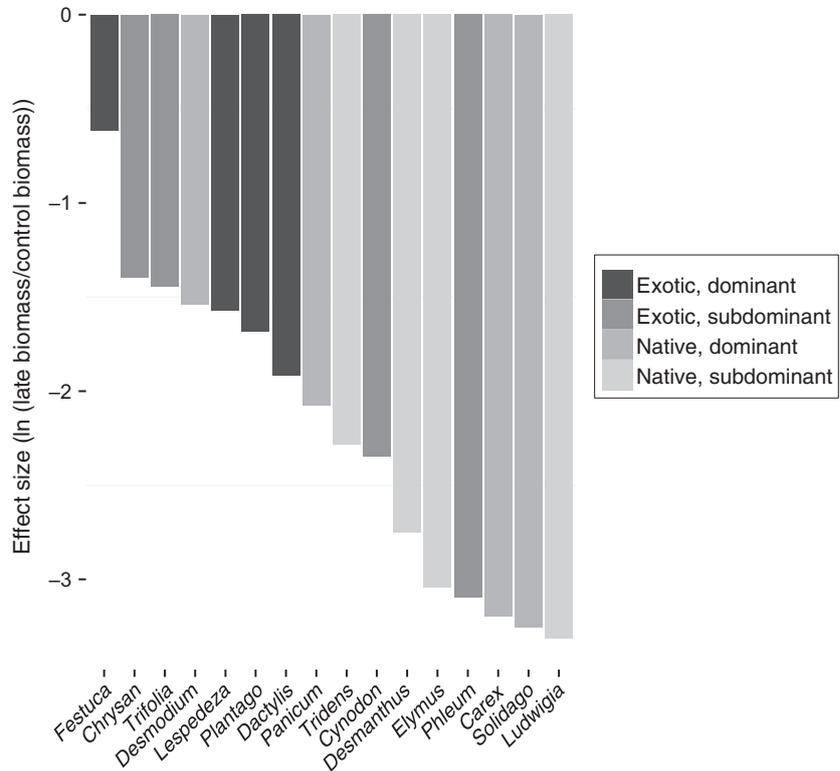
**Table 3.** ANOVA table of a) benefit associated with arriving in early group and b) cost associated with arriving in late group across species groups

Factor	d.f.	F-value	P-value
(a) $\ln(\text{early/control})$			
Dominance	1, 10	0.82	0.39
Invasion status	1, 10	0.14	0.72
Functional group	3, 10	0.97	0.45
(b) $\ln(\text{late/control})$			
Dominance	1, 10	3.05	0.11
Invasion status	1, 10	11.31	0.01
Functional group	3, 10	3.09	0.08

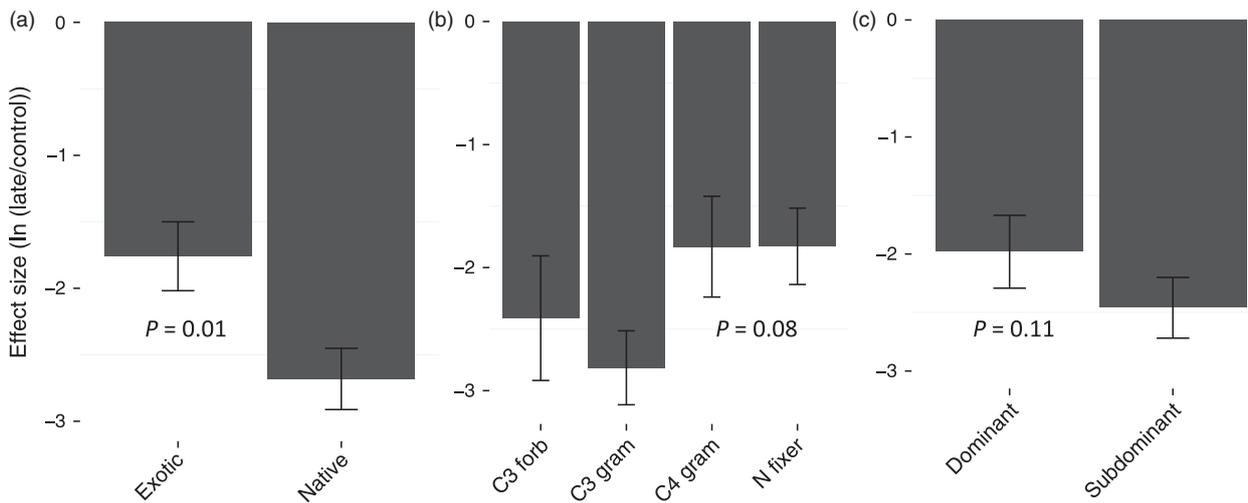
benefit these species received from early arrival did not differ across groups (native v. exotic; dominant v. subordinate; functional groups). Unlike growth, priority did not differentially affect survival across exotic and native species (Appendix S1). These findings are important as priority effects can drive community composition (Körner *et al.* 2008; Porensky, Vaughn & Young 2012; Vaughn & Young 2015). Our finding that exotic species do not benefit from priority to a greater extent than natives is likely driven, in part, by the fact that we used seedlings instead of seeds to propagate our mesocosms, thereby eliminating the priority advantage conferred to exotics by their generally quicker rate of germination and focusing instead on the relative potential for both native and exotic species to capitalize on early arrival in a community. In the case of exotic species, it is often postulated that at least part of their success arises as a result of priority effects: the benefit exotic species gain from arriving (Maron & Marler 2008) and germinating early (Wainwright, Wolkovich & Cleland 2012; Wilsey, Barber & Martin 2015). To be sure, the ability of exotics to occupy open habitat early and in high abundances can contribute to their ability to invade.

Vannette & Fukami (2014) suggest that the strength of priority effects are not driven solely by the impact a species has on resource levels, but also by a species' sensitivity to environmental shifts and overlap between competing species in resource needs. Thus, in addition to being driven by the advantage received by early arrival, the strength of priority could presumably work on the back end, allowing some species to cope better with late arrival than others. In fact, species introduced into already populated communities tend to establish at relatively low abundances, but establishment success can vary substantially across species with important implications for community composition (Burke & Grime 1996; Moles & Westoby 2002).

Though there is evidence that exotic species may benefit from early arrival to a greater extent than do natives (Dickson, Hopwood & Wilsey 2012), some studies have found no difference in the strength of priority benefits incurred by native and exotic plant species (Cleland, Esch & McKinney 2015). Such differences in results among studies likely stem from important differences among species and study systems, such as potentially different effects of priority on annual and perennial-dominated systems (the Dickson, Hopwood &



**Fig. 1.** Effect size representing the cost associated with late arrival (as compared to arrival in the control group) across all 16 study species. Fill colour indicates origin and commonness. There was a significant cost of arriving late (as compared to arrival in the control group) for 16 old-field plant species. However, the cost of arriving late was generally lower for exotic species compared to native species, regardless of dominance status.



**Fig. 2.** Effect size representing the cost associated with late arrival (compared to arrival in the control group) for (a) native vs. exotic species, (b) the four functional groups and (c) dominant vs. subdominant species. We found that (a) the cost was significantly greater for native species relative to exotic species, (b) C3 graminoids and forbs had marginally greater costs associated with late arrival relative to C4 graminoids and nitrogen-fixers, and (c) subdominant species exhibited higher costs associated with late arrival relative to dominance species, though the effect was not significant.

Wilsey (2012) study took place in a perennial-dominated system, while the Cleland, Esch & McKinney (2015) study was in an annual-dominated grassland in which only two of the eight study species were perennials). Our study provides a potential avenue by which priority effects may promote the success of exotic species, even in the absence of a strong benefit associated with early arrival. There are at least two possible mechanisms for the enhanced ability of exotic

species to tolerate late arrival over native species. First, exotic species may be more tolerant of low concentrations of resources (Byers 2000), thereby allowing them to thrive when arriving in a community in which other individuals are already usurping resources. That is to say, exotic species may be particularly adept at tolerating high levels of competition. Alternatively, exotic species may compete more strongly with native species than natives do with exotics

(Petren & Case 1996; Maron & Marler 2008), thereby making it more difficult for native species to garner adequate resources in a community already populated with exotic species.

Functional traits are known to influence community assembly (Kraft *et al.* 2014). We therefore conducted this experiment using native and exotic species from a range of functional groups. Across invasion status and dominance, we found C<sub>3</sub> graminoids were negatively impacted by late arrival to a greater extent than were C<sub>4</sub> graminoids and nitrogen-fixing forbs. Dickson, Hopwood & Wilsey (2012) found that C<sub>3</sub> grasses benefited the least from priority, while legumes benefited the most, which, combined with our results, may suggest that at establishment stages N-fixers may be particularly robust, benefiting from arriving early but paying little to arrive late.

Mesocosm studies such as the one described here have both benefits, as well as limitations. The glasshouse allowed us to closely control abiotic conditions, as well as important biotic factors such as herbivory that can differentially affect native and exotic species (Agrawal & Kotanen 2003; HilleRisLambers *et al.* 2010). However, in the context of the glasshouse, exotic species were only exotic in respect to their lack of co-evolutionary history with our native species. It is also impossible to know whether the observed size discrepancies would lessen over time, though we believe that the fact that exotic species seem to experience less slowed growth in response to late arrival compared to native species is likely indicative of an important community dynamic with lasting consequences for community composition. In fact, longer-running studies of priority effects have found that qualitative results did not change substantially after 2 months (Kardol, Souza & Classen 2013) and the effects of priority can be detected after multiple growing seasons and harvests (Körner *et al.* 2008; Vaughn & Young 2015). The timing of arrival also has the potential to influence our results. In this study, our early arrivers were added 2.5 weeks before late-arriving species, which is well within the typical range of 1–3 weeks often used in studies of priority (Dickson, Hopwood & Wilsey 2012; Kardol, Souza & Classen 2013; Cleland, Esch & McKinney 2015). However, we might imagine that increasing the time between the addition of early- and late-arriving species may serve to strengthen priority effects, though 2.5 weeks seems to be enough to elicit effects (Kardol, Souza & Classen 2013). Finally, we note that the species establishing the greatest biomass were a mixture of native (*Ludwigia* and *Solidago*) and exotic species (*Cynodon*), thereby limiting the possibility that more robust exotic species may be driving the results of this experiment.

Arriving early is generally beneficial to species, but we suggest ecologists consider the costs associated with arriving late, as well. In some cases, it may not be the benefits associated with early arrival that set some species apart as much as the differences in their ability to tolerate arriving late. This differential ability to tolerate arriving in a community already populated by competitors may drive how priority effects shape communities. The potential for exotic species to arrive

late with little cost may provide a secondary mechanism via which priority effects aid in the success of exotic species.

## Acknowledgments

We thank K. Bacon, M. Morrison and M. Schartz for help in the greenhouse. We also thank J. Chase, S. Kuebbing and D. Simberloff for feedback that helped to improve this manuscript. Funding support was provided by the Junior Faculty Fellowship Program at the University of Oklahoma to LS.

## Data accessibility

Biomass data are archived with the Oklahoma Biological Survey and can be accessed on their website at [http://biosurvey.ou.edu/StubleandSouza2016/PriorityData\\_Archive.xlsx](http://biosurvey.ou.edu/StubleandSouza2016/PriorityData_Archive.xlsx).

## References

- Agrawal, A.A. & Kotanen, P.M. (2003) Herbivores and the success of exotic plants: a phylogenetically controlled experiment. *Ecology Letters*, **6**, 712–715.
- Burke, M.J.W. & Grime, J.P. (1996) An experimental study of plant community invasibility. *Ecology*, **77**, 776–790.
- Byers, J.E. (2000) Competition between two estuarine snails: implications for invasions of exotic species. *Ecology*, **81**, 1225–1239.
- Chase, J.M. (2003) Community assembly: when should history matter? *Oecologia*, **136**, 489–498.
- Cleland, E.E., Esch, E. & McKinney, J. (2015) Priority effects vary with species identity and origin in an experiment varying the timing of seed arrival. *Oikos*, **124**, 33–40.
- Cole, B.J. (1983) Assembly of mangrove ant communities: patterns of geographical distribution. *Journal of Animal Ecology*, **52**, 339–347.
- Connell, J.H. & Slayter, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *The American Naturalist*, **111**, 1119–1144.
- Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plant: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 183–211.
- Dickson, T.L., Hopwood, J.L. & Wilsey, B.J. (2012) Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biological Invasions*, **14**, 2617–2624.
- Ejmaes, R., Bruun, H.H. & Graae, B.J. (2006) Community assembly in experimental grasslands: suitable environment or timely arrival? *Ecology*, **87**, 1225–1233.
- Fox, J. & Weisberg, S. (2011) *An (R) Companion to Applied Regression*, 2nd edn. Sage, Thousand Oaks, CA, USA.
- Grman, E. & Suding, K.N. (2010) Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. *Restoration Ecology*, **18**, 664–670.
- Hedges, L.V., Gurevitch, J. & Curtis, P.S. (1999) The meta-analysis of response ratios in experimental ecology. *Ecology*, **80**, 1150–1156.
- HilleRisLambers, J., Yelenik, S.G., Colman, B.P. & Levine, J.M. (2010) California annual grass invaders: the drivers or passengers of change? *Journal of Ecology*, **98**, 1147–1156.
- Hoelzle, T.B., Jonas, J.L. & Paschke, M.W. (2012) Twenty-five years of sagebrush steppe plant community development following seed addition. *Journal of Applied Ecology*, **49**, 911–918.
- Kardol, P., Souza, L. & Classen, A.T. (2013) Resource availability mediates the importance of priority effects in plant community assembly and ecosystem function. *Oikos*, **122**, 84–94.
- Körner, C., Stöcklin, J., Reuther-Thiébaud, L. & Pelaez-Riedl, S. (2008) Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist*, **177**, 698–705.
- Kraft, N.J.B., Crutsinger, G.M., Forrester, E.J. & Emery, N.C. (2014) Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. *Oikos*, **123**, 1391–1399.
- Kuebbing, S.E., Classen, A.T., Sanders, N.J. & Simberloff, D. (2015) Above- and below-ground effects of plant diversity depend of species origin: an experimental test with multiple invaders. *New Phytologist*, **208**, 727–735.
- Levine, J.M., Vilà, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions.

- Proceedings of the Royal Society of London B: Biological Sciences*, **207**, 775–781.
- Mariotte, P. (2014) Do subordinate species punch above their weight? Evidence from above- and below-ground. *New Phytologist*, **201**, 16–21.
- Maron, J.L. & Marler, M. (2008) Field-based competitive impacts between invaders and natives at varying resource supply. *Journal of Ecology*, **96**, 1187–1197.
- Moles, A.T. & Westoby, M. (2002) Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos*, **99**, 241–248.
- Petren, K. & Case, T.J. (1996) An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology*, **77**, 118–132.
- Porensky, L.M., Vaughn, K.J. & Young, T.P. (2012) Can initial intraspecific spatial aggregation increase multi-year coexistence by creating temporal priority? *Ecological Applications*, **22**, 927–936.
- Pyšek, P., Jarošík, V., Hulme, P.E., Pergl, J., Hejda, M., Schaffner, U. & Vilá, M. (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18**, 1725–1737.
- Rabinowitz, D. & Rapp, J.K. (1981) Dispersal abilities of seven sparse and common grasses from a Missouri prairie. *American Journal of Botany*, **68**, 616–624.
- Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1661.
- Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, **83**, 263–282.
- Simberloff, D., Souza, L., Nuñez, M.A., Barrios-Garcia, M.N. & Bunn, W. (2012) The natives are restless, but not often and mostly when disturbed. *Ecology*, **93**, 598–607.
- Souza, L., Bunn, W.A., Simberloff, D., Lawton, M. & Sanders, N.J. (2011) Biotic, abiotic, and landscape factors influence exotic plant richness across spatial scales in old-field communities. *Functional Ecology*, **25**, 1106–1112.
- Tan, J., Pu, Z., Ryberg, W.A. & Jiang, L. (2012) Species phylogenetic relatedness, priority effects, and ecosystem functioning. *Ecology*, **93**, 1164–1172.
- Van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **12**, 235–245.
- Vannette, R.L. & Fukami, T. (2014) Historical contingency in species interactions: towards niche-based predictions. *Ecology Letters*, **17**, 115–124.
- Vaughn, K.J. & Young, T.P. (2015) Short-term priority over exotic annuals increases the initial density and longer-term cover of native perennial grasses. *Ecological Applications*, **25**, 791–799.
- Vilá, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y. & Pyšek, P. (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–708.
- van de Voorde, T.F.J., van der Putten, W.H. & Bezemer, T.M. (2011) Intra- and interspecific plant-soil interactions, soil legacies and priority effects during old-field succession. *Journal of Ecology*, **99**, 945–953.
- Wainwright, C.E., Wolkovich, E.M. & Cleland, E.E. (2012) Seasonal priority effects: implications for invasion and restoration in a semi-arid system. *Journal of Applied Ecology*, **49**, 234–241.
- Wilsey, B.J., Barber, K. & Martin, L.M. (2015) Exotic grassland species have stronger priority effects than natives regardless of whether they are cultivated or wild genotypes. *New Phytologist*, **205**, 928–937.
- Wilsey, B.J., Daneshgar, P.P. & Polley, H.W. (2011) Biodiversity, phenology and temporal niche differences between native and novel exotic-dominated grasslands. *Perspectives in Plant Ecology, Evolution and Systematics*, **13**, 265–276.
- Young, T.P., Zefferman, E.P., Vaughn, K.J. & Fick, S. (2015) Initial success of native grasses is contingent on multiple interactions among exotic grass competition, temporal priority, and effect size. *AoB Plants*, **7**, plu081.

Received 4 December 2015; accepted 5 April 2016

Handling Editor: Meghan Avolio

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Effect size indicating the benefit associated with early arrival as compared with arrival in the control group by (A) invasion status; B) functional group; and C) rarity.

**Appendix S1.** Analysis of seedling survival across treatments.

**Table S1.** ANOVA table of percent of individuals surviving across treatments, functional groups, invasion status and dominance.