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Flowering phenology of invasive alien plant species compared with native species in three Mediterranean-type ecosystems

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• *Background and Aims* Flowering phenology is a potentially important component of success of alien species, since elevated fecundity may enhance invasiveness. The flowering patterns of invasive alien plant species and related natives were studied in three regions with Mediterranean-type climate: California, Spain and South Africa's Cape region.

• *Methods* A total of 227 invasive–native pairs were compared for seven character types across the regions, with each pair selected on the basis that they shared the same habitat type within a region, had a common growth form and pollination type, and belonged to the same family or genus.

• *Key Results* Invasive alien plant species have different patterns of flowering phenology from native species in the three regions. Whether the alien species flower earlier, later or at the same time as natives depends on the climatic regime in the native range of the aliens and the proportion of species in the invasive floras originating from different regions. Species invading at least two of the regions displayed the same flowering pattern, showing that flowering phenology is a conservative trait. Invasive species with native ranges in temperate climates flower earlier than natives, those from Mediterranean-type climates at the same time, and species from tropical climates flower later. In California, where the proportion of invaders from the Mediterranean Basin is high, the flowering pattern did not differ between invasive and native species, whereas in Spain the high proportion of tropical species results in a later flowering than natives, and in the Cape region early flowering than natives was the result of a high proportion of temperate invaders.

• *Conclusions* Observed patterns are due to the human-induced sympatry of species with different evolutionary histories whose flowering phenology evolved under different climatic regimes. The severity of the main abiotic filters imposed by the invaded regions (e.g. summer drought) has not been strong enough (yet) to shift the flowering pattern of invasive species to correspond with that of native relatives. It does, however, determine the length of the flowering season and the type of habitat invaded by summer-flowering aliens. Results suggest different implications for impacts at evolutionary time scales among the three regions.

Key words: Biological invasions, flowering phenology, genetic inertia, Cape Floristic Region, California, Spain, Mediterranean-type ecosystems, water availability, climatic origin.

INTRODUCTION

The timing of sexual reproduction is a critically important determinant of plant reproductive success. Flowering at the optimum time ensures fecundity and good development of seeds and fruits (Mazer, 1987). Flowering phenology is mediated by the interaction of internal factors (Murfet, 1977; Putterill *et al.*, 2004) with external environmental signals such as temperature (Hollister *et al.*, 2005), daylength (Imaizumi and Kay, 2006) or drought (Fox, 1990*a*). In general, plant species in their native ranges have coupled the sensitive flowering period to the optimal climatic conditions through natural selection, thus maximizing their reproductive success. The main selective factors acting upon flowering phenology differ between ecosystems. In Mediterranean-type ecosystems (MTEs), which occur in five widely separated

regions of the world (Cowling *et al.*, 1996), summer drought and rainfall variability (Cowling *et al.*, 2005) modulate the flowering plant response. Drought is one of the most limiting factors for vegetative growth and flower development (Mitrakos, 1980; Roche *et al.*, 1997). Flowering is concentrated in spring and autumn in most native plants in MTEs, which can be interpreted with reference to avoidance of summer water stress (Orshan, 1989; Johnson, 1993; Castro-Díez and Montserrat-Martí, 1998; Perez-Latorre and Cabezudo, 2002).

Rainfall variability plays an important role in the start and length of flowering phenology in these ecosystems. In less predictable regimes there is selection for a largely plastic response of start of flowering in order to cope with the uncertain moisture conditions of spring; this also occurs in other seasonally dry ecosystems (Borchert *et al.*, 2004). Climate-change studies focused on responses of wide-ranging plant species occurring

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along latitudinal gradients corroborate the idea of high phenological plasticity in fluctuating environments (Arft *et al.*, 1999; Parmesan, 2006). However, phylogenetic and genetic inertia of flowering phenology imposes limits to this plasticity (Rathcke and Lacey, 1985; Herrera, 1992). Consequently, plasticity of flowering, measured as the length of temporal internal plant sensitivity to flower development, is a conservative trait, since it has a genetic base (Ausin *et al.*, 2005), and plant species may be unable to shift their timing of flowering when they are introduced into a new region.

Widespread introductions of plant species to areas outside their natural ranges provide the opportunity to gain new insights into the importance of flowering phenology as a component of success of alien species in a new region, since enhanced fecundity appears to be an important trait associated with invasiveness (Pyšek and Richardson, 2007). To be a successful invader, introduced plants must first cope with the abiotic filters imposed by the new region and then reproduce (Richardson *et al.*, 2000); this requires them to flower at the appropriate time of year, which will depend on the plant's requirements. Flowering phenology has been shown to be fairly flexible in within-alien comparisons. For example, successful invaders generally display early flowering or long blooming periods (Goodwin *et al.*, 1999; Pyšek *et al.*, 2003), since the chance of acquiring improved fitness via effective pollination visits is increased. On the other hand, late, short flowering gives insufficient time for completion of the life cycle or results in a shorter time for pollination, reducing opportunities for fruit and seed development (Roche *et al.*, 1997). In the case of alien–native comparisons, many authors have found that invasive alien species flower earlier than natives (Cadotte and Lovett-Doust, 2001; Lake and Leishman, 2004). Others have found that alien species that flower later than natives are more abundant (Celesti-Grapow *et al.*, 2003; Lloret *et al.*, 2005). Exhibiting a different flowering pattern compared with native species may be more frequent in those alien species which have evolved under climatic conditions markedly different from those of the invaded region. This premise is based on the following argument: if plant species maintain their genetic inertia of timing of flowering when they are introduced in a new ecosystem, different flowering phenology between invasive and native species may occur as a direct result of different strategies of reproduction selected by evolution. On the other hand, invasive species with the same climatic conditions in their native and invaded ecosystems will not show any difference in flowering phenology.

MTEs probably provide the best opportunity to test this hypothesis, since they have been severely affected by invasions of introduced (alien) plant species (Groves and di Castri, 1991). Many studies have sought reasons for differential success of different alien plant species in the different MTE regions [see Lloret *et al.* (2005) for the Mediterranean Basin; Rejmánek and Randall (1994) for California; Jimenez *et al.* (2008) and Sax (2002) for California and central Chile; and Richardson and Cowling (1992) and Richardson *et al.* (1992) for the Cape region of South Africa]. The fate of introduced species has clearly been influenced by many factors, including numerous inherent features of the different regions and differences in cultural links between the regions and colonial powers, which shaped the magnitude, timing and nature of early introductions and dissemination within regions. In addition, recent socio-economic developments and human-mediated modification of landscapes have also driven further introductions and their dissemination within the regions (Wilson *et al.*, 2007).

This study examines the flowering phenology of invasive alien species in three different regions with Mediterranean-type climate. The following questions were addressed. (*a*) Does the flowering phenology of invasive alien species differ from that of native species? (*b*) Are there differences between regions? (*c*) Is the flowering phenology of invasive alien species explained by the climate in their regions of origin?

MATERIALS AND METHODS

Climatic characteristic of selected regions

Three MTE regions were selected to represent a gradient of summer drought and rainfall reliability severity among regions of the world with this climatic regime (Cowling *et al.*, 2005). The California region has the lowest summer precipitation [San Francisco (SF) = 4·9 mm, San Diego (SD) = 4·8 mm] and a high water deficit in this season (SF = −296·4 mm, SD = −298·5 mm), the Cape region has a relative high summer precipitation [Cape Town (CT) = 47 mm, Port Elizabeth (PE) = 110 mm] and the lowest water deficit (CT = −96·0 mm, PE = −13·7 mm; Fig. 1). The Spanish Mediterranean region falls somewhere between these two regions, although with a remarkable variability in summer rainfall along latitudinal and coast–inland gradients. Water deficit was calculated as the difference between the precipitation and the potential evapotranspiration in each month. In this sense, potential evapotranspiration was calculated using the method of Jensen *et al.* (1990). This method is considered the most accurate from latitudes $0°$ to $60°$. It takes into account the latitude of the studied region, mean of the maximum and minimum temperatures, mean altitude and total irradiance considering the number of hours of sun. Climatic data for a 30-year period were used; for California and the Cape region, data were obtained from NOAA (1961–1990), and Spanish data were obtained from the national meteorological institute for the same period (INM 1971–2000).

Species selection and data compilation

To standardize between regions, the data set comprised introduced plant species that were clearly invasive (*sensu* Pyšek *et al.*, 2004), with clear impact on the native ecosystems (transformer species, *sensu* Richardson *et al.*, 2000). Three major sources were used to compile the lists of invaders: *Invasive plants of California's wildlands* (Bossard *et al.*, 2000), *Atlas de las plantas alóctonas invasoras en España* (Sanz Elorza *et al.*, 2004) and *The complete guide to declared weeds and invaders in South Africa* (Henderson, 2001). For California, all species listed by Bossard *et al.* (2000) were included, since the criteria used by these authors for inclusion of species in their book match those in the present study. For Spain, all listed species were selected, except those alien plants that are invasive only in the Canary Islands (non-Mediterranean climate) and those that are naturalized but not invasive *sensu* (Pyšek *et al.*, 2004). For South Africa, all species listed by
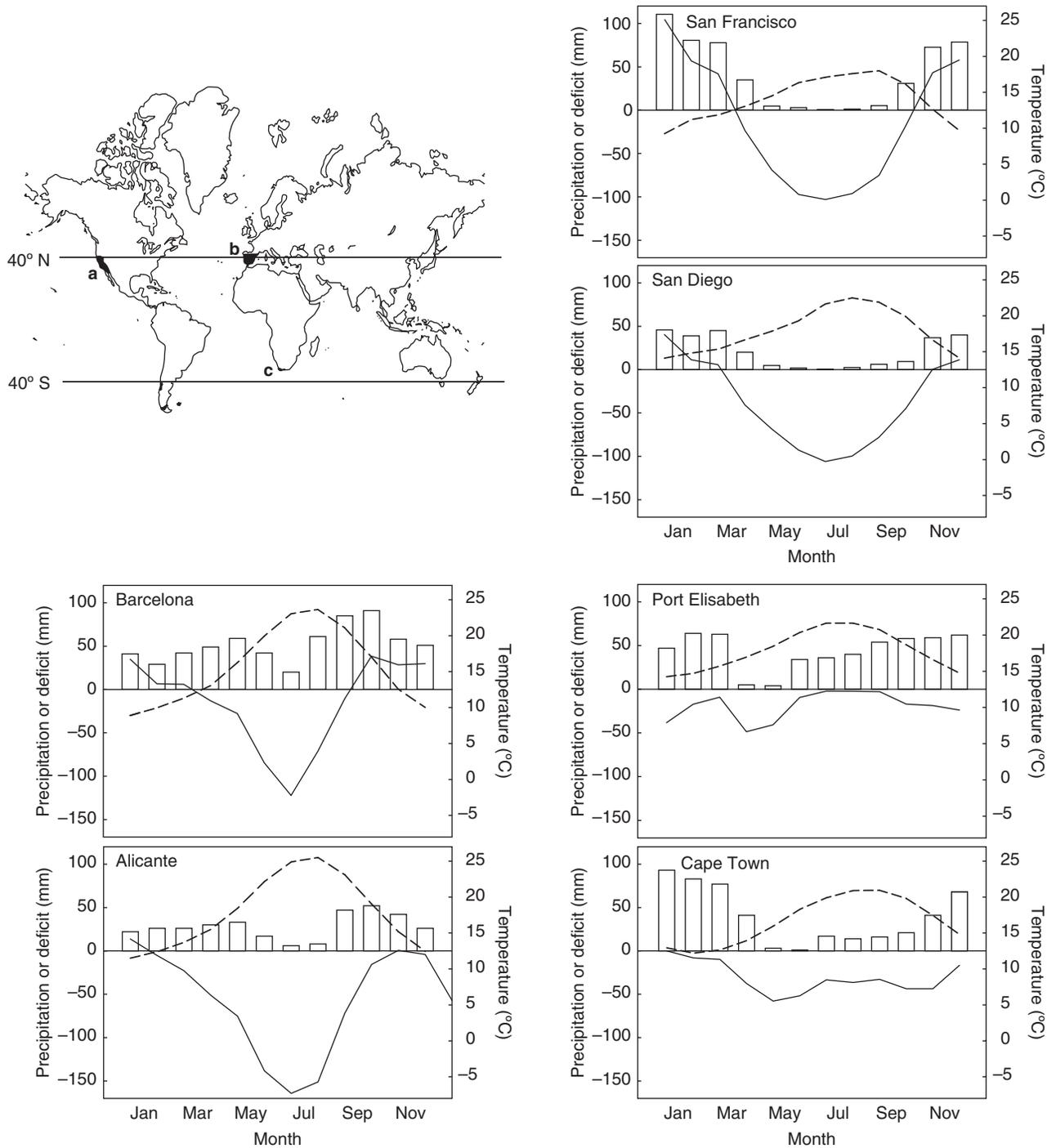
FIG. 1. Climatic characteristic of the three Mediterranean-type ecosystems studied: (a) California, (b) Spain and (c) the Cape region of South Africa. The three regions represent a gradient of summer drought severity. California has the driest and the Cape region has the mildest summers. Climatic charts of two different localities in each region illustrate this gradient. Columns represent the precipitation; solid lines the temperature; and dashed lines the water deficit in each month. Charts of the southern hemisphere localities (Cape region) have been modified to show drought between June and July for clearer comparison with Northern Hemisphere localities.

Henderson (2001) with mapped occurrence in the Cape Floristic Region were included. A total of 227 alien species were selected (see Supplementary Data, available online).

Each of the selected species was coded for seven characters (Table 1), using primarily information from the sources mentioned above. Climatic origin of the invasive species in their former native range was considered important since plants have a genetic inertia on flowering development due to climatic conditions under which they evolved (Rathcke and Lacey, 1985; Herrera, 1992). Four main habitats that are representative of

TABLE 1. *List of characters for which data were scored and used in ecological pair construction and invasive–native comparisons.*

Character	Character state
Climatic origin	Tropical, temperate, Mediterranean type-ecosystems (MTE)
Habitat type	Disturbed areas, coastal areas, lakes and rivers, shrub and woodland
Growth form	Woody, herbaceous, climber
Start, end and length of flowering of invasive and native species in the three MTEs	January to December (months)*
Pollination type	Animal, wind

* Flowering times for the Cape region were transformed to the Northern Hemisphere calendar.

invaded habitats across the regions were selected, as differences in timing of flowering are sometimes explained by habitat conditions rather than different flowering strategies (Thies and Kalko, 2004). Growth form was selected because environmental variables that affect flowering differ for woody and herbaceous plants (Arft *et al.*, 1999; Post and Stenseth, 1999). Pollination type was considered important because different flowering strategies have been documented for animal- and wind-pollinated plants (Rathcke and Lacey, 1985). Finally, data on the start, duration and end of flowering were also compiled.

In order to compare characters of invasive species with those of native plants with similar ecological requirements each invasive species was paired with one closely related native species based on four criteria: (1) within each pair, the native must be recorded in the region where the alien species is invasive; (2) native and invasive alien species must share the same habitat type – to be potential competitors; (3) the two species must belong to the same growth form and pollination type; and finally (4) the two species must belong to the same genus or family, to obtain phylogenetic independent contrasts (Ackerly, 2000). Native species with small distribution ranges and those listed in any IUCN threatened category were excluded. Criterion 4 was only realized for California and the Cape region since there were large phylogenetic differences between invasive and native floras in Spain. Thus, phylogenetic relatedness was taken into account *a posteriori* in Spain. In this case, total phylogenetic distances were collected for each species through the angiosperm plant phylogenetic supertree described by Soltis *et al.* (2000) and modified by Bremer *et al.* (2003). Currently, these studies are the most highly resolved and strongly supported topology obtained for angiosperms. Next, tests were conducted to determine whether the differences in the start and the end of flowering between invasive and native species were influenced by a phylogenetic relationship between each pair of species. Analysis of covariance (ANCOVA) testing for differences in flowering time demonstrated no phylogenetic effects on the results due to the native species selection for construction of the ecological pairs (start of flowering, $F = 0.23$ $P = 0.632$; end of flowering, $F = 1.21$ $P = 0.274$). In this sense, the phylogenetic relationship of the Spanish pairs was the covariable calculated as the mean of phylogenetic distance to the first common ancestor of both of the paired species.

Characteristics of Californian native species as well as their flowering phenology were collated from the Online Interchange for California Floristics (2007), based on *The Jepson manual of higher plants of California* (Hickman, 1993). For Spain, native plant characters were collated from the *Flora Ibérica. Plantas vasculares de la Península Ibérica e Islas Baleares (todos los vols)* (Castroviejo, 1986–2005). Unfortunately, accounts of some Spanish native species are yet to be published in the *Flora Ibérica*. Characters for these species were compiled from regional floras such as *Flora of Western Andalucía* (Valdés *et al.*, 1987) and *Flora of Catalonia* (Bolòs and Vigo, 1984–2001). Because the information was obtained from three different sources, differences in flowering onset and cessation in 31 species common among floras were tested with a one-way analysis of variance (ANOVA). No differences were found either in the start ($F = 7.7$E-4, $P = 0.978$) or in the end of flowering time ($F = 0.723$, $P = 0.402$). Finally, Goldblatt and Manning (2000) provided the best reference on the required information for the native plants of the Cape region.

Statistical analyses

Chi-square tests were applied to test for differences between the exotic floras of the three regions in the spectra of climatic origin, life form and type of invaded habitat. An orthogonal general lineal model (GLM) for unbalanced designs was used to test for significant variables affecting differences in the start, end and length of flowering between native and invasive species. Categorical predictors were the invaded Mediterranean regions plus those used to create invasive–native pairs (growth form, pollination type and invaded habitat). Pairwise Watson–William *F*-tests for dependent samples in circular statistic were performed to test for differences in flowering phenology between: (*a*) all invasive alien and native species pairs in the three regions; (*b*) those species pairs in each region where the alien invasive species shared the same climatic origin or pollination type; (*c*) those species pairs that are animal-pollinated and for which the invaders share the same climatic origin; and (*d*) differences in flowering phenology between invasive alien species present in at least two different regions. These analyses were performed with the ORIANA package (Kovach, 1994). In all circular analyses, flowering phenology data followed a Von Mises distribution (circular version of normal distribution) so no transformation was needed. *t*-tests for paired samples were performed to test for differences in the length of flowering between invasive alien and native species. SPSS 12·0 (SPSS, Inc.) was used for non-circular statistic analysis.

RESULTS

Characteristic of invaders

Invasive species in the three MTEs showed different patterns of climatic origin, growth form and invaded habitats (Fig. 2). The invasive flora of California had the smallest proportion of tropical species and a high proportion of invaders with Mediterranean and temperate origin. Spain and the Cape region had almost the same proportion of Mediterranean
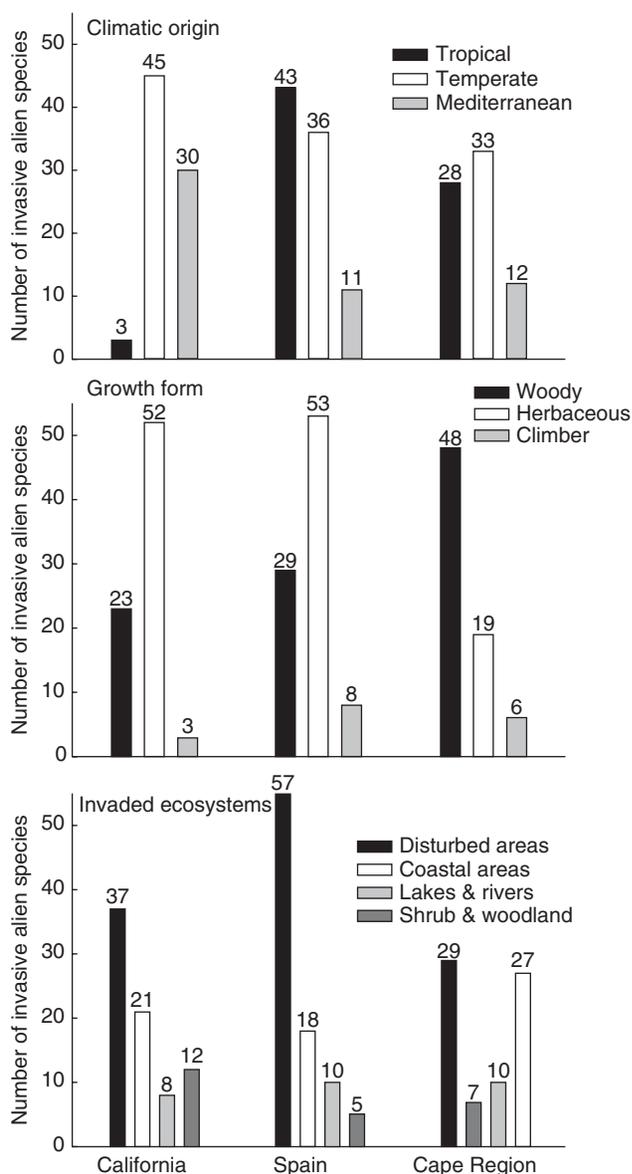
FIG. 2. Proportions of invasive species according to their climatic origin, growth form and invaded ecosystem in the three Mediterranean climate regions.

invaders (approx. 15 % of species). However, the alien flora of the Cape region showed a higher proportion of temperate species, while in Spain tropical species were more abundant. Herbaceous plants were the principal growth form in the invasive floras of California and Spain, and disturbed areas had the highest percentages of invasive species. However, a higher proportion of the invasive flora in the Cape region was made up by woody plants, and invaded habitats were mostly natural shrubland. The proportion of climbers is similarly low in the three MTEs.

Differences in flowering phenology between invasive and native species

Differences in the start of flowering between invasive and native species were significantly influenced by the invaded region and by the interaction between region and pollination type (Table 2). These differences in the start were generally lower in California than in Spain and the Cape region. In addition, wind-pollinated species had higher differences than animal-pollinated species in California, whereas in the Cape region the pattern was the opposite. Differences in the end of flowering were significantly influenced by the interaction between region and growth form (Table 2). In this sense, only invasive climbers in California had lower differences in the end of flowering compared with the invasive climbers in Spain and the Cape Region. Finally, differences in the length of flowering varied significantly depending of the invaded region, being shorter in California (Tables 2 and 3).

Variation of flowering phenology of invasive species between regions

The flowering length of invaders was positively correlated with the climatic conditions of the three regions. Invasive species flower for longer periods where the summer precipitation is higher. Thus, invasive alien plants in the Cape region bloom over 5·2 months, in Spain over 4·8 months and in California over 4·1 months on average. Overall, no differences in flowering length were found between invasive–native pairs, except in the Cape region where invasive species flower for longer than natives (Table 3). When considering the climatic origins of invasive species, only tropical plants showed different patterns between the invaded region and the length of flowering. In Spain, tropical invaders flowered over a shorter period than the natives, whereas invaders of tropical origin in the Cape region flowered for longer than the natives (Table 3).

For different regions, invasive species flowered earlier, later or at the same time as co-occurring natives. In California, the start and the end of the flowering period was similar for invasive alien and native species. However, when the comparison only included those pairs where the invasive had a Mediterranean origin, invaders started flowering 1 month earlier and finished 1 month earlier than natives. In contrast, in Spain invasive species started and ended flowering later than native species. This result was true for those species pairs where the alien has either tropical or temperate origin, but not for the Mediterranean group (Table 3). Timing of flowering of tropical invasive species in Spain and California showed the same pattern. This suggests that a displacement of flowering phenology may also occur in the latter region. However, no significant differences were found, probably due to the small sample size. In the Cape region, invasive species flowered earlier than natives, due to the early onset of flowering of invaders of temperate origin (Table 3). Tropical species ended flowering later than their native pairs, but no differences were found when the comparison was conducted with the full set of native species. Although native species showed a large variation in their spring onset of flowering, the flower development corresponded with those months with a mean temperature of 18 °C and with relatively low water deficits (Fig. 1, Table 3).

Finally, the 28 species that are invasive in at least two regions showed no displacement of flowering phenologies, either for the initiation ($F = 0·11$, $P = 0·745$) or for the cessation of flowering ($F = 0·22$, $P = 0·638$). Overall, these results suggest that

TABLE 2. *Results of a general lineal model (GLM) of the differences in the start, end and length of flowering phenology (dependent variables) between invasive and native species pairs, for region (California, Spain and the Cape region of South Africa), growth form, habitat invaded and pollination type as categorical predictors (see Table 1)*

Variable	Start of flowering			End of flowering			Length of flowering		
	d.f.	F	P	d.f.	F	P	d.f.	F	P
Region (R)	2	5·233	**<0·01**	2	2·974	0·053	2	8·949	**<0·001**
Growth form (GF)	2	1·998	0·138	2	0·144	0·866	2	1·422	0·244
Pollination type (PT)	1	0·002	0·963	1	0·411	0·522	1	2·129	0·146
Habitat type (HT)	3	0·93	0·427	3	0·359	0·783	3	0·166	0·919
R × GF	4	1·147	0·335	4	2·822	**<0·05**	4	0·701	0·592
R × PT	2	3·506	**<0·05**	2	2·99	0·052	2	0·187	0·83
GF × PT	2	0·647	0·525	2	0·299	0·742	2	0·85	0·429
R × HT	6	1·722	0·117	6	1·449	0·198	6	1·305	0·256
GF × HT	6	1·157	0·331	6	0·596	0·733	6	0·332	0·92
PT × HT	3	1·355	0·258	3	0·41	0·746	3	0·833	0·477

Three and higher order interactions are not showed for clarity and because they were not significant. To perform this analysis, flowering times for the Cape region were transformed to the Northern Hemisphere calendar (i.e. January–July). Significant values of *P* are indicated in bold.

TABLE 3. *Mean values of flowering phenology parameters between invasive and native plant species according to climatic origin and pollination type in the three Mediterranean climate regions*

Parameter	All species	Tropical	Temperate	Mediterranean	Animal-pollinated	Wind-pollinated
California	(n = 78)	(n = 3)	(n = 45)	(n = 30)	(n = 60)	(n = 18)
Start of flowering						
Invasive	29 April	17 May	19 May	25 March	11 April	19 May
Native	5 May	17 February	19 May	26 April	10 May	3 May
F-value	0·63 ns	0·64 ns	1·22E-04 ns	4·83*	2·44 ns	0·88 ns
End of flowering						
Invasive	21 July	16 October	13 August	6 June	24 July	23 July
Native	22 July	11 August	6 August	13 July	8 August	6 July
F-value	9·10E-4 ns	1·31 ns	0·13 ns	4·62*	0·73 ns	1·04 ns
Flowering duration (months)						
Invasive	4·1	6·7	3·9	3·9	4·2	3·6
Native	3·9	6·0	3·6	3·6	3·9	3·2
t-value	0·67 ns	0·36 ns	1·20 ns	0·67 ns	0·98 ns	1·27 ns
Spain	(n = 90)	(n = 43)	(n = 36)	(n = 11)	(n = 67)	(n = 23)
Start of flowering						
Invasive	4 June	14 June	2 June	20 May	30 May	30 May
Native	18 April	9 April	16 April	2 May	19 April	9 April
F-value	21·85***	27·82***	11·48***	0·42 ns	11·09***	11·63***
End of flowering						
Invasive	28 September	2 October	8 October	5 September	27 September	28 September
Native	4 September	3 September	2 September	7 September	18 August	24 September
F-value	3·72*	3·88*	4·42*	0·01 ns	4·02*	0·04 ns
Flowering duration (months)						
Invasive	4·8	4·7	4·8	5·5	4·8	4·6
Native	5·3	5·9	5·2	4·9	4·9	5·7
t-value	−1·47 ns	−2·53**	−0·93 ns	0·54 ns	−0·44 ns	−2·27*
Cape region	(n = 73)	(n = 28)	(n = 33)	(n = 12)	(n = 53)	(n = 20)
Start of flowering						
Invasive	15 September	29 October	27 August	8 September	11 September	26 September
Native	5 November	3 November	14 November	22 September	12 November	22 October
F-value	22·20***	0·05 ns	37·52***	1·56 ns	21·21***	2·53 ns
End of flowering						
Invasive	25 January	4 April	10 December	9 February	25 January	22 January
Native	13 January	26 January	5 February	8 March	15 January	5 January
F-value	0·51 ns	3·97*	1·26 ns	0·61 ns	0·33 ns	0·25 ns
Flowering duration (months)						
Invasive	5·2	6·1	4·5	5·2	5·1	5·4
Native	4·3	4·4	4·0	5·1	4·1	4·8
t-value	2·59**	2·96**	1·16 ns	0·86 ns	2·51*	0·86 ns

Circular mean values were transformed to days of the year for easier interpretation.
Watson–Williams *F*-values and *t*-test values are given: *P < 0·05; **P < 0·01; ***P < 0·001; ns, P > 0·05.

the differences in flowering phenology of invasive species are due to the differences in climatic origin of invaders rather than the particular species composition of the invasive flora.

Animal-pollinated species and climatic origin

Animal-pollinated invasive species displayed the same pattern as for the entire invasive–native comparison (Table 3, Fig. 3). This means that in California they had the same flowering phenology as native species, in Spain they started and finished their flowering later, and in the Cape region they started their flowering earlier, while invasive and native species finished at the same time. When comparing between regions, different climatic origins of animal-pollinated invaders showed differences in the onset of flowering. In California, Mediterranean invaders started flowering earlier than temperate invaders (Julian day Mediterranean species = 89, Julian day temperate species = 127; $F = 4.65$, $P < 0.05$). In Spain, tropical invaders started later than temperate invaders, but these differences were not significant (Julian day temperate species = 132, Julian day tropical species = 162; $F = 3.56$, $P = 0.065$). In the Cape region, tropical invasive species started significantly later than temperate ones (Julian day temperate species = 233, Julian day tropical species = 307; $F = 20.65$, $P < 0.001$) and also than Mediterranean ones (Julian day Mediterranean species = 232, Julian day tropical species = 307; $F = 7.2$, $P < 0.01$).

Invasive alien species had a different end of flowering in relation to their climatic origin. In California, tropical invaders finished flowering later than invaders from the Mediterranean (Julian day Mediterranean species = 181, Julian day tropical specis = 285; $F = 4.6$, $P < 0.05$). In Spain, no differences between groups were found for the offset of flowering. Lastly, in the Cape region, temperate invaders finished flowering earlier than tropical (Julian day temperate species = 338, Julian day tropical species = 76; $F = 27.1$, $P < 0.001$) or Mediterranean invaders (Julian day temperate species = 338, Julian day Mediterranean species = 72; $F = 7.1$, $P < 0.01$).

In summary, these differences suggest that a segregation of timing of flowering is occurring depending on the climatic origin of invasive species. Temperate invaders start flowering first, followed by the Mediterranean invaders and then the tropical invaders.

DISCUSSION

The three Mediterranean climate regions dealt with here occur along a gradient of summer drought severity, and their invasive floras differ in terms of the proportion of growth forms, their climatic origins and the habitats most invaded. Depending on the region selected, invasive species flowered earlier, later or at the same time as natives. Thus, a different flowering phenology pattern between groups is context dependent. It must be taken into account that, for a different timing of flowering between invasive and native species, two events must co-occur: (1) a small proportion of invasive species have to belong to the same climatic origin as the invaded region, i.e. Mediterranean climate; and (2) climatic and habitat conditions must minimize summer drought to allow invasive plants to survive. Related to the former premise, species tend to show a genetic inertia for the

time of flowering because flowering phenology is an adaptive trait selected to avoid unfavourable climatic conditions in the regions where the plants evolved (Fox, 1990*b*; Herrera, 1992; Johnson, 1993). In this sense, invasive species maintain the same flowering phenology when they are introduced to regions with the same climatic characteristics. Twenty-eight invasive species shared between at least two regions showed the same flowering phenology in both invaded regions, providing support for this idea. In general, invasive species from the Mediterranean flowered predominantly in spring, whereas tropical invaders continued flowering further into summer. On the other hand, temperate aliens flowered in early spring (in the Cape region) or in summer (in Spain) depending on whether they are woody or herbaceous species.

Recent studies have highlighted the importance of studying historical factors (e.g. the links between regions and colonial powers or human-mediated modifications to landscapes) as these factors are thought to shape the composition and magnitude of introductions (Lockwood *et al.*, 2007; Wilson *et al.*, 2007). Such anthropogenic factors may also influence the biotic interactions between invasive and native species as can occur with animal-pollinated plants. For example, no difference was noted in flowering phenology between invasive and native species in California, because the proportion of invaders from the Mediterranean Basin is high. This is due to California's historical links with Europe and especially with Spain as a colonial power (Bancroft, 1890). As both groups flower at the same time, they may compete for pollinators (Lopezaraiza-Mikel *et al.*, 2007). Competition for pollinators is thought to be an important form of disruption of plant–animal interactions caused by invasive species (Traveset and Richardson, 2006). However, in the Cape region and in Spain, flowering phenology of invaders was different from that of natives, since the proportion of invaders from Mediterranean climate regions is small. A high proportion of invaders of temperate and tropical origin in the Cape region are attributable to two events. From the 17th to the 19th century the current South Africa and thus the Cape region was a European colony. The influence and trade with countries such as The Netherlands and especially the UK increased the rate of deliberate introductions (Henderson, 2001). Temperate alien species were introduced from Europe or other European colonies such as Australia (e.g. *Hypericum perforatum* from Europe*, Acacia* species from Australia). On the other hand, more recently, tropical species (e.g. *Araujia sericifera, Passiflora caerulea*) have also been deliberately introduced for horticulture (Henderson, 2001). Although the introductions of alien species in both historical situations were for different reasons, the ecological result is convergent. Invasive species flower at a different time compared with the natives, filling an empty temporal niche. Flowering at a different time compared with natives may be an advantage for invasive species. It increases sexual fitness due to avoidance of pollen limitation and competition for pollinators with natives (Sargent and Ackerly, 2008). In contrast to the situation in the Cape region, most of the invasive plants in Spain were introduced accidentally with the trade of plants for agricultural purposes (Lloret *et al.*, 2005). Tropical summer weeds invading croplands and disturbed areas highlight the importance of the Spanish past linked to their American colonies.
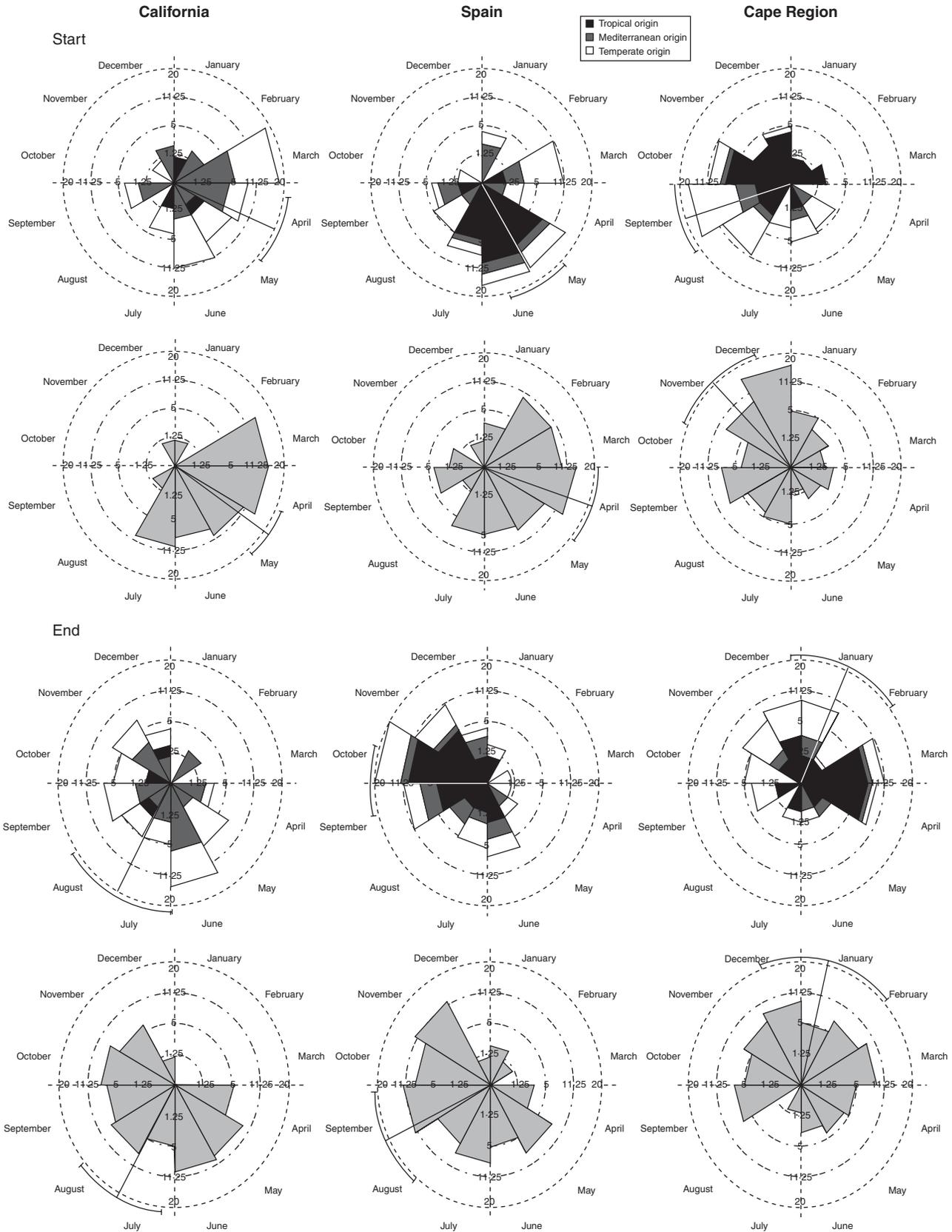
FIG. 3. Circular histograms for the start and the end of flowering in animal-pollinated invasive species and corresponding native species (see text). The triangles represent the number of species that flower in that month. Black areas indicate alien species of tropical origin; white areas indicate species with temperate origin; and dark grey areas show species with Mediterranean origin. Native species are shown separately in light grey below. Means and s.d. are also shown.

The reason for some invaders flowering in summer (the least favourable period for flower development in MTEs) is due to the type of habitat they invade. Disturbed areas are generally the most susceptible to invasion (Lake and Leishman, 2004; Cadotte *et al.*, 2006). Some disturbed habitats such as irrigated summer croplands and riparian habitats seldom experience water stress, allowing invasive plants to survive the summer drought in Mediterranean-type climates (Lake and Leishman, 2004). The importance of disturbed areas as a microenvironment for avoiding abiotic filters of the invaded region depends on the severity of summer drought. In California and Spain, where summer drought is intense, most of the species on the lists invade disturbed areas. In the Cape region, however, where summer drought is relatively mild, invasive species seem less limited by drought and can invade natural areas (Fig. 2).

Climatic and habitat environmental conditions can also influence the growth form of invaders and thus the length of flowering phenology of invasive species (Castro-Diez *et al.*, 2003). For example, disturbed areas have the advantage of minimizing abiotic unfavourable conditions, but limit the type of growth form that can invade. Annuals and short-lived plants are better adapted to rapid changes and disturbance conditions of this type of habitat (Grime, 1974). These types of invaders which can complete their life cycles in a few months showed a short flowering period associated with their short-lived cycle. Mainly herbaceous invaders of tropical origin in Spain (e.g. *Datura stramonium*, *Xanthium strumarium*) illustrate this situation. They show significantly shorter flowering periods than natives (Table 1). On the other hand, tropical invaders in the Cape region are mainly woody species that invade natural areas and flower longer than natives (Tables 1 and 2, and Fig. 2).

Previous studies have shown that successful invaders generally display early flowering or long blooming periods (Goodwin *et al.*, 1999; Pyšek *et al.*, 2003). Also, in alien–native comparisons, many authors have found that invasive alien species flower earlier than natives (Cadotte and Lovett-Doust, 2001; Lake and Leishman, 2004). Those results suggest that invasive species capitalize on an early blooming strategy to increase their reproductive success since the chance to acquire improved fitness via effective pollination visits is also increased (Goodwin *et al.*, 1999; Pyšek *et al.*, 2003). This idea is supported by other authors who have found that late, short flowering for pollination reduced opportunities for fruit and seed development of alien species (Roche *et al.*, 1997). However, the present results show that early flowering is not the only reproductive strategy for successful invaders. They can also flower at the same time or later than native species and be successful. Therefore, the possible different flowering phenology is mainly a consequence of different nature, historical and human factors that drive the reproductive relationship between groups. If this argument is correct, the same alien plant flowering phenological pattern should be found in regions with homogenous environmental conditions and the same history of introductions. This seems to apply for regions within the Mediterranean Basin. Dominance of summer flowering among invasive species in Spain (Table 3) is in agreement with previous results found for Italy (Celesti-Grapow *et al.*, 2003) and Mediterranean Islands (Lloret *et al.*, 2005).

Most invasion ecology studies relate traits of alien species to their capacity to invade, with the overall aim of unravelling aspects of the invasion process and aiming to predict future invasions. However, not all the observed plants traits identified as being associated with invasiveness in aliens really confer invasiveness, since other causes often underlie the observed pattern. This seems to be the case with flowering phenology. Although several studies have found a positive relationship between flowering phenology of aliens and their invasiveness potential (Goodwin *et al.*, 1999; Cadotte and Lovett-Doust, 2001; Pyšek *et al.*, 2003; Lake and Leishman, 2004), flowering phenology of invasive species and the possible differences relative to natives is only a consequence of different history of human-orchestrated introductions. The results of this study proved that under the same climatic conditions in three widely separated regions, invasive alien species do not display a common flowering phenology pattern. Instead, they flower earlier, later or at the same time as native species depending on the climatic regime in the region where they evolved.

SUPPLEMENTARY DATA

Supplementary data are available at *Annals of Botany* online and consists of a checklist of the 227 plant species (alien–native comparisons) in the three Mediterranean-type regions, California, Spain and the Cape region of South Africa.

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