Timing is everything: does early and late germination favor invasions by herbaceous alien plants?

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Abstract

\textbf{Aims}
Plant invasions represent a unique opportunity to study the mechanisms underlying community assembly rules and species distribution patterns. While a superior competitive ability has often been proposed as a major driver of successful plant invasions, its significance depends crucially on the timing of any competitive interaction. We assess whether a mismatch in germination phenology can favor the establishment of alien species, allowing them to exploit vacant niches where competition is low. As well as having important effects on the survival, growth and fitness of a species, asymmetric competition and potential soil legacies resulting from early or late germination can also impact on species recruitment. However, early or late germination comes at a cost, increases the risks of exposure to unfavorable conditions and requires an enhanced abiotic resistance if it is to lead to successful establishment.

\textbf{Important Findings}
While there are several anecdotal accounts of early and late germination for invasive species, there are limited comparative data with resident species growing under natural conditions. Available evidence from grassland communities indicates that a short-term germination advantage or priority (few days/weeks) provides invasive species with a strong competitive advantage over native species and is a critical factor in many invasions. While the exploitation of periods of low competition is a plausible mechanism for the successful establishment of many invasive plants, direct evidence for this strategy is still scarce. This is particularly true with regard to the exploitation of late germination niches. Consequently, long-term comparative monitoring of the germination phenology of invasive and native plants \textit{in situ} is needed to assess its significance in a range of ecosystems and its impact on community dynamics.

\textbf{Keywords:} competition, germination, invasive plants, phenology, temporal niche

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INTRODUCTION

Addressing the global issue represented by invasions by alien plants requires understanding the key processes and mechanisms that may promote or hamper their establishment and spread following their introduction into novel geographic ranges. The invasion success of many alien plants is attributed to their superior competitive ability, given the capacity of many to form a larger biomass and grow faster (Daehler 2003; Dawson \textit{et al.} 2011; Elton 1958; Levine \textit{et al.} 2003), often under suboptimal conditions (Funk 2013; Funk and Vitousek 2007) and/or to benefit disproportionately more than native species from increases in resources (Daehler 2003; Dawson \textit{et al.} 2011; Funk 2013; see Gioria and Osborne 2014 for a review). However, invasive species are not necessarily strong competitors (Funk 2013; Funk and Vitousek 2007) and there is evidence that invasive species can be outcompeted by native (Corbin and D’Antonio 2004; Mangla \textit{et al.} 2011; McGlone \textit{et al.} 2012) or other invasive species in the longer term (Gioria \textit{et al.} 2011).

While several studies have compared the competitive abilities of alien and native species, only few studies have accounted for the temporal dimension of competitive interactions between the compared groups (Gioria and Osborne 2014). However, the timing of competition can play a crucial role in determining the successful establishment of alien species in novel environments (Beckmann \textit{et al.} 2011; Blair and Wolfe 2004) and their persistence. In the presence of...
differences in the timing of germination, in fact, an alien species does not need to possess an inherently greater ability to use resources than native species to become established and ultimately invasive, although a capacity to use resources under less than optimal conditions might be needed (Funk and Vitousek 2007; Gioria and Osborne 2014; Tilman 1999).

The concept of niche differentiation, generally interpreted as differences in resource use or resource availability (Davis et al. 2000; Levine et al. 2008), becomes very important in this context. Niche differentiation, reflecting differential resource requirements between species, makes the coexistence of competitively inferior and superior species possible (e.g. Chesson 2000; MacDougall et al. 2009). Phenological niches arising from differences in the timing of developmental phases between alien and native species can create windows of opportunity for alien species with phenologies that contrast with those that have evolved in native communities (Johnstone 1986; Kardol et al. 2013; Körner et al. 2008; Wolkovich and Cleland 2011), promoting the invasiveness of such species and/or the invasibility of the recipient communities (Gioria and Osborne 2014; Pucheta et al. 2011).

While the interest in assessing the role of flowering phenology and extended leaf phenology in plant invasions has increased substantially in recent years (e.g. DeFalco et al. 2007; Fridley 2012; Godoy et al. 2009; McEwan et al. 2009; Wainwright et al. 2012; Wilsey et al. 2011; Wolkovich et al. 2013), the contribution of differences in germination phenology between alien and co-occurring native species to the successful establishment (naturalization phase) and spread (invasion phase) of invasive species has received comparatively little attention. The timing of germination determines the post-germination conditions experienced by seedlings (Donohue 2003, 2005), including the competitive environment (Forbis 2010) and can thus strongly affect the fitness, growth and survival of a species in a community (Donohue 2005; Donohue et al. 2010; Fenner and Thompson 2005; Harper 1977; Simons and Johnston 2000; Verdú and Traveset 2005) and thus its invasion potential.

With a focus on grassland communities, (i) we discuss the benefits and associated risks arising from the exploitation of early or late germination niches at times when competition from resident species (native and other alien species) is low; (ii) we speculate whether such benefits are important only during the establishment phase or also for the spread and persistence of invasive species in the invaded communities and (iii) we discuss available evidence of how invasive species respond (including plastic and adaptive responses) to variation in the environmental conditions, including climatic changes, with respect to their germination timing. Understanding the role of germination phenology in plant invasions is critical to predict future invasions and develop sustainable control and restoration programs. We follow Richardson et al. (2000) in defining alien and invasive species. We refer to alien species when a clear distinction between naturalized and invasive species is not made in the studies examined in this paper, i.e. whether they have become established and formed self-sustaining populations, or whether they have also spread from the loci of introduction.

DEFINING TEMPORAL GERMINATION NICHES

In this paper, we focus on within-year phenological differences in the timing of germination between invasive and co-occurring native species (Grman and Suding 2010; Wolkovich and Cleland 2011; Wolkovich et al. 2013). We refer to ‘early germination’ or ‘early windows of opportunity’ when a species germinates before the majority of other species present in a community, while ‘late germination’ or ‘late windows of opportunity’ occur when a species germinates after the majority of the other species present in a community. For instance, in temperate grassland communities dominated by winter annual species, early germination refers to species germinating early in autumn, while for communities dominated by summer annual species, early germination occurs when a species germinates early in spring. Facultative winter annuals can behave as both winter and short-lived summer annuals (ephemerals), with seeds germinating in autumn and in spring and seed set being completed in late spring/early summer for both cohorts (Benech-Arnold et al. 2000; Lu et al. 2016). The timing of germination for these species may alter the phenology of other life stages, including flowering as well as seed production (e.g. Lu et al. 2016).

The term ‘delayed germination’ is used in the literature to describe the fact that a certain proportion of fresh seeds may enter primary or secondary dormancy to prevent the germination of all dispersed seeds, leading to the formation of a seed bank (Fenesi et al. 2014; Rice and Dyer 2001; Venable and Lawlor 1980). Delayed germination should not be confused with late germination, as the former relates to germination of fresh seed and does not refer to any specific (early and/or late) window of opportunity. On the other hand, early germination does not refer to the germination of fresh seeds but to a specific window of opportunity.

BENEFITS OF EARLY AND LATE GERMINATION

A capacity for early germination has long been regarded as an important trait conferring weediness or invasiveness (Baker 1974; Pyšek and Richardson 2007). Species that germinate earlier than other species can benefit from the early access to (some) resources (or space) and reduced competition at the initial stage of establishment (Gioria and Osborne 2014; Godoy et al. 2009; Wainwright et al. 2012) and can thus achieve substantial size increases before other species (Abraham et al. 2009; Grman and Suding 2010; Ross and Harper 1972; Seabloom et al. 2003). Positive effects of early germination on growth and fecundity have been reported for several invasive

The timing of germination of a species can have a large impact on community assembly (Kardol et al. 2013). By affecting the timing of competition and thus the intensity of competitive interactions (Forbis 2010; Vannette and Fukami 2014), differences in germination timing can also affect the fitness of neighboring individuals, both within and between species (Abraham et al. 2009; Miller et al. 1994; see Verdú and Traveset 2005 for a review), potentially promoting the dominance of the early-germinating species (Dickson et al. 2012). Resource pre-emption by early-germinating species can have a significant impact on the establishment of later-germinating species via size-asymmetric competition (Abraham et al. 2009; Freckleton and Watkinson 2001; Weiner 1990) as well as via soil legacies (Grman and Suding 2010), potentially exerting a founder control over native species that emerge later in the season (Körner et al. 2008).

Many early-germinating invasive species are reported to have strong negative effects on the establishment of native species and on the diversity of native plant communities, both above-ground (Dickson et al. 2012; Gioria and Osborne 2010; Ross and Harper 1972) and/or below-ground (Gioria et al. 2014; Gioria and Pyšek 2016). There is ample experimental evidence that even short-term differences in the timing of planting (one to three weeks) can have strong effects on initial community assembly and plant diversity (Abraham et al. 2009; Cleland et al. 2015; Deering and Young 2006; Dickson et al. 2012; Ejrnaes et al. 2006; Grman and Suding 2010; Hoelzle et al. 2012; Kardol et al. 2013; Stevens and Fehmi 2011; von Gillhaussen et al. 2014; Vaughtni and Young 2015; Young et al. 2015).

Early germination by a fast-growing, dominant species can be highly detrimental to light-demanding species that achieve maximum carbon gain/cover before canopy closure. This is particularly relevant for spring ephemerals (Grime 1998, 2001), many of which accumulate most of their annual biomass increment during periods of direct irradiance (Rothstein and Zak 2001), or in native perennial grasslands where native species germinate later than annual invasive species (Abraham et al. 2009; Abraham et al. 2009; Deering and Young 2006; Wainwright and Cleland 2013).

The magnitude and direction of the effects of differences in the germination phenology of invasive and co-occurring native species are strongly dependent on the identity of the interacting species (Cleland et al. 2015) and on the prevailing environmental conditions, including the strength of competitive interactions (Arthur et al. 1973; Donohue et al. 2010; Kardol et al. 2013; Rathcke and Lacey 1985). Experimental studies show that invasive species characterized by high growth rates generally benefit more from reduced competition associated with early germination than do native species (Dickson et al. 2012; Stevens and Fehmi 2009). High resource availability is reported to enhance (Kardol et al. 2013; Pérez-Fernández et al. 2000) or reduce (Young et al. 2015) the competitive advantages associated with early germination, depending on the type of resources and their combinations. In general, high nutrient levels increase the benefits of early germination for alien species with growth rates higher than those of native species (Abraham et al. 2009; Kardol et al. 2013).

Water deficits seem to delay germination less in alien species than in native species. In her review of invasive species’ traits in low-resource environments, Funk (2013) showed that in arid and semi-arid ecosystems, early germination is more pronounced in invasive than native species under low water availability. This suggests a more opportunistic resource-use strategy for invasive species, resulting in efficient exploitation of short-term pulses of resources, despite the increased risk of mortality associated with this strategy. Pérez-Fernández et al. (2000) showed that water deficits postponed germination to a greater extent in seven native species compared to seven alien species co-occurring in Banksia woodlands in south-western Australia. These findings indicate that a drought event could increase temporal differences in germination, potentially promoting the invasiveness of alien species in such ecosystems. Increases in water availability in regions characterized by seasonal precipitation patterns can, however, reduce the benefits associated with early germination. For instance, in an experimental study conducted in perennial grasslands in north-central California, Young et al. (2015) showed that increases in water availability allowed native perennial grasses to germinate and grow despite the presence of early-germinating alien species.

Competition for resources is both affected by (Weiner 1990; Vannette and Fukami 2014) and affects the timing of germination, with studies reporting that intense inter- and intra-specific competition often promotes rapid seed germination (Dyer et al. 2000; Grime et al. 1981; Miller et al. 1994; Rathcke and Lacey 1985; Verdú and Traveset 2005). Competition can also affect the direction and magnitude of the effects of early germination (Ross and Harper 1972), as shown in many comparisons between alien/invasive and native species (Abraham et al. 2009; Dickson et al. 2012; Grman and Suding 2010; Körner et al. 2008; Seabloom et al. 2003; Stevens and Fehmi 2011; Young et al. 2015), with such effects predicted to be stronger if the competing species (i) have a high resource use overlap; (ii) their impact on the environment is strong and (iii) their growth rate is more sensitive to changes in the environment (Vannette and Fukami 2014). As predators and pathogens are a major cause of seed and seedling mortality (Harper 1977), seasonally restricted predators or pathogens could also select for timing of germination (Rathcke and Lacey 1985).

While the benefits of early germination have been explored experimentally in several studies (see Cleland et al. 2015; Wolkovich et al. 2013), the significance of late germination in plant invasions has received comparatively less attention (but see Pucheta et al. 2011). Late windows of opportunity associated with germination after that of the majority
of native species could be as important as early germination as a mechanism to avoid competition and thus promote the successful establishment and spread of late-emerging invasive species. Late windows of opportunity arising from germination at the end of the growing season in temperate regions would be characterized by decreasing rather than increasing temperature, thus this window of opportunity would be beneficial only if seedlings tolerated the increasing abiotic constraints associated with late-season growth and reached a developmental stage that allows them to over-winter successfully. A key feature in this window of opportunity would be the establishment of a competitive advantage in the following spring by providing the potential for earlier growth. This could place a particular emphasis on the environmental conditions associated with the late-season period that facilitates successful establishment and growth. This is likely the case for cheatgrass *Bromus tectorum*, which is dependent on specific temperatures and soil moisture conditions during the coolest part of the growing season for its successful invasion (see *Harris 1967*).

**RISKS OF EARLY AND LATE GERMINATION**

The seedling stage is the most vulnerable time in the life cycle of a plant (*Baskin and Baskin 2014; Fenner and Thompson 2005; Harper 1977*). Whether early or late germination promote the establishment of a species in a community depends on the post-germination environmental conditions experienced by its seedlings (see *Donohue et al. 2010*). Ideally, germination should be timed to occur only when conditions for seedling growth and development are suitable, while unfavorable abiotic (e.g. low resources, non-optimal temperatures) or biotic (e.g. plant pathogens, competition) conditions should be avoided. Thus, the optimal timing of germination (e.g. early, intermediate or late) is likely to vary substantially in space and time (*Donohue et al. 2010*). To gain an advantage, germination in alien species should be fine-tuned to occur earlier (or later) than that of native species, when competition is low, but not so early (or late) that it would be detrimental to seedling survival (*Rathcke and Lacey 1985*).

Early or late germination do not necessarily result in the establishment of a species (*Kardol et al. 2013; Sans et al. 2004*). In temperate regions, early germination generally reduces the probability of survival of seeds of herbaceous species, despite increases in reproductive success associated with this strategy have often been reported (see *Rathcke and Lacey 1985; Verdú and Traveset 2005* and references therein). In fact, early germination inevitably carries risks associated with the possibility that those environmental conditions that have promoted germination might not signal the actual beginning of suitable conditions for growth and development (*Fenner and Thompson 2005; Grime 1977; Wainwright et al. 2012*). Thus, the potential benefits of early or late germination in seasonal environments must be balanced by a capacity to tolerate growth-limiting conditions (*Gioria and Osborne 2014; Verdú and Traveset 2005; Wainwright et al. 2012*). Alterations in herbivory pressure can also affect the establishment of early-germinating species (*Lambrinos 2006; Wainwright et al. 2012; Willis et al. 2014*).

In temperate regions, the main risk of early germination is represented by late frosts or suboptimal temperatures (*Baskin and Baskin 2014; Skálová et al. 2011*). A seedling’s frost tolerance is critical to the establishment of early-germinating species and is an important determinant of their distribution range (*Berger et al. 2007; Gioria and Osborne 2013; Perrins et al. 1993; Skálová et al. 2011*). High seedling tolerance to suboptimal conditions is particularly important for those alien species that are expanding their range northwards (e.g. *Berger et al. 2007*) or towards higher altitudes (e.g. *Pauchard et al. 2009; Pyšek et al. 2011*).

In regions characterized by seasonal rainfall, seedlings of early-germinating species can be exposed to water deficits and/or high temperatures after small rainfall events that had promoted seed germination (*Wainwright et al. 2012; Willis et al. 2014*). For instance, *Wainwright et al. (2012)* assessed the performance of alien and native species in an invaded coastal sage scrub community in the Mediterranean climate of California, simulating ambient rainfall timing (winter rains) and a pre-growing season rainfall event (late-summer), to test whether early-germination confers a performance advantage. They found that, under ambient rainfall timing, alien annual grasses and forbs germinated earlier and reached higher abundances than native species. Many alien annual grasses germinated also following the pre-seasonal watering treatment, while annual or perennial native species did not germinate under those conditions, indicating that native species possess more constrained germination cues than alien species. Alien species that germinated under those pulses, however, did not survive until the start of natural rains, suggesting that early germination might not be a successful strategy for the establishment of a species in that ecosystem (*Wainwright et al. 2012*). Tolerance to heat and/or to low water availability may benefit early-germinating invasive species in such regions. In contrast, in many temperate regions, high water availability (waterlogging) combined with low air/soil temperatures may constrain germination and seedling development as well as increase the risk of pathogen infestation, such as in the invasive *Gunnera tinctoria* in Ireland (*Gioria and Osborne 2009a*).

Clearly, the risks of early/late germination depend on the overall germination strategy of a species and on the proportion of the soil seed bank that germinates in a given year. Synchronous germination early in the season is regarded as a major factor in the success of several invasive herbaceous species (*Beerling and Perrins 1993; Dreyer et al. 1987; Gioria and Osborne 2009b; Laube et al. 2015; Navie et al. 2004; Pucheta et al. 2011*). However, this strategy increases the vulnerability of a species to unfavorable conditions that could follow germination and cause high seedling mortality. This could have
substantial negative effects on the persistence of such populations, especially for species not forming a persistent soil seed bank (sensu Thompson et al. 1997).

In contrast, asynchronous germination (Fig. 1) increases the probability of germination occurring at a ‘safe site’ (sensu Harper 1977) and mitigates mortality risks associated with unfavorable post-germination conditions as well as the effects of inter- and intra-specific competition among neighboring seedlings (Brändle et al. 2003; Donohue et al. 2010). The formation of a soil seed bank composed of seeds possessing varying degree of dormancy and differing in their germination requirements is particularly favorable where environmental conditions are highly variable (Venable and Brown 1988; Venable and Lawlor 1980) or where the period suitable for seedling establishment is long (Rathcke and Lacey 1985). Asynchronous germination can result in the creation of vacant germination niches throughout the year, potentially contributing to the successful establishment of invasive species.

Late germination niches can arise from seeds that germinate asynchronously over an extended period (Fig. 1) as well as from seeds that germinate synchronously but in a different season from the season when germination of the majority of native species occur (Gioria and Osborne 2009a; Pucheta et al. 2011; Fig. 1). For instance, Pucheta et al. (2011) suggested that the exploitation of a late germination niche is important in promoting the invasiveness of the alien winter annual grass *Schismus barbatus* in a desert community in Argentina, where the native annual flora is mainly composed of summer annual species. These authors found that germination of this invader was highly synchronous, with more than 90% of seed emerging from samples collected in autumn, at which time annual species that compete for sporadic cool-season rain are absent.

**Figure 1:** Example of highly asynchronous germination leading to early and late windows of opportunity for an invasive species. The number of seedling of the invasive herb *Gunnera tinctoria* germinating from samples collected from invaded sites in western Ireland (Site 1: coastal grassland along a cliff; Site 2: wet meadow; and Site 3: coastal grassland), at two sampling occasions, coinciding with periods when the majority of seedlings had already germinated in the field (May) and after seed dispersal of this species (October; n = 20 of soil cores, 5 cm diameter, 15 cm depth, in total 120 samples), is plotted over time. The samples had been placed in pots over sand and kept under temperature, light and water availability conditions that were similar to those experienced at the sites of collection. Seedling emergence began one week after the potting of soil samples, in June, and was monitored over 74 weeks (19 months). Germination during the second growing season began at the end of February, consistent with field observations and approximately a month earlier than seedlings of native species in the field (early window of opportunity). Germination was high late in spring and early in the summer, with peaks in May, June and July and continued throughout September, while in November it started declining to almost no germination. The absence of seedlings from November till March is consistent with germination patterns observed under natural conditions (Hickey 2002). These germination patterns indicate a capacity for this species to exploit temporal niches associated with differences in the germination of native species, including early temporal niches (February/March), late temporal niches (germination over the summer and in late autumn, after the germination of seeds of native species, when *senescence* has already begun in native species).

**PERSISTENCE OF THE EFFECTS OF EARLY AND LATE GERMINATION OVER TIME**

While the benefits of early germination during the establishment phase have been tested in several studies, their role in the spread of invasive species remains unclear. Comparisons of germination patterns between invasive and non-invasive congeners under experimental conditions show that invasive species tend to germinate earlier (lower time to germination) than non-invasive congeners or less invasive congeners (Pyšek and Richardson 2007; Perglóva et al. 2009; Skálová et al. 2011), suggesting that early germination is an important determinant of species’ invasiveness. However, comparisons under natural conditions are scarce. Laube et al. (2015) reported no significant differences in germination timing between the invasive *Impatiens glandulifera* and the less
invasive congener *I. parviflora*, both under experimental and natural conditions at different elevations. These somewhat contradictory findings seem to suggest that early germination provides these aliens with a competitive advantage over native species, but traits other than germination timing are eventually responsible for the differences in the invasive status of these species. Clearly, such differences could be associated with those in propagule pressure and residence time, although this information is rarely available.

Whether the benefits of differences in germination timing between invasive and native species change over time remains unclear. The majority of studies on this topic have been conducted over one season or one year only, while only a few studies have explored the effects of differences in the timing of germination between alien and native species under multiple years (De Luis et al. 2008; Vaughni and Young 2015; Young et al. 2001). Evidence of the persistence of community effects associated with early germination by one or more species is equivocal, showing that the initial advantage of early germination increases (Vaughni and Young 2015) or decreases over time (Körner et al. 2008; Verdú and Traveset 2005) or is perpetuated for several years (De Luis et al. 2008).

The duration of the benefits of early or late germination for alien species and their persistence in a community will depend on several factors, including (i) the duration of the temporal niche and the availability of resources during this period; (ii) the functional group of alien and co-occurring native species; (iii) changes at the ecosystem-level promoted by an invasive species; (iv) variation in the environmental conditions after seed germination; (v) a capacity for plastic or adaptive responses and (vi) biotic interactions, such as those with natural enemies. Moreover, climatic changes could impact on all of these factors, by altering the timing and duration of any early or late window of opportunity, the environmental conditions during seed maturation and post-germination, as well as the timing of biotic interactions (Walck et al. 2011).

In experimental studies, greater temporal differences in the timing of arrival (planting or sowing advantage) of a species have stronger effects on the germination or growth of neighboring species (Kardol et al. 2013; Orloff et al. 2013; von Gillhaussen et al. 2014). For instance, Kardol et al. (2013) showed that increases in planting interval, simulating seedling emergence (0, 5, 10, 15 or 20 days), resulted in a greater divergence of plant communities from the control, indicating that the duration of early germination niches has major effects on plant community assembly. This divergence was stronger at high than at low nutrient supply, consistent with studies showing that the effects of early germination tend to increase with increases in nutrients via the more rapid/higher biomass produced by early-germinating species (Dickson et al. 2012; Kardol et al. 2013; Pérez-Fernández et al. 2000; Stevens and Fehmi 2009). In an experimental study manipulating the order of arrival, von Gillhaussen et al. (2014) also found that a larger interval between successive sowings had a stronger effect on plant communities, with a reduced number of individuals and lower plant species richness in six-week sowing interval groups, compared to three-week sowing interval groups.

Experimental studies also show that the benefits of early germination differ with the functional group that arrives (or is sown) first (Ejrnaes et al. 2006; Körner et al. 2008; von Gillhaussen et al. 2014), with stronger effects on productivity, species composition and above-ground biomass in legume-start communities than in grass- or herb-start communities (Körner et al. 2008; von Gillhaussen et al. 2014). However, Körner et al. (2008) found that legume-start communities did not perpetuate their initial advantage, arriving at similar final functional group composition and above-ground biomass after 56 weeks. In contrast, for grass- and herb-start communities, the effects of differences in the timing of arrival on community composition persisted until the end of the experiment (56 weeks), suggesting that more time is required for these effects to disappear in such communities than in legume-start communities.

These findings also suggest that a nitrogen-fixing capacity could be important in the early establishment of some alien plants in regions with a limited availability of combined nitrogen due to low/high soil water availability and/or low temperatures that restrict mineralization. However, over time, nitrogen fixation could create conditions that would be beneficial to the establishment and persistence of nitrophilous (often alien) species (Gioria and Osborne 2013), potentially reducing the benefits associated with early germination, while inhibiting the germination of species with low-resource requirements (Funk 2013; Gioria and Osborne 2014; Grman and Suding 2010; Marushia et al. 2010); much of this would depend on how much nitrogen that is initially fixed is available to other species. This is consistent with findings by Grman and Suding (2010) showing that within-year soil legacies associated with the early germination of alien species strongly affect native California grassland communities.

With regard to life history, annual species tend to germinate earlier than perennial species, regardless of their origin (native vs. alien; Abraham et al. 2009; Deering and Young 2006; Grime et al. 1981; Reynolds et al. 2001; Rice and Dyer 2001; Verdú and Traveset 2005; Wainwright and Cleland 2013). Moreover, annual species more commonly produce seeds that vary in their germination requirements than perennial species, potentially increasing the probability of exploiting suitable germination niches for growth and development (Harper 1977; Rathcke and Lacey 1985). For annual plant species in communities dominated by perennials, early germination is an important strategy ensuring their persistence (Rees and Long 1992).

Early germination is recognized as a major factor in the establishment and persistence of alien annual species in arid and semi-arid ecosystems, such as in native perennial California grasslands (e.g. Deering and Young 2006; DeFalco et al. 2007; Freckleton and Watkinson 2001; Lulow 2006; Rice and Dyer 2001; Seabloom et al. 2003; Vaughni and Young
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Germination responses to environmental variation, including climate change

The germination phenology of invasive species in their non-native range can differ from that in their native range due to a range of factors, including plastic and/or evolutionary changes (Anderson et al. 2012) that determine their phenological ‘flexibility’ (Wolkovich et al. 2013). Phenotypic plasticity is considered to play a major role in determining the success of many invasive plants (Nicotra et al. 2010; Pyšek and Richardson 2007; Richards et al. 2006), by affecting both the short-term response of plant populations to environmental variation and their long-term persistence (Matesanz et al. 2012). The role of phenotypic plasticity in the establishment of alien species and in promoting species’ invasiveness, however, remains unclear (Lande 2015), with contrasting results being reported in many species traits (Davidson et al. 2011; Godoy et al. 2011; Palacio-Lopez and Gianoli 2011).

Plasticity in germination traits altering the environment experienced by a plant can be regarded as a means of habitat selection and niche construction (Donohue 2003, 2005; Donohue et al. 2005). Plastic changes resulting in the earlier (or later) germination of alien species compared to native ones could be important in determining their invasion potential, although available experimental evidence is equivocal. In a comparison of alien and native species that are common in a coastal sage scrub in California, Wainwright and Cleland (2013) found that alien species exhibited greater germination plasticity, across multiple cues (temperature, day-length and soil moisture) than native species, germinated more rapidly and responded more strongly to favorable conditions (warm temperatures and high soil moisture). In contrast, using 10 herbaceous invasive alien and 10 non-invasive alien species that occur in central-eastern Europe, Ruprecht et al. (2014) reported no differences in plasticity in germination traits (including time to germination, potentially promoting earlier germination), suggesting that higher plasticity in germination traits is not a reliable predictor of invasiveness.

2015; Verdú and Traveset 2005; Wainwright et al. 2012; Young et al. 2015). In desert ecosystems, many alien annual species often germinate rapidly and earlier than the majority of native forbs, which often have strict environmental requirements for germination (Marushia et al. 2010) and more constrained than many invasive (non-desert) species (Wainwright et al. 2012; see Marushia et al. 2010 and references therein).

Early-germinating annuals can strongly affect the growth and survival of late-spring germinating annuals. For instance, Abul-Fatih and Bazzaz (1979) showed that the invasive annual Ambrosia trifida, which germinates early in spring, increased mortality and reduced seed production of late-spring germinating annuals. Germination niches arising from differences in the timing of germination of winter and summer annuals can be detrimental to invasive species. Raynal and Bazzaz (2012; see Marushia 2010 and references therein).

In desert ecosystems, many alien annual species germinate more rapidly than many invasive (non-desert) species (Wainwright et al. 2010). Manipulating the timing of germination of native and invasive species has been recently recommended as a cost-effective restoration method, especially where there is a need to promote the establishment of less-competitive species (Abraham et al. 2009; Deering and Young 2006; Dickson et al. 2012; Grman and Suding 2010; Marushia et al. 2010; Stevens and Fehmi 2011; Vaughn and Young 2015; Young et al. 2015).

Knowledge of the persistence of the species- and community-level effects of early or late germination is necessary to assess the long-term implications of plant invasions on native communities and ecosystems, as well as for the development of sustainable restoration measures that would otherwise fail if the growth of invasive species that germinate before or after native species is not suppressed (see Marushia et al. 2010).
Acquired genetic differences in germination phenology could also play an important role in determining the successful establishment and persistence of invasive species. There is increasing evidence that the timing of phenological events is adaptive (e.g. Levin 2006; Volis 2007) and that phenological traits can evolve relatively rapidly (Erfmeier and Bruelheide 2005; Levin 2006).

Several experimental studies report that seed of many invasive species collected in their non-native range germinate more rapidly (they require lower time to germination, and shorter stratification period, or have higher germination rates) than those collected in the native range, including Ambrosia artemisiaefolia (Leiblein-Wild et al. 2014), Echium species (Hock et al. 2015), Eupatorium adenophorum (Li and Feng 2009), Rhododendron ponticum (Erfmeier and Bruelheide 2005), Silene latifolia (Blair and Wolfe 2004), Ulmus pumila (Hirsch et al. 2012) and Verbascum species (Hock et al. 2015). These differences have been interpreted as evidence of adaptive changes in the non-native range that result in the earlier germination of these species in their non-native range and indicative that early germination is an important determinant of invasiveness. However, factors other than rapid local adaptation, such as founder effects and random genetic drift (Colautti and Lau 2013; Drügoci et al. 2015; Hantsch et al. 2013), as well as maternal effects (e.g. Baskin and Baskin 2014; Donohue et al. 2010; Lu et al. 2016; Rathcke and Lacey 1985), could be responsible for differences in species traits in their native and non-native range.

The benefits of any plastic or adaptive change leading to earlier (or later) germination in their non-native range will depend on the degree of risk experienced by seedlings after germination (see Volis and Bohrer 2013). In unpredictable environments, early (or late) germination represents a highly risky strategy potentially leading to high seedling mortality. Thus, changes leading to earlier or later germination would need to be balanced by joint changes in other traits, such as an improved tolerance to suboptimal conditions for growth and development or a higher proportion of dormant seeds (Venable and Brown 1988; Volis and Bohrer 2013). A correlation between germination patterns and post-germination environmental conditions in their non-native range has been reported for invasive herbs such as A. artemisiaefolia (Leiblein-Wild et al. 2014), Centaurea solstitialis (Hierro et al. 2009) and Cardamine hirsuta (Kudoh et al. 2007).

For instance, an expansion of the germination temperature niche of A. artemisiaefolia in non-native European populations compared to native North American populations, which could allow the exploitation of an early germination niche once the duration, was correlated with an improved resistance to sub-zero temperatures (Leiblein-Wild et al. 2014). A strong correlation between germination timing and elevation has been reported for invasive Impatiens species (Laube et al. 2015) and for Ageratina adenophora (Li and Feng 2009) in their non-native range, suggesting that adaptive and/or plastic changes in germination phenology might play an important role in the invasion success of these species in their non-native range.

Adaptive increases in plasticity resulting in earlier germination than that of native or other alien species could also play an important role in successful invasions. However, these would depend on a range of factors, including differences in environmental variation and predictability in the native and introduced range, the cost of plasticity, residence time and the type of plasticity (one-shot plasticity vs. labile plasticity, i.e. continuous and reversible changes in phenotype throughout the lifetime of an individual) (see Lande 2015 for a review on this topic). Plasticity in germination timing influences the expression of post-germination of life-history characters as well as natural selection of those characters (Donohue 2003). Habitat selection via, for instance, changes in germination timing can alter the degree of environmental variation experienced by an individual at later life stages and can thus affect the evolution of plasticity of later characters (Donohue 2003). The evolutionary effects of the response(s) of invasive species to the environmental conditions experienced in the novel range and their role in determining species’ invasiveness is an important question that deserves further investigation.

While the above-mentioned studies report a lower time to germination under experimental conditions for seeds of many invasive species in their non-native range than in their native range, caution should be used when attempting to estimate the timing of germination under natural conditions (Cristado et al. 2014; Verdu and Traveset 2005). Moreover, the environmental conditions during seed maturation, maternal effects, as well as seed storage conditions or the timing of seed collection, can strongly affect germination patterns (Baskin and Baskin 2014; Donohue et al. 2010; Hierro et al. 2009; Rathcke and Lacey 1985), thus limiting the validity of the findings of studies that compare germination patterns for populations located in different regions/ecosystems, if these factors are not accounted for.

Changes in the timing of phenological events are among the major indicators of climate change (Cleland et al. 2007; Fitter and Fitter 2002). Climatic changes can affect the timing of germination and the survival of seeds of both alien and native species in many ways (Johnson 2014; Walck et al. 2011). These include (i) shorter winters, with spring temperatures occurring earlier in the year (Rosenzweig et al. 2007; Walther et al. 2002); (ii) changes in precipitation patterns, including increases in the frequency of extreme climatic events and changes in snow cover and in the timing of snow melting, which could either promote or delay germination and (iii) alterations in the germination of species with specific temperature-related requirements (see Walck et al. 2011 and references therein). Species that can detect climatic changes and respond to them more rapidly, via plastic and/or adaptive changes, are predicted to gain an advantage over slow-responding species (Dickson et al. 2012; Fridley 2012). Climatic changes are thus expected to favor species with flexible germination cues (Wainwright et al. 2012), as well as those that germinate under a broad range of environmental conditions, synchronously or asynchronously.
Whether climatic changes may create early or late germination niches or alter their duration, and ultimately benefit the establishment and spread of invasive alien plants is highly context-dependent and further evidence is required. Such changes can have opposite effects on seed germination timing and seedling survival of alien and native species. For instance, for a species requiring cold stratification, short winters could prevent or postpone rather than advance germination (Pyšek et al. 1998; Walck et al. 2011), while in arid- and semi-arid ecosystems changes in precipitation patterns could improve the competitive ability of later-germinating native species or alter the probability of seedling survival.

Other environmental cues, including photoperiod, can interfere with temperature (Baskin and Baskin 1985; Laube et al. 2014; Newman 1963) or precipitation patterns (Padgett et al. 2000, see Donohue et al. 2010), and affect the response of invasive plants to climate change, with respect to their germination timing. Species whose germination patterns and growth are largely determined by climatic triggers and not by day-length (day-neutral species) would take advantage of climatic changes resulting in a longer growing season to a greater extent than those determined by photoperiod, enabling them to germinate earlier. Quantitative information on this topic is needed to improve our understanding of the effects of climate change on plant invasions.

**CONCLUSIONS**

Despite the plausibility of the belief that early or late phenological niches play a key role in promoting successful invasions, quantitative field observations recording the timing of germination of seeds of alien and co-occurring native species in natural communities are lacking. Yet, pre-existing or adaptive phenological differences that allow an alien species to germinate at times when competition from native species is low could play a crucial role in determining its invasiveness in novel environments. Besides allowing a species to benefit from a ‘privileged’ access to resources, for a certain period of time, early and/or late germination can suppress the germination and establishment of native species and even create soil legacies that may further benefit early- or late-germinating alien species. Clearly, the benefits of these germination strategies in the establishment and spread of invasive species will strongly depend on the post-germination environmental conditions, including the competitive environment and the potential effects of climate change. Such effects could be detrimental to those species that germinate too early or too late in the season.

Given the high vulnerability of the seedling stage, high mortality risks associated with early or late germination could hamper the persistence of invasive species, especially those that do not form a soil seed bank or only form a transient one (sensu Thompson et al. 1997). Understanding whether the benefits of early or late germination persist over time and their role in determining species’ invasiveness requires further evidence. That some highly invasive early-germinating species are reported to decrease their abundance over time at sites were they had long been invasive suggests that early germination is beneficial at the initial stages of the invasion process, while it is not a sufficient condition for persistence. Moreover, the fact that native species (including invasive species in their native ranges) are reported to possess stricter germination cues compared to alien species under experimental conditions suggests that more constrained temperature- or water-related signals or photoperiodic signals might represent a more successful strategy for the long-term persistence of a species in a community.

Knowledge of the germination phenology of alien, invasive and native species is crucial for predicting the identity of species that could establish successfully in future and to develop sustainable control and restoration measures. This is also important to predict how climate change will affect competitive interactions between alien and co-occurring native plants via alterations in their germination phenology. For some invasive species and in some ecosystem/biome types, differences in germination phenology between invasive and native species could be the key attribute explaining successful invasions. This would reconcile the fact that some species traits that are often cited as promoting plant invasions (e.g. a superior competitive ability or high resource use efficiency) are not a necessary condition for invasiveness.

Long-term monitoring is needed to improve our understanding of the role of germination phenology in promoting successful invasions. Studies linking the germination phenology of invasive and native species with other traits, including reproductive and physiological traits, would improve our capacity to predict the mechanisms and processes underlying invasive success and identify those communities that are more susceptible to plant invasions.

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