

RESEARCH PAPER

Different flowering phenology of alien invasive species in Spain: evidence for the use of an empty temporal niche?

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ABSTRACT

Flowering phenology is an important and poorly understood plant trait that may possibly be related to the invasiveness potential of alien species. The present work evaluates whether flowering time of invasive alien species is a key trait to overcome the climatic filters operating in continental Mediterranean ecosystems of Spain (characterised by summer drought and low temperatures in winter). We conducted comparisons between the flowering phenology of the invasive species in their native range and in Spain, and between flowering phenology of 91 coexisting invasive–native species pairs. For the alien species, geographical change from the native to the invaded region did not result in shifts in the start and the length of the flowering period. Overall, climatic conditions in the native range of species selected for a flowering pattern is maintained after translocation of the species to another region. Flowering of tropical and temperate invasive alien species peaked in summer, which contrasts with the spring flowering of native and invasive alien species of Mediterranean climate origin. By exploiting this new temporal niche, these invasive alien species native to tropical and temperate regions benefit from reduced competition with natives for abiotic and biotic resources. We suggest that human-mediated actions have reduced the strength of the summer drought filter in particular microhabitats, permitting the invasion of many summer-flowering aliens.

INTRODUCTION

Understanding the causes of biological invasions by non-native plants and the ecological consequences is key for biodiversity conservation (Huenneke *et al.* 1990; Mack *et al.* 2000; Theoharides & Dukes 2007). Among the potentially important traits observed in invasive alien species, appropriate flowering phenology is a key trait for achieving high fecundity, which is a recurrent property of invasive species (Cadotte & Lovett-Doust 2001; Lake & Leishman 2004; Pyšek & Richardson 2007). Interactions between genetic factors (Murfet 1977) and environmental variables, such as day length (Orshan 1989; Imaizumi & Kay 2006), drought (Fox 1990) or temperature (Orshan

1989; Hollister *et al.* 2005) determine the period when a plant flowers.

Climatic conditions under which plants have evolved determine flowering phenology, although this trait might change if a plant is transported to a new region (Rathcke & Lacey 1985; Dlugosch & Parker 2008). Plant species native to tropical regions are known to flower either as a response to the tropical wet season, as a consequence of phylogenetic constraints, or both, mainly corresponding to the summer of temperate regions (Wright & Calderon 1995; Singh & Kushwaha 2006). In temperate regions, where winter cold is the main limiting environmental factor, flowering time can extend from early spring to late summer (Rathcke & Lacey 1985). By contrast, in

Mediterranean-type ecosystems (MTEs, *e.g.* Spain), where continental regions are characterised by two unfavourable periods for plant activity – a cold winter and an arid summer (Mitrakos 1980; Orshan 1989) – plant species have a narrow window of time for completing their life cycle, and flower mainly in spring (Castro-Díez & Montserrat-Martí 1998; Perez-Latorre *et al.* 2007).

The climatic conditions of any region can represent an abiotic filter for newly arrived aliens (Richardson *et al.* 2000). The permeability of this filter is expected to depend on the extent to which climatic conditions match between the native and the invaded region of the species (Thuiller *et al.* 2005) (see conceptual model Fig. 1). If the climate in the new range is similar to the original range, then alien species will not be expected to change their flowering phenology, and will bloom at the same time as native species (Fig. 1A). If the climate in the new range differs from that in the original range, then the success of alien species depends on a combination of the magnitude of the climatic differences, the species intrinsic ability to flower despite different climatic conditions and the capacity of the species to adapt (Fig. 1B), either by local adaptation through evolution, phenotypic plasticity or a combination of both (Dudley 2004).

The degree of change of functional traits (such as flowering phenology) between the invaded and the native region is related to the severity of the climatic filters. If such filters are not very limiting (Fig. 1C), invaders will preserve the flowering phenology of their native range. This may lead to different flowering phenology as compared to natives so that invasive alien species can start flowering before and for longer periods than natives (Pyšek & Richardson 2007) or later (Celesti-Grapow *et al.* 2003). Finally, if climatic conditions are strongly limiting (Fig. 1D), the favourable period for flowering will be short, and successful invaders will be those able to shift

and match their phenology to that of the native species. In this sense, Roche *et al.* (1997) experimentally demonstrated that late-flowering phenology of an invasive alien species enormously reduces its success in a region with a strong summer drought, such as Mediterranean-type ecosystems.

So far, it remains unclear whether the flowering phenology pattern observed in invasive plants is due to a species-specific reproductive strategy involving a variable degree of local adaptation and plasticity, or if invaders simply conserve the flowering phenology of their native region. Previous studies in different parts of the Mediterranean Basin found that summer-flowering invaders are the most abundant (Celesti-Grapow *et al.* 2003; Lloret *et al.* 2005) when *a priori* summer is an unfavourable period for flowering (Roche *et al.* 1997). This suggests that other factors, such as the characteristics of the invaded habitat, may play an important role in the invasion success of alien species, lessening the importance of abiotic filters (Fig. 1, transition from D to C) (Lake & Leishman 2004).

The objective of the present study was to compare the flowering phenology of invasive plant species with that of native species in Spain, and to examine whether the flowering phenology of invasive alien plants differs between their native and invaded range. We addressed the following questions: (i) Does flowering phenology of invasive alien plants in Spain differ from that shown in their native region?; (ii) Do invasive plant species differ in flowering phenology from the native species of the shared habitat? and (iii) If so, do the particular features of each invaded habitat play an important role in explaining such differences? A total of 91 invasive–native ecological pairs of species from Spain were selected, and a list of their habitat, growth form and flowering phenology features were recorded to address the above questions.

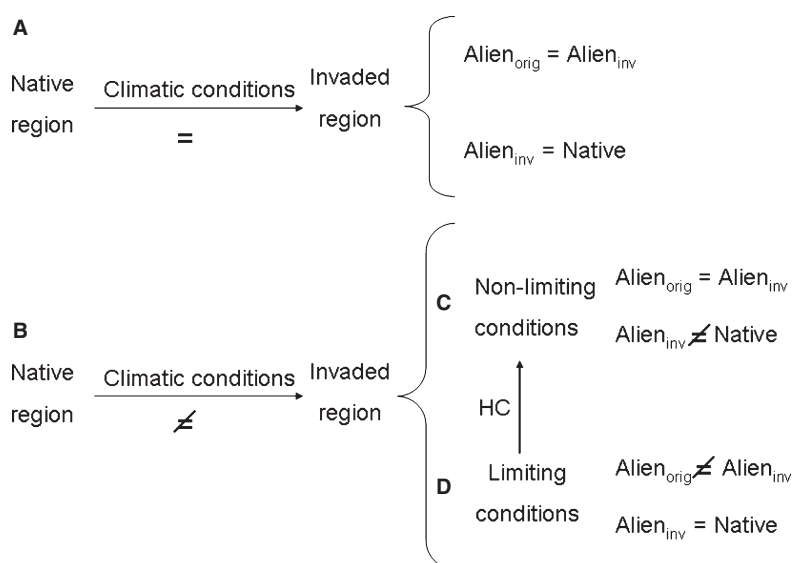


Fig. 1. Conceptual diagram showing flowering phenology similarities of the invasive species in their native range ($\text{Alien}_{\text{orig}}$) and in Spain ($\text{Alien}_{\text{inv}}$), and between flowering phenology of coexisting invasive ($\text{Alien}_{\text{inv}}$) and native species (Native). Environmental conditions are similar (A) and different (B) between the native and the invaded region. Case (C) refers to local environmental conditions being low-limiting factors for flowering phenology, whereas in case (D) environmental conditions are high-limiting factors for flowering. Changes in habitat characteristics (HC) of the invaded region may lead to a transition from (D) to (C).

MATERIALS AND METHODS

Species selection and data compilation

Data of invasive plants in Spain were taken from the atlas of invasive alien species in Spain (Sanz Elorza *et al.* 2004). All the listed alien species were selected, except those that are invasive only in the Canary Islands (non-Mediterranean climate) and those that are *naturalised* but not *invasive*, *sensu* Pyšek *et al.* (2004), *i.e.* have a small population whose demographic pattern is unclear. Each of the selected species was coded for a set of characters considered relevant in this study.

1 *Climatic origin of invasive species* in their native range was selected according to three main climatic regions (Tropical, Temperate and Mediterranean), which covered the possible origin of all alien species. Tropical category refers to species living between the Tropics of Cancer and Capricorn; Temperate category refers to species living between the tropics and the Arctic and Antarctic circles; and, finally, Mediterranean category refers to the regions described by Cowling *et al.* (1996) and situated around latitude 40° north or south. If the native region of an alien covers two or more climatic region categories, the region where the species is more abundant was taken for the analyses.

2 *Habitat type*. Four main habitats cover most of the invaded habitat types in Spain. This information was selected because differences in timing of flowering are often explained by differences in habitat conditions rather than different flowering strategies (Thies & Kalko 2004). ‘Disturbed areas’ category refers to habitats intensely modified by humans, while the other three categories refer to natural areas where human impact is low. The category ‘coastal areas’ covers habitats where temperature amplitude is low throughout the year because of the influence of the sea. ‘Mesic inland areas’ category covers inland habitats where high-soil water content has a large influence on plant development, *e.g.* marshes or riparian forests. Finally, ‘shrub and woodland’ category covers habitats dominated by woody vegetation, where summer drought is a limiting factor for plant development.

3 *Growth form* was included because environmental variables that affect flowering may differ between woody and herbaceous plants (Post & Stenseth 1999). Three categories – woody (trees and shrubs), herbaceous (annual and perennial herbs) and climber species – cover the growth form spectra in our data set.

4 *Pollination type (wind and animal pollination)* was considered important because different flowering strategies have been documented between animal- and wind-pollinated plants (Rathcke & Lacey 1985).

5 *Flowering phenology* was recorded as the month of start, end and duration of flowering of invasive species (both in Spain and in their native range) and their native partner species used as control (see below). Flowering phenology of alien species in their native range was collected from an extensive set of national floras from throughout the world (see Supporting Information).

To compare the above attributes between alien invasive and native plants, each invasive species was paired with one native species based on three criteria: (i) within each pair, the native must be recorded in the region where the alien species is invasive; (ii) the native and invasive alien species must share the same habitat type, *i.e.* be potential competitors and (iii) the species pair must belong to the same growth form and pollination type. Expert knowledge and published literature was used to create and corroborate the native species selection (Bolòs & Vigo 1984–2001; Castroviejo 1986–2005; Valdés *et al.* 1987; Casado *et al.* 2004; De Miguel *et al.* 2005) (see Supporting Information).

Data on flowering phenology of native plants was collected mostly from Iberian flora (Castroviejo 1986–2005). Unfortunately, some native species have not yet been included in the Iberian flora. In these cases, information was collected from regional floras, such as the flora of western Andalucía (Valdés *et al.* 1987) and the flora of Catalonia (Bolòs & Vigo 1984–2001). Because the information was obtained from three different sources, we tested differences in flowering onset and cessation in 31 species reported in multiple floras using a one-way ANOVA. No differences were found either for the start ($F = 7.7E-4$, $P = 0.978$) or the end ($F = 0.723$, $P = 0.402$) of flowering time.

Statistical analyses

Chi-square tests were applied to test for differences between invasive alien species in the spectra of climatic origin, life form and type of invaded habitat. Pairwise Watson–William F-tests for dependent samples in circular statistics were performed to test for differences in the start and end of flowering time (i) of invasive alien species between their native range and the Spanish invaded range and (ii) between invasive alien species and their native partner species (*i.e.* using the structure of pairs), either considering the whole data set, or for subsets where the exotics have the same origin or the same pollination type. Data for Southern hemisphere species were transformed to Northern hemisphere climatically equivalent months (*i.e.* January = July). Circular histograms are presented for a better interpretation of these circular data. The first analysis was computed with a subset of 60 invasive–native pairs, because native range flowering information was not available for the rest of the chosen species. This data subset was consistent, given that (i) the proportion of missing species (51% tropical, 39% temperate, 10% Mediterranean) was similar to the total proportion of the invasive species used for this study (compare results in Fig. S1). These analyses were performed with the ORIANA package (Kovach 1994). In all circular analyses, flowering phenological data followed the Von Mises distribution (circular version of normal distribution), therefore no transformation was required.

To rule out the possibility that native–exotic differences were due to a bias in taxonomic selection, a phylogenetic

non-independence test was conducted to control for the effect of phylogenetic distance within invasive–native pairs on the results. Thus, an analysis of covariance (ANCOVA) was performed to test for differences in flowering phenology between invasive and native species, depending on climatic origin of the invasive species (dependent variable was difference in month between pairs), with phylogenetic distance between the two species in each pair as a covariate to control for possible phylogenetic bias. Phylogenetic relatedness was recorded as the mean phylogenetic distance to the first common ancestor between the two species in each pair. Species gene distances were collected through the angiosperm plant phylogenetic supertree described by Soltis *et al.* (2000).

Finally, paired *t*-tests were performed to test for flowering length difference between invasive species in their

native range and the Spanish invaded range, and between invasive and native species in Spain. SPSS 12.0 (SPSS, Inc) was used for non-circular statistical analysis.

RESULTS

Among the invasive plant species in Spain, the herbaceous growth form is significantly more frequent than climber and woody growth forms; those of tropical and temperate origins are more frequent than Mediterranean origin species; and more species invade disturbed habitats than natural habitats (Fig. S1).

Flowering phenological pattern of invasive alien species in Spain was similar between the native and invaded range (Fig. 2) (flowering length mean = 4.96 SD = 2.82 in the native range, and mean = 4.80 SD = 2.20 in Spain,

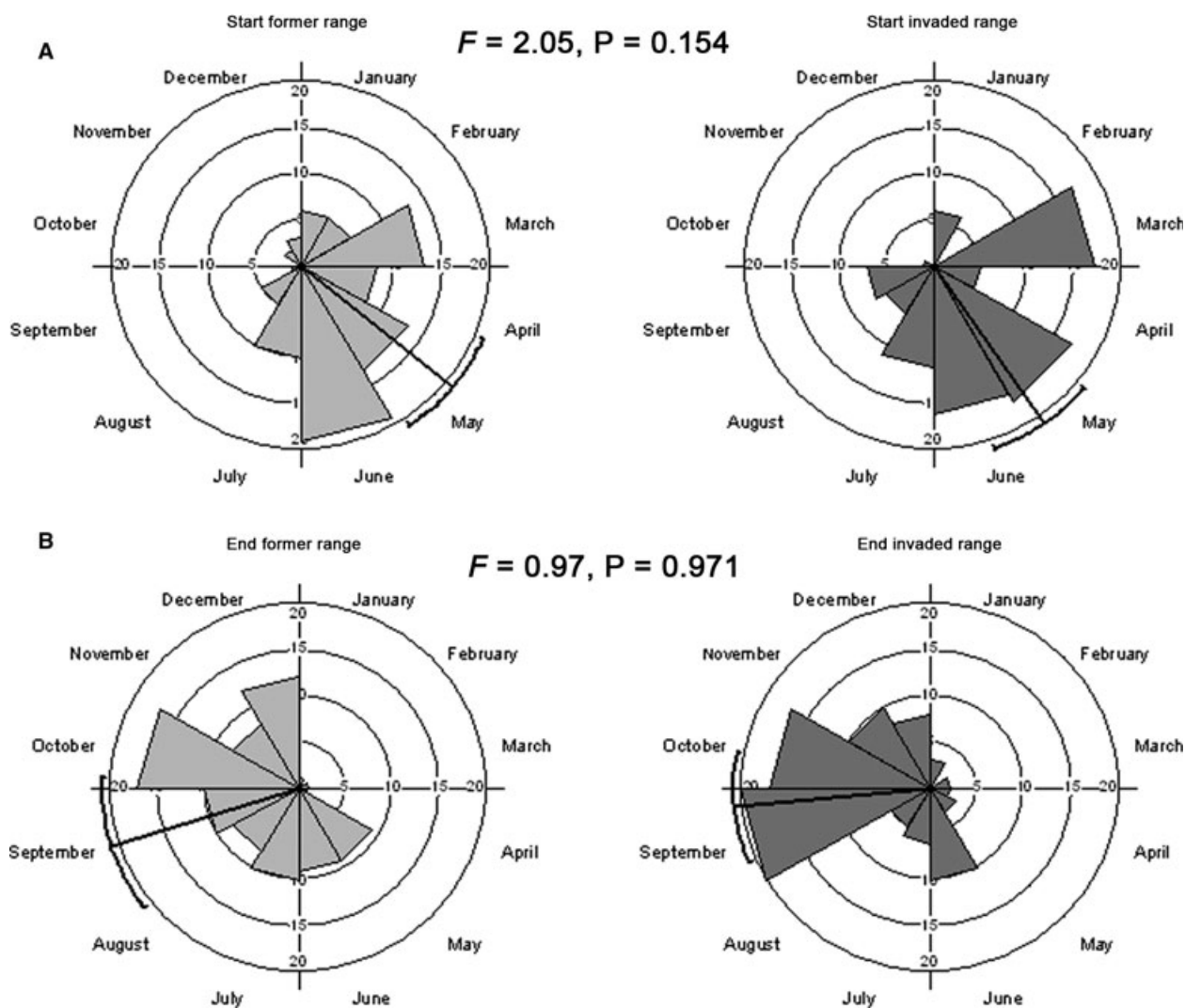


Fig. 2. Circular histogram of flowering phenology for invasive species showing (A) start and (B) end of flowering time in their former native range (left) and in their invaded Spanish range (right). Flowering phenology did not differ between native and invaded range of the alien species. Each triangle represents the number of species that flower in each month. Mean vector and standard deviation are also shown ($P > 0.05$ n.s.; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Table 1. Mean values of flowering phenology parameters for invasive and native plant species of Spain according to climatic origin and pollination type.

parameter	status	all species n = 91	tropical n = 43	temperate n = 37	mediterranean n = 11	animal pollinated n = 63	wind pollinated n = 28
start of flowering	Invasive	4 June	14 June	2 June	20 May	9 June	30 May
	Native	18 April	9 April	16 April	2 May	25 April	9 April
F-value, P		21.85***	27.82***	11.48***	0.42 n.s.	11.09***	11.63***
end of flowering	Invasive	28 September	2 October	8 October	5 September	28 September	28 September
	Native	4 September	3 September	2 September	7 September	23 August	24 September
F-value, P		3.72*	3.88*	4.42*	0.01 n.s.	6.39*	0.04 n.s.
flowering length	Invasive	4.8	4.7	4.8	5.5	4.9	4.6
	Native	5.3	5.9	5.2	4.9	4.9	5.7
t-value, P		-1.47 n.s.	-2.53**	-0.93 n.s.	0.54 n.s.	-0.04 n.s.	-2.27*

Circular mean values were transformed to days of the year for better interpretation. Flowering length is represented in months. Watson–Williams F and t-test values are also represented (P > 0.05 n.s.; *P < 0.05; **P < 0.01; ***P < 0.001).

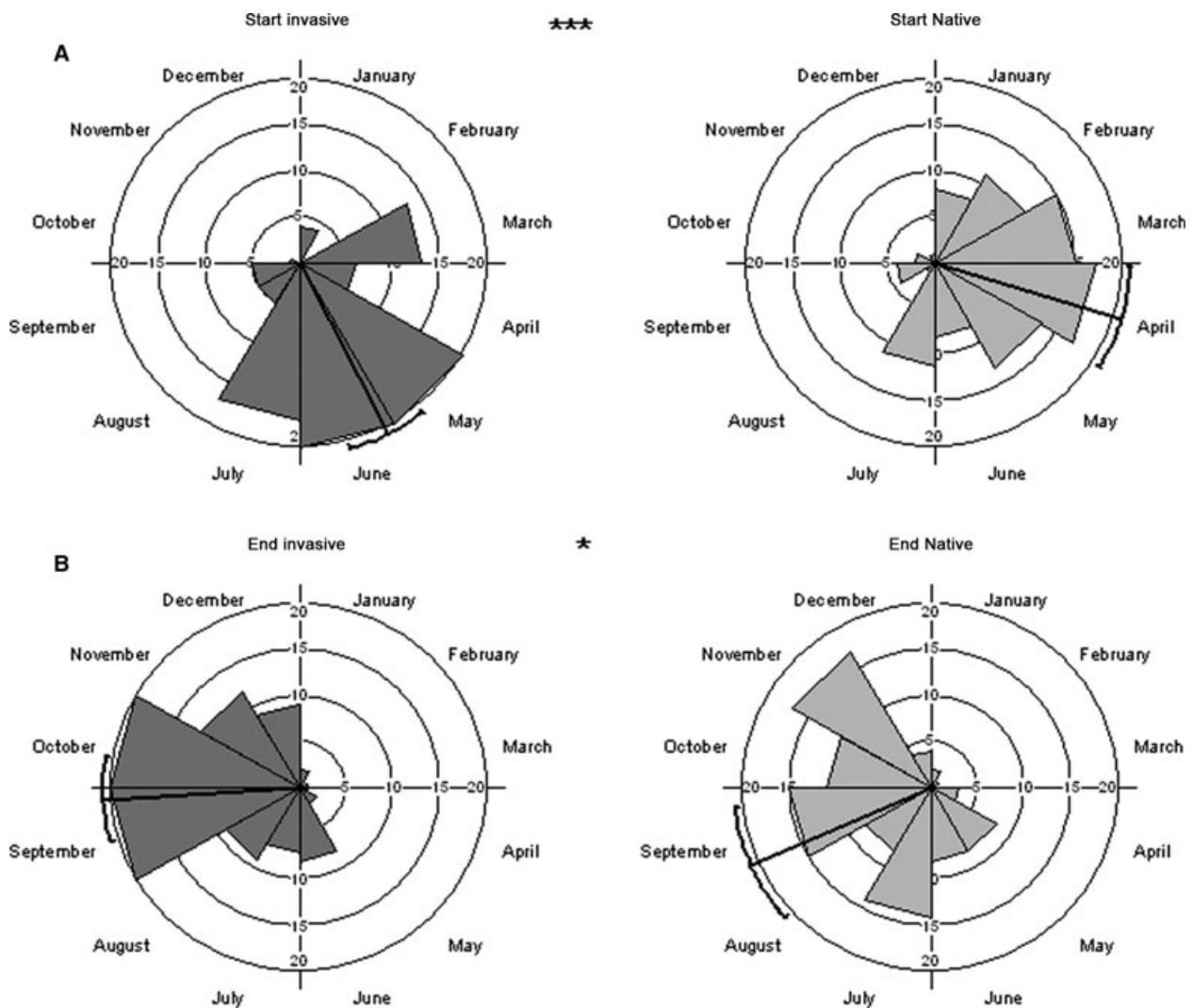


Fig. 3. Circular histogram of flowering phenology showing (A) start and (B) end of flowering time for invasive species (left) and native species (right). Flowering phenology of invasive species started and ended later than that of the native species. Each triangle represents the number of species that flower in each month. F-values are shown in Table 1. Mean vector and standard deviation are also shown (P > 0.05 n.s.; * P < 0.05; **P < 0.01; ***P < 0.001).

$t = 0.41$, $P = 0.682$). The same result was obtained when the analysis was performed separately for each climatic origin group (data not shown). Invasive–native comparisons revealed different flowering patterns between groups (Table 1, Fig. 3). On average, invasive species started flowering in June, while native species started flowering in April. Length of flowering period did not differ between groups; therefore, the significant differences continued to the end of flowering, which, in invasive species, was the end of September, and in native species, the start of September.

The invasive–native flowering differences were accounted for by those pairs where the invasive had a tropical or temperate origin, but not by pairs where the invasive species was of Mediterranean origin. Length of flowering was significantly shorter in aliens of tropical origin (Table 1). Animal-pollinated invasive plants also started and ended flowering later than their ecological native pair. However, for wind-pollinated invasive plants, only the start date was later and the length of flowering was shorter than for their native partner (Table 1).

The ANCOVA for the effects of invasive origin and phylogenetic distance between paired invasive and native species on the invasive–native differences at the start and end of flowering confirmed the significant effect of origin (start of flowering: $df = 1$, $F = 19.7$, $P < 0.001$, end of flowering: $df = 1$, $F = 3.48$, $P < 0.05$). There was no significant effect of phylogenetic distance between paired species (start of flowering: $df = 1$, $F = 0.23$, $P = 0.632$, end of flowering: $df = 1$, $F = 1.21$, $P = 0.274$). Tropical invaders started flowering 2.1 months later than natives, and temperate invaders started flowering 1.8 months later (Table 1).

DISCUSSION

Our results show that invasive alien species do not significantly shift the start, end and total length of their flowering between the invaded range in Spain and their native range. In consequence, invasive alien plants exhibited later flowering phenology (on average from early June to late September) compared to their corresponding native ecological partner (from mid-April to early September). Invasive alien species native to a non-Mediterranean region (tropical and temperate) were responsible for this pattern, whereas invaders native to other Mediterranean regions had the same flowering phenology as their native species pair. This suggests that the observed pattern is due to the different evolutionary histories of aliens driven by the climatic conditions of their native region, and that flowering phenology of alien species is a genetically determined trait that is little modified when they invade a new region.

The spring peak of flowering shown by species native to Spain, as well as by invasive aliens from Mediterranean-type ecosystems, agrees well with the assumption that, in these regions, summer drought and winter cold are highly limiting abiotic factors for plant performance in general and for flowering in particular (Mitrakos 1980; Orshan

1989; Herrera 1992; Castro-Díez & Montserrat-Martí 1998; Perez-Latorre *et al.* 2007) (Fig. 1, Table 1). By contrast, invasive species native to tropical and non-Mediterranean temperate regions do not exhibit this flowering pattern, since they have not evolved under the evolutionary pressure of an arid summer. For example, in temperate ecosystems, winter and autumn frosts are limiting factors for flowering, which primarily occurs from spring to summer (Rathcke & Lacey 1985). Under tropical climatic conditions, where temperature limitations do not exist, the flowering pattern is influenced by internal plant factors, pollinator activity and soil moisture (Wright & Calderon 1995; Singh & Kushwaha 2006; Sloan *et al.* 2007).

Given that alien species conserve their flowering phenology when they invade a new region, climatic conditions of the Mediterranean climate will be a filter only for those species whose flowering time is not matched to favourable local conditions for blooming. If species cannot shift their flowering phenology when they invade a new region, and summer drought appears to have been a strong evolutionary pressure for selecting spring flowering in native species, why are tropical and temperate species so frequent among invaders in Spain? We suggest that human-mediated actions may have widened this window by expanding habitats with a mitigated summer drought (transition from D to C, Fig. 1). Numerous studies have targeted disturbed areas as the most important habitats for biological invasions, since the specific conditions of these invaded ecosystems play an important role for the establishment and spread of invasive species (Cadotte *et al.* 2006). These particular microenvironments, such as summer-irrigated fields, recreational areas, canals and disturbed riparian forests, where water is available during summer, minimise the drought limitations on plant survival, growth and reproduction (Lake & Leishman 2004). Specifically for Mediterranean Basin regions, Vilà *et al.* (2008) recently demonstrated the importance of water availability for the establishment and population persistence of alien species. Therefore, most of the invaders of Spain and of other Mediterranean Basin regions live in human-created habitats where summer drought is less pronounced (Lloret *et al.* 2005). In these microenvironments, summer is an empty temporal niche that can be effectively invaded by many alien species that are not particularly adapted to drought (Fig. S1). Accordingly, the flowering difference between native and exotic species is greater in disturbed than in natural habitats (Table S1).

A possible advantage of the delayed flowering pattern observed in many aliens is the reduction in competition for both abiotic resources (*e.g.* water and nutrients) and biotic resources (*e.g.* pollinators) demanded for flowering. However, disturbed areas are habitats with especially rapid dynamics, particularly suited for species with a ruderal strategy (Grime 1974). In fact, Recasens *et al.* (2005) demonstrated that these kinds of invaders (*e.g.* *Abutilon theophrasti*, *Datura stramonium*) complete their life cycle in a short period (less than 3 months), which allows the population to increase more than twenty times per year,

also increasing the chances of persistence in the introduced range.

The phenological asynchrony between invasive and native plants can be expected to be more advantageous for animal- than for wind-pollinated invaders. Given that invasive species have peak flowering in summer, when few natives are blooming (Table 1) and pollinators are still abundant (Herrera 1990), they may have an extra reproductive benefit by reducing or avoiding competition for pollinators (Gómez 2000; Picó *et al.* 2002). A reduction in the number of co-flowering native plants can increase the number of pollinator visits to invasive plant flowers, particularly when invasive plants are more effective in attracting pollinators, as found in some species (Moragues & Traveset 2005; Lopezaraiza-Mikel *et al.* 2007). Although self-pollination is a common feature among invasive plants (Schueller 2004; van Kleunen *et al.* 2007), an increase in out-cross pollination may augment seed production (Parker 1997).

Our study suggests that the observed flowering phenology of alien species results from multiple interactions between the abiotic filters of the invaded region, flowering phenology of alien species in their region of origin and human-mediated actions that have modified important habitat characteristics. Our results on the summer phenology of alien invasive plants cannot be directly extrapolated to other Mediterranean climate regions such as California or the Cape region of South Africa because the proportion of invasive plants coming from each climatic region varies between areas (Bossard *et al.* 2000; Goldblatt & Manning 2000; Godoy *et al.* 2008). However, our results, together with those of Celesti-Gradow *et al.* (2003) and Lloret *et al.* (2005), suggest that summer flowering of invasive alien species is a recurrent pattern across the Mediterranean Basin.

In coastal Mediterranean regions, the number of invasive alien species is higher than in more continental areas. This may be attributed to the history of introductions, but also to the harsher climatic conditions of the inner Iberian Peninsula (Sanz Elorza *et al.* 2004; Vilà *et al.* 2008). Thus, another case of filling an empty temporal niche could occur under a climate change scenario. Since the severity of winters is expected to decrease in most climate change models (Christensen *et al.* 2007), alien species with a flowering phenology that could benefit from ameliorated winters might become increasingly successful in continental Mediterranean regions where they are currently absent or few.

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SUPPORTING INFORMATION

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

Figure S1. Number of invasive species according to their climatic origin, invaded ecosystem in Spain and growth form. Chi-square values and their significance are also shown above each character ($P > 0.05$ n.s., * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

Table S1. Mean values of flowering phenology parameters for invasive and native plant species of Spain according to the habitat type that they invade. Circular mean values were transformed to days of the year for better interpretation. Length of flowering is measured in months. Watson–Williams F and *t*-test values are also represented ($P > 0.05$ n.s.; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$).

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