Different flowering phenology of invasive alien species in Spain:

Evidence for the use of an empty temporal niche?

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Running head: Different invasive flowering phenology compared to natives in Spain

Diferente fenología de floración de las especies exóticas invasoras en España. ¿Evidencias del uso de un nicho temporal vacío?

Resumen

La fenología de floración es posiblemente un rasgo vegetal relacionado con el potencial invasor de las especies exóticas que todavía es poco comprendido. El presente trabajo evalúa si el tiempo de floración de las especies exóticas invasoras es un rasgo clave para sobrepasar los filtros climáticos que operan en los ecosistemas mediterráneos continentales de España (los cuales están caracterizados por la sequía estival y bajas temperaturas en invierno). Llevamos a cabo comparaciones entre la fenología de floración mostrada por la especies invasoras en su rango nativo y en España y además entre la fenología de floración de 91 pares invasora-nativa. Para las especies exóticas, cambios geográficos de la región nativa a la región que invaden no suponen cambios en el comienzo y duración del periodo de floración. En general, la floración en el rango de origen se mantiene después del traslado al rango donde invaden las especies exóticas. El pico de floración de las especies invasoras exóticas tropicales y templadas es en verano, lo que contrasta con el pico de floración primaveral de las especies nativas y las invasoras de clima mediterráneo. Explotar este nuevo nicho temporal, puede favorecer a estas especies invasoras una serie de beneficios derivados de una reducción de la competencia por los recursos bióticos y abióticos. Por ultimo, sugerimos que la acción humana sobre el territorio ha disminuido la importancia de la sequía estival en micro hábitat particulares, permitiendo la invasión de gran cantidad de especies de floración estival.

Palabras clave: Comparación invasora-nativa, areas perturbadas, origen climático, rasgos heredados, filtros abióticos.

Abstract

Flowering phenology is possibly an important plant trait related to the invasiveness potential of alien species that is still poorly understood. 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 (which are characterized by summer drought and low temperatures in winter). We conducted comparisons between the flowering phenology displayed by 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 changes from the native to the invaded region did not result shifts in the start and the length of 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 natives and invasive alien species from Mediterranean-climate origins. By exploiting this new temporal niche, these invasive alien species native to tropical and temperate regions benefit from a reduced competition with natives for abiotic and biotic resources. We suggest that human-mediated actions have diminished the strength of the summer drought filter in particular microhabitats, permitting the invasion of many summer-flowering aliens.

Key words: invasive-native comparison, disturbed areas, climatic origin, inherited trait, abiotic filters.

1 **Introduction**

2 Understanding the causes of biological invasions by non-native plants and their
3 ecological consequences is a key topic for biodiversity conservation (Huenneke et al.,
4 1990; Mack et al., 2000; Theoharides and Dukes 2007). Among the potentially
5 important traits observed in invasive alien species, a suited flowering phenology is a
6 key trait for achieving a high fecundity, which is one the properties recurrently found in
7 invasive species (Cadotte and Lovett-Doust 2001; Lake and Leishman 2004; Pyšek and
8 Richardson 2007). Interactions between genetic factors (Murfet 1977) and
9 environmental variables, such as day length (Orshan 1989; Imaizumi and Kay 2006),
10 drought (Fox 1990) or temperature (Orshan 1989; Hollister et al., 2005) determine the
11 period when a plant flower.

12 Climatic conditions under which plants have evolved determine flowering
13 phenology, although this trait might change if a plant is transported to a new region
14 (Rathcke and Lacey 1985; Dlugosch and Parker 2008). Plant species native to tropical
15 regions are known to flower either as a response to the tropical wet-season, as a
16 consequence of phylogenetic constraints or both, mainly corresponding with the
17 summer of temperate regions (Wright and Calderon 1995; Singh and Kushwaha 2006).
18 In temperate regions, where winter cold is the main environmental limiting factor,
19 flowering time can extend from early spring to late summer (Rathcke and Lacey 1985).
20 By contrast, in Mediterranean-type ecosystems (MTEs, e.g. Spain), where continental
21 regions are characterized by two unfavourable periods for plant activity a cold winter
22 and an arid summer (Mitrakos 1980; Orshan 1989), plant species have a narrow window
23 of time for completing their life cycle, flowering mainly in spring (Castro-Díez and
24 Montserrat-Martí 1998; Perez-Latorre et al., 2007).

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

12 The degree of change of functional traits (such as flowering phenology) between
13 the invaded and the native region is related to the severity of the climatic filters. If they
14 are not very limiting (Fig. 1c) invaders will preserve the flowering phenology of their
15 native range. This may lead to different flowering phenology as compared to natives so
16 invasive alien species can start flowering before and for longer periods than natives
17 (Pyšek and Richardson 2007) or later (Celesti-Grapo et al., 2003). Finally, if climatic
18 conditions are strongly limiting (Fig. 1d), the favourable period for flowering will be
19 short, and successful invaders will be those able to shift and match their phenology to
20 that of the native species. In this sense, Roche et al., (1997) have experimentally
21 demonstrated that a late flowering phenology of an invasive alien species reduces
22 enormously its success in a region with high summer drought, like the Mediterranean-
23 type ecosystems.

24 So far, it remains unclear whether the flowering phenology pattern observed in
25 invasive plants is due to a species specific reproductive strategy involving a variable

1 degree of local adaptation and plasticity, or invaders just conserve their flowering
2 phenology from their native region. Previous works in different places of the
3 Mediterranean Basin showed that summer-flowering invaders are the most abundant
4 (Celesti-Grapo et al., 2003; Lloret et al., 2005), when *a priori* summer is an
5 unfavourable period for flowering (Roche et al., 1997). This suggests that other factors,
6 such as the characteristics of the invaded habitat, may play an important role in the
7 invasion success of alien species, lessening the importance of abiotic filters (Fig. 1,
8 transition from d to c) (Lake and Leishman 2004).

9 The objective of the present study was to compare the flowering phenology of
10 invasive plant species with that of native ones in Spain and to study whether the
11 flowering phenology of invasive alien plants differs between their native and invaded
12 range. We addressed the following questions: i) Does flowering phenology of invasive
13 alien plants in Spain differ from that shown in their native region? ii) Do invasive plant
14 species differ in flowering phenology from the native species they share habitat with?
15 iii) If so, do the particular features of each invaded habitat play an important role
16 explaining such differences? A set of 91 invasive-native ecological pairs of species
17 from Spain were selected and a list of habitat, growth form and flowering phenology
18 features were recorded to address these questions.

20 **Materials and Methods**

21 *Species selection and data compilation*

22 Data of invasive plants in Spain were recorded from the Atlas of Invasive alien species
23 in Spain (Sanz-Elorza et al 2004). All listed species were selected, except those alien
24 plants that are invasive only in the Canary Islands (non-mediterranean climate) and
25 those that are *naturalized* 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 cover the possible origins of all alien species. Tropical category is referred to those species living between the tropic of Cancer and Capricorn; Temperate category is referred to those species living between the tropics and the Arctic and Antarctic circles; and finally, Mediterranean category, it is referred to the regions described by Cowling et al., (1996) and situated around the latitude 40° north or south; If the native region of an alien covers two or more climatic regions category, the region where the species was 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 type conditions rather than different flowering plant strategies (Thies and Kalko 2004). “Disturbed areas” category is referred to those habitats intensely modified by humans, while the other three categories are refer to natural areas where human impact is low. The category “coastal areas” covers those habitats where temperature amplitude is low during the year due to the sea influence. “Mesic inland areas” category covers inland habitats where high soil water content has a great influence on plant development, like 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 and Stenseth 1999).

Three categories - woody (trees and shrubs), herbaceous (annual and perennial herbs) and climber species - cover all 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 and Lacey 1985).

5-Flowering phenology was recorded by 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 controls (see below). Flowering phenology of alien species in their native range was collected from an extensive set of national floras over the world (see references in Supplementary Material).

To compare the above attributes between alien invasive and native plants, each invasive species was paired with one native species based on three 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, i.e. to be potential competitors; and (3) the two species 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 and Vigo 1984-2001; Castroviejo 1986-2005; Valdés et al., 1987; Casado et al., 2004; De Miguel et al., 2005;) (See Supplementary Material).

Data on flowering phenology of native plants was collected mostly from Iberian Flora (Castroviejo 1986-2005). Unfortunately, some native species have not been published yet in the Iberian Flora. In these cases, information was collected 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, we tested differences in flowering onset and cessation in 31

species reported in multiple flora books with a one-way ANOVA. No differences were found either in the start ($F=7.7E-4$, $p=0.978$) or in the end of flowering time ($F=0.723$, $p=0.402$).

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 statistic were performed to test for differences in the start and the end of flowering time 1) of invasive alien species between their native range and in the Spanish invaded range, and 2) 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 exotic have the same origin or the same pollination type. Data of Southern hemisphere species were transformed to Northern hemisphere climatically-equivalent months (i.e. January = July). Circular histograms are presented for a better interpretation of 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 species. This data subset was consistent, given that 1) 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 with results in Fig.1 of Supplementary material),. These analyses were performed with ORIANA package (Kovach Computing Services (Kovach 1994)). In all circular analysis, flowering phenological data followed a Von Mises distribution (circular version of normal distribution), therefore no transformation was needed.

To rule out the possibility that native-exotic differences were due to a bias in the taxonomic selection, a phylogenetic non-independence test was conducted to control for

the effect of the 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 the climatic origin of invasive species (the dependent variable was month difference between pairs), including 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 statistic analysis.

Results

Among the invasive plant species in Spain, the herbaceous growth form is significantly more frequent than the climber and woody growth forms; those with tropical and temperate origins are more frequent than Mediterranean-origin ones; and more species invade disturbed habitats than natural habitats (Fig. 1 Supplementary material).

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, $t = 0.41$, $p = 0.682$). The same result was obtained when the analysis was performed for each climatic origin group separately (data not shown). Invasive-native comparisons revealed a different flowering pattern between groups (Table 1, Fig. 3). On average, invasive species started flowering in

June, while the native species started flowering in April. Length of flowering period not differs between groups. Therefore, the significant differences continued to the end of flowering, which in invasive species was at the end of September and in native species at the start of September.

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

ANCOVA analysis testing for the effects of invasive origin and phylogenetic distance between paired invasive and native species on the invasive-native differences in the start and end of flowering time, 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 1.8 months later (Table 1).

Discussion

Our results show that invasive alien species do not significant shift the start, end and total length of their flowering between the invaded range in Spain and their native range. The consequence is that invasive alien plants exhibited a later flowering phenology (on average from early June to late September) compared to their

1 corresponding native ecological partners (from mid April to early September). Invasive
2 alien species native to a non-Mediterranean region (tropical and temperate) were
3 responsible for this pattern, whereas invaders native to other Mediterranean regions
4 showed the same flowering phenology as their native species pairs. This suggest that the
5 observed pattern is due to the different evolutionary histories of aliens driven by the
6 climatic conditions of their native region, and that flowering phenology of alien species
7 is a genetically determined trait that is little modified when they invade a new region.

8 The spring peak of flowering shown by species native to Spain, as well as by
9 invasive aliens from Mediterranean-type ecosystems, agrees well with the assumption
10 that in these regions summer drought and winter cold are highly limiting abiotic factors
11 for plant performance in general and for flowering in particular (Herrera 1992; Mitrakos
12 1980; Orshan 1989; Castro-Díez and Montserrat-Martí 1998; Perez-Latorre et al., 2007)
13 (Fig. 1) (Table 1). By contrast, invasive species native to tropical and non-
14 mediterranean temperate regions do not exhibit this flowering pattern, since they have
15 not evolved under the evolutionary pressure of an arid summer. For example, in
16 temperate ecosystems winter and autumn frosts are limiting factors for flowering, which
17 primarily occurs from spring to summer (Rathcke and Lacey 1985). Under tropical
18 climatic conditions, where temperature limitations do not exist, the flowering pattern is
19 influenced by internal plant factors, pollinator activity, and soil moisture (Wright and
20 Calderon 1995; Singh and Kushwaha 2006; Sloan et al., 2007).

21 Given that alien species conserve their flowering phenology when they invade a
22 new region, climatic conditions of Mediterranean-climate will be a filter only for those
23 species whose flowering time is unmatched with favourable local conditions for
24 blooming. If species cannot shift their flowering phenology when they invade a new
25 region and summer drought appears to have been a strong evolutionary pressure

1 selecting spring flowering in native species, how can tropical and temperate species be
2 so frequent among invaders in Spain? We suggest that human-mediated actions may
3 have widened this window by expanding those habitats with mitigated summer drought
4 (transition from d) to c) situation, Fig.1). Numerous studies targeted disturbed areas as
5 the most important habitats for biological invasions, since the specific conditions of
6 these invaded ecosystems play an important role for the establishment and spread of
7 invasive species (Cadotte et al., 2006). These particular microenvironments, such as
8 summer irrigated fields, recreational areas, canals and disturbed riparian forests, where
9 water is available during summer, minimise the drought limitations on plant survival,
10 growth and reproduction (Lake and Leishman 2004). Specifically for Mediterranean-
11 basin regions, Vilà et al, (2008) have recently demonstrated the importance of water
12 availability for the establishment and population persistence of alien species. Therefore,
13 most of the invaders of Spain and of other Mediterranean-basin regions live in human-
14 created habitats where summer drought is less pronounced (Lloret et al., 2005). In these
15 microenvironments, summer is an empty temporal niche that can be effectively invaded
16 by many alien species that are not particularly adapted to drought (Fig.1 Suppl.
17 material). Accordingly, the flowering difference between native and exotic species is
18 greater in disturbed than in natural habitats (Table 1 Suppl. material).

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

1 twenty times per year, increasing also the chances for persistence in the introduced
2 range.

3 The phenological asynchrony between invasive and native plants can be
4 expected to be more advantageous for animal- than for wind-pollinated invaders. Given
5 that invasive species peaked their flowering in summer when few natives are blooming
6 (Table 1) and pollinators are still abundant (Herrera, 1990), they may have an extra
7 reproductive benefit by diminishing or avoiding competition for pollinators (Gómez
8 2000; Picó et al., 2002). A reduction of the number of coflowering native plants can
9 increase the number of pollinator visits to invasive flowers, particularly when invasive
10 plants are more effective in attracting pollinators, as it has been found in some cases
11 (Moragues and Traveset 2005;Lopezaraiza-Mikel et al., 2007). Although self-
12 pollination is a common feature among invasive plants (Schueller 2004; van Kleunen et
13 al., 2007), an increase of the out-cross pollination may augment seed production (Parker
14 1997).

15 Our study suggests that the observed flowering phenology of alien species
16 results from multiple interactions between the abiotic filters in the invaded region, the
17 flowering phenology of alien species in their region of origin and the human-mediated
18 actions that have modified important habitat characteristics. Our results on the summer
19 phenology of alien invasive plants cannot be directly extrapolated to other
20 Mediterranean-climate regions such as California or the Cape Region of South Africa
21 because the proportion of invasive plants coming from each climatic region vary
22 between them (Bossard et al., 2000; Goldblatt and Manning 2000; Godoy et al., 2008).
23 However, our results, together with those found by Celesti-Grapow et al., (2003) and
24 Lloret et al. (2005), suggest that summer flowering of invasive alien species is a
25 recurrent pattern all across the Mediterranean basin.

In coastal Mediterranean regions, the number of invasive alien species is higher than in more continental regions. This may be attributed to the history of introductions, but also to the harsher climatic conditions of the inner Iberian Peninsula (Vilà et al, 2008; Sanz Elorza et al., 2004). 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 benefit from ameliorated winters could become increasingly successful in continental Mediterranean regions where they are currently absent or little abundant.

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References

- Bolòs, O., and Vigo, J. (1984-2001) *Flora dels Països Catalans* Barcelona: Barcino.
- Bossard, C.C., Randall, J.M., and Hoshovsky, M.C. (2000) *Invasive Plants of California's Wildlands*. Berkeley, CA: University of California Press.
- Cadotte, M.W., and Lovett-Doust, J. (2001) Ecological and taxonomic differences between native and introduced plants of southwestern Ontario. *Ecoscience*, 8(2), 230-238.
- Cadotte, M.W., Murray, B.R., and Lovett-Doust, J. (2006) Ecological patterns and biological invasions: Using regional species inventories in macroecology. *Biological Invasions*, 8(4), 809-821.
- Casado, M.A., Castro, I., Ramirez-Sanz, L., Costa-Tenorio, M., de Miguel, J.M., and Pineda, F.D. (2004) Herbaceous plant richness and vegetation cover in Mediterranean grasslands and shrublands. *Plant Ecology*, 170(1), 83-91.

- 1 Castroviejo, S. (1986-2005) Flora Ibérica. Plantas Vasculares de la Península Ibérica e
2 Islas Baleares. Madrid: Real Jardín Botánico-CSIC.
- 3 Celesti-Grapow, L., Di Marzio, P., and Blasi, C. (2003) Temporal niche separation of
4 the alien flora of Rome. In *Plant Invasions: Ecological Threats and Management*
5 *Solutions* (L.E. Child, J.H. Brock, G. Brundu, P. Prack, P. Pyšek, P.M. Wade,
6 and M. Williamson, eds), Leiden: Backhuys, pp 101-111.
- 7 Christensen, J. H., B. Hewitson, A. Busuioc, A. Chen, X. Gao, I. Held, R. Jones, R. K.
8 Kolli, W.-T. Kwon, R. Laprise, V. M. Rueda, L. Mearns, C. G. Menéndez, J.
9 Räisänen, A. Rinke, and A. S. P. Whetton. 2007. Regional Climate Projections.
10 Contribution of Working Group I to the Fourth Assessment Report of the
11 Intergovernmental Panel on Climate Change. Pages 847-943 *in* S. Solomon, D.
12 Qin, M. Manning, Z. Chen, M. Marquis, K. B. Averyt, M. Tignor, and H. L.
13 Miller, editors. *Climate Change 2007: The Physical Science Basis*. Cambridge
14 University Press, Cambridge, United Kingdom and New York, NY, USA.
- 15 Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.K., and Arianoutsou, M.
16 (1996) Plant diversity in Mediterranean-climate regions. *Trends in Ecology &*
17 *Evolution*, 11(9), 362-366.
- 18 De Miguel, J.M., Ramirez-Sanz, L., Castro, I., Costa-Tenorio, M., Casado, M.A., and
19 Pineda, F.D. (2005) Plant species richness and spatial organization at different
20 small scales in western Mediterranean landscapes. *Plant Ecology*, 176(2), 185-
21 194.
- 22 Dlugosch, K.M., and Parker, I.M. (2008) Invading populations of an ornamental shrub
23 show rapid life history evolution despite genetic bottlenecks. *Ecology Letters*,
24 11(7), 701-709.
- 25 Dudley, S.A. (2004) *Plasticity and the Functional Ecology of Plants In Phenotypic*
26 *Plasticity: Functional and Conceptual Approaches* (T.J. De Witt, and S.M.
27 Scheiner, eds): Oxford University Press.
- 28 Fox, G.A. (1990) Drought and the Evolution of Flowering Time in Desert Annuals.
29 *American Journal of Botany*, 77(11), 1508-1518.
- 30 Godoy, O., Richardson, D.M., Valladares, F., and Castro-Díez, P. (2008) Flowering
31 phenology of invasive alien plant species compared with native species in three
32 Mediterranean-type ecosystems. *Annals of Botany*, doi:10.1093/aob/mcn232
- 33 Goldblatt, P., and Manning, J. (2000) *Cape Plants: A conspectus of the Cape flora of*
34 *South Africa: Strelitzia* 9.
- 35 Gómez, J.M. (2000) Effectiveness of ants as pollinators of *Lobularia maritima* : effects
36 on main sequential fitness components of the host plant. *Oecologia*, 122(1), 90-
37 97.
- 38 Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*,
39 250(5461), 26-31.
- 40 Groves, R.H., and Di Castri, F. (1991) *Biogeography of Mediterranean invasions*
41 Cambridge: Cambridge University Press.
- 42 Herrera, C.M. (1990) Daily patterns of pollinator activity, differential pollinating
43 effectiveness, and floral resource availability, in a summer-flowering
44 mediterranean shrub. *Oikos*, 58(3), 277-288.
- 45 Herrera, C.M. (1992) Individual Flowering Time and Maternal Fecundity in a Summer-
46 Flowering Mediterranean Shrub - Making the Right Prediction for the Wrong
47 Reason. *Acta Oecologica-International Journal of Ecology*, 13(1), 13-24.
- 48 Hollister, R.D., Webber, P.J., and Bay, C. (2005) Plant response to temperature in
49 Northern Alaska: Implications for predicting vegetation change. *Ecology*, 86(6),
50 1562-1570.

- 1 Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A., and Vitousek, P.M. (1990)
- 2 Effects of Soil Resources on Plant Invasion and Community Structure in
- 3 Californian Serpentine Grassland. *Ecology*, 71(2), 478-491.
- 4 Imaizumi, T., and Kay, S.A. (2006) Photoperiodic control of flowering: not only by
- 5 coincidence. *Trends in Plant Science*, 11(11), 550-558.
- 6 Kovach, W.L. (1994) Oriana for Windows, ver 2.01. In UK: Kovach Computing
- 7 Services.
- 8 Lake, J.C., and Leishman, M.R. (2004) Invasion success of exotic in natural
- 9 ecosystems: the role of disturbance, plant attributes and freedom from
- 10 herbivores. *Biological Conservation*, 117(2), 215-226.
- 11 Lopezaraiza-Mikel, M.E., Hayes, R.B., Whalley, M.R., and Memmott, J. (2007) The
- 12 impact of an alien plant on a native plant-pollinator network: an experimental
- 13 approach. *Ecology Letters*, 10(7), 539-550.
- 14 Lloret, F., Medail, F., Brundu, G., Camarda, I., Moragues, E., Rita, J., Lambdon, P., and
- 15 Hulme, P.E. (2005) Species attributes and invasion success by alien plants on
- 16 Mediterranean islands. *Journal of Ecology*, 93(3), 512-520.
- 17 Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., and Bazzaz, F.A.
- 18 (2000) Biotic invasions: Causes, epidemiology, global consequences, and
- 19 control. *Ecological Applications*, 10(3), 689-710.
- 20 Mitrakos, K.A. (1980) A theory for Mediterranean plant life. *Acta Oecologica*, 1, 245-
- 21 252.
- 22 Moragues, E., and Traveset, A. (2005) Effect of *Carpobrotus* spp. on the pollination
- 23 success of native plant species of the Balearic Islands. *Biological Conservation*,
- 24 122(4), 611-619.
- 25 Murfet, I.C. (1977) Environmental Interaction and The Genetics of Flowering. *Annual*
- 26 *Review of Plant Physiology*, 28(1), 253-278.
- 27 Orshan, G. (1989) Plant pheno-morphological studies in Mediterranean type
- 28 ecosystems. . Dordrecht: Kluwer Academic Publishers.
- 29 Parker, I.M. (1997) Pollinator limitation of *Cytisus scoparius* (Scotch broom), an
- 30 invasive exotic shrub. *Ecology*, 78(5), 1457-1470.
- 31 Perez-Latorre, A.V., Gavira, O., and Cabezudo, B. (2007) Ecomorphology and
- 32 phenopormology of Mediterranean heathlands (SW Iberian Peninsula). .
- 33 *Phytocoenologia*, 37(2), 239-268.
- 34 Picó, F.X., de Kroon, H., and Retana, J. (2002) An extend flowering and fruting season
- 35 has a few demographic effects in a Mediterranean perennial herb. *Ecology*,
- 36 83(7), 1991-2004.
- 37 Post, E., and Stenseth, N.C. (1999) Climatic variability, plant phenology, and northern
- 38 ungulates. *Ecology*, 80(4), 1322-1339.
- 39 Pyšek, P., and Richardson, D.M. (2007) Traits Associated with Invasiveness in Alien
- 40 Plants: Where do we stand? In *Biological Invasions* (M.M. Caldwell, ed:
- 41 Springer Berlin Heidelberg, pp 97-125.
- 42 Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M., and
- 43 Kirschner, J. (2004) Alien plants in checklist and floras: towards better
- 44 communication between taxonomist and ecologist. . *Taxon*, 53, 131-143.
- 45 Rathcke, B., and Lacey, E.P. (1985) Phenological Patterns of Terrestrial Plants. *Annual*
- 46 *Review of Ecology and Systematics*, 16, 179-214.
- 47 Recasens, J., Calvet, V., Cirujeda, A., and Conesa, J. (2005) Phenological and
- 48 demographic behaviour of an exotic invasive weed in agroecosystems.
- 49 *Biological Invasions*, 7(1), 17-27.

- 1 Richardson, D.M., Pyšek, P., Rejmanek, M., Barbour, M.G., Panetta, F.D., and West,
2 C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions.
3 Diversity and Distributions, 6(2), 93-107.
- 4 Roche, C.T., Thill, D.C., and Shafii, B. (1997) Prediction of flowering in common
5 crupina (*Crupina vulgaris*). Weed Science, 45(4), 519-528.
- 6 Sanz Elorza, M., Dana Sanchez, D., and Sobrino Vesperinas, E. (2004) Atlas de las
7 Plantas Alóctonas Invasoras en España. Madrid: Ministerio de Medio Ambiente,
8 pp.378.
- 9 Schueller, S.K. (2004) Self-pollination in island and mainland populations of the
10 introduced hummingbird-pollinated plant, *Nicotiana glauca* (Solanaceae).
11 American Journal of Botany, 91(5), 672-681.
- 12 Singh, K.P., and Kushwaha, C.P. (2006) Diversity of Flowering and Fruiting Phenology
13 of Trees in a Tropical Deciduous Forest in India. Ann Bot, 97(2), 265-276.
- 14 Sloan, S.A., Zimmerman, J.K., and Sabat, A.M. (2007) Phenology of *Plumeria alba* and
15 its herbivores in a tropical dry forest. Biotropica, 39(2), 195-201.
- 16 Soltis, D.E., Soltis, P.S., Chase, M.W., Mort, M.E., Albach, D.C., Zanis, M.,
17 Savolainen, V., Hahn, W.H., Hoot, S.B., Fay, M.F., Axtell, M., Swensen, S.M.,
18 Prince, L.M., Kress, W.J., Nixon, K.C., and Farris, J.S. (2000) Angiosperm
19 phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. Botanical
20 Journal of the Linnean Society, 133(4), 381-461.
- 21 Theoharides, K.A., and Dukes, J.S. (2007) Plant invasion across space and time: factors
22 affecting nonindigenous species success during four stages of invasion. New
23 Phytologist, 176(2), 256-273.
- 24 Thies, W., and Kalko, E.K.V. (2004) Phenology of neotropical pepper plants
25 (Piperaceae) and their association with their main dispersers, two short-tailed
26 fruit bats, *Carollia perspicillata* and *C. castanea* (Phyllostomidae). Oikos, 104(2),
27 362-376.
- 28 Thuiller, W., Richardson, D.M., Pyšek, P., Midgley, G.F., Hughes, G.O., and Rouget,
29 M. (2005) Niche-based modelling as a tool for predicting the risk of alien plant
30 invasions at a global scale. Global Change Biology, 11(12), 2234-2250.
- 31 Valdés, B., Talavera, S., and Fernández-Galiano, E. (1987) Flora vascular de Andalucía
32 Occidental (3 volúmenes) Barcelona: Ketres.
- 33 van Kleunen, M., Fischer, M., and Johnson, S.D. (2007) Reproductive assurance
34 through self-fertilization does not vary with population size in the alien invasive
35 plant *Datura stramonium*. Oikos, 116(8), 1400-1412.
- 36 Weber, E.F. (1997) The alien flora of Europe: a taxonomic and biogeographic review.
37 Journal of Vegetation Science, 8(4), 565-572.
- 38 Vilà, M., Siamantziouras, A.-S.D., Brundu, G., Camarda, I., Lambdon, P., Médail, F.,
39 Moragues, E., Suehs, C.M., Traveset, A., Troumbis, A.Y., and Hulme, P.E.
40 (2008) Widespread resistance of Mediterranean island ecosystems to the
41 establishment of three alien species. Diversity and Distributions, 14(5), 839-851.
- 42 Wright, S.J., and Calderon, O. (1995) Phylogenetic Patterns among Tropical Flowering
43 Phenologies Journal of Ecology, 83(6), 937-948.

1 Tables Captions

2 Table 1 Mean values of flowering phenology parameters for invasive and native plant species of Spain according to their climatic origin and
3 pollination type. Circular mean values were transformed to days of the year for better interpretation. Flowering length is represented in months.
4 Watson-Williams F value and t-test value are also represented ($p > 0.05$ ns, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Parameters	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 ns	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 ns	6.39*	0.04 ns
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 ns	-2.53**	-0.93 ns	0.54 ns	-0.04 ns	-2.27*

1 **Figures Captions**

2 Figure 1 Conceptual diagram showing flowering phenology similarities of the invasive species in their native range ($\text{Alien}_{\text{orig}}$) and in Spain
3 ($\text{Alien}_{\text{inv}}$), and between flowering phenology of coexisting invasive ($\text{Alien}_{\text{inv}}$) and native species (Native). Environmental conditions are similar
4 (a) and different (b) between the native and the invaded region. Case c) refers to local environmental conditions as low-limiting factors for
5 flowering phenology, whereas in case d) environmental conditions are high-limiting factors for flowering. Changes in habitat characteristic (HC)
6 of the invaded region may lead to a transition from d) to c).

1

2

1 Figure 2 Circular histogram of flowering phenology for invasive species showing (a) start and (b) end of flowering time in their former native
2 range (left graphs) and in their invaded Spanish range (right graphs). Flowering phenology did not differ between native and invaded range of
3 alien species. Each triangle represents the number of species that flowers in each month. Mean vector and standard deviation are also shown.
4 (p>0.05 ns, * p<0.05, ** p<0.01, ***p<0.001)

5

1 Figure 3 Circular histogram of flowering phenology showing (a) start and (b) end of flowering time for invasive species (left graphs) and native
2 species (right graphs). Flowering phenology of invasive species started and ended later than the one of native species. Each triangle represents
3 the number of species that flowers in each month. F-values are shown in Table 1. Mean vector and standard deviation are also shown. ($p > 0.05$ ns,
4 * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

5

1 **Supplementary material**

- 2 Table 1 Mean values of flowering phenology parameters for invasive and native plant species of Spain according to habitat type they invade.
- 3 Circular mean values were transformed to days of the year for better interpretation. Length of flowering is measured in months. Watson-Williams
- 4 F value and t-test value are also represented ($p > 0.05$ ns, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

Parameters	Status	Disturbed areas n=58	Coastal areas n=18	Mesic inland areas n=10	Shrub & Woodland n=5
Start of	Invasive	6 June	16 May	4 June	4 February
flowering	Native	3 April	21 April	19 May	21 April
	F-value, p	30.04***	0.61 ns	0.57 ns	4.01 ns
End of	Invasive	1 October	20 August	15 September	20 November
flowering	Native	14 September	7 August	6 September	6 June
	F-value, p	15.95***	0.12 ns	0.38 ns	5.92*
Flowering	Invasive	3.9	3.2	3.6	8.2
length	Native	5.2	3.8	3.9	1.4
	t-value, p	-2.63**	-0.57 ns	-0.38 ns	2.7*

- 1 Figure 1 Number of invasive species according to their climatic origin, invaded ecosystem in Spain and growth form. Chi-square values and
- 2 their significance are also shown above each character. ($p>0.05$ ns, * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

3

4

1 Start and end of flowering of 91 ecological invasive-native pairs of plant species. Flowering phenology of invasive alien species in their native
2 range were collected from Atlas of Floras over the world (Flora of Australia, Flora of Canada, Flora of the Cape Region of South Africa, Flora of
3 China, Flora of Israel, Flora of Japon, Missouri Botanical Garden, Flora of Nicaragua, Flora of North America, Flora of Pakistan, Flora of URSS,
4 Flora of Western Australia). Flowering dates of invasive alien species that are natives to the southern hemisphere were transformed to the
5 northern hemisphere calendar (e.g. January to July).

6

Invasive Family/Species	Start of flowering	End of flowering	Start of flowering	End of flowering	Native Family/Species	Start of flowering	End of flowering
NATIVE RANGE			SPAIN				
Aceraceae <i>Acer negundo</i>	March	April	March	April	Oleaceae <i>Fraxinus angustifolia</i>	December	January
Agavaceae <i>Agave americana</i>	April	June	July	September	Lamiaceae <i>Rosmarinus officinalis</i>	September	May
Aizoaceae <i>Carpobrotus acinaciformis</i>	February	June	January	June	Apiaceae <i>Crithmum maritimum</i>	May	July
Anacardiaceae <i>Schinus molle</i>	---	---	May	June	Anacardiaceae <i>Pistacia lentiscus</i>	March	May
Apocynaceae <i>Vinca diformis</i>	March	May	January	December	Caryophyllaceae <i>Silene latifolia</i>	April	July
Asclepiadaceae							

<i>Gomphocarpus fruticosus</i>	November	April	June	August	Apocynaceae <i>Nerium oleander</i>	May	September
<i>Araujia sericifera</i>	January	December	May	September	Smilacaceae <i>Smilax aspera</i>	September	November
<i>Asclepias curassavica</i>	January	December	May	October	Lamiaceae <i>Ballota hirsuta</i>	May	July
Asteraceae							
<i>Achillea filipendulina</i>	July	August	June	October	Scrophulariaceae <i>Verbascum pulverulentum</i>	May	July
<i>Ambrosia artemisifolia</i>	July	October	June	November	Brassicaceae <i>Cakile Maritima</i>	February	October
<i>Arctotheca calendula</i>	January	May	March	June	Polygonaceae <i>Polygonum aviculare</i>	April	October
<i>Artemisia verliorum</i>	---	---	July	November	Asteraceae <i>Artemisia vulgaris</i>	July	November
<i>Baccharis halimifolia</i>	August	November	August	October	Chenopodiaceae <i>Halimione portulacoides</i>	August	November
<i>Bidens aurea</i>	August	September	September	January	Polygonaceae <i>Polygonum hydropiper</i>	July	October
<i>Bidens frondosa</i>	June	October	September	November	Polygonaceae <i>Polygonum lapathifolium</i>	June	November
<i>Bidens pilosa</i>	April	September	July	October	Brassicaceae <i>Rorippa palustris</i>	April	November
<i>Bidens subalternus</i>	---	---	August	November	Ranunculaceae <i>Ranunculus sceleratus</i>	March	October
<i>Conyza bonariensis</i>	January	December	March	September	Fabaceae <i>Melilotus officinalis</i>	May	November
<i>Conyza canadiensis</i>	June	December	July	November	Asteraceae <i>Crepis vesicaria</i>	February	June
<i>Conyza sumatrensis</i>	---	---	July	November	Polygonaceae <i>Rumex pulcher</i>	April	July
<i>Cotula coronopifolia</i>	May	November	March	August	Asteraceae <i>Aster tripolium</i>	October	November
<i>Helianthus tuberosus</i>	August	October	August	October	Asteraceae <i>Calendula arvensis</i>	January	December

<i>Senecio inaequidens</i>	---	---	May	October	Asteraceae <i>Centaurea aspera</i>	March	November
<i>Senecio mikanioides</i>	---	---	September	December	Rosaceae <i>Rubus ulmifolius</i>	June	August
<i>Xanthium spinosum</i>	July	October	July	October	Asteraceae <i>Sonchus oleraceus</i>	January	December
<i>Xanthium strumarium</i>	July	October	July	September	Asteraceae <i>Sonchus asper</i>	February	September
Boraginaceae							
<i>Heliotropium crassavicum</i>	May	September	June	October	Asteraceae <i>Pulicaria dysenterica</i>	July	October
Brassicaceae							
<i>Isatis tinctoria</i>	May	June	April	July	Brassicaceae <i>Sisymbrium austriacum</i>	April	August
Buddlejaceae							
<i>Buddleja davidii</i>	---	---	June	November	Cornaceae <i>Cornus sanguinea</i>	May	July
Cactaceae							
<i>Opuntia dillenii</i>	---	---	June	July	Rhamnaceae <i>Rhamnus lycioides</i>	March	May
<i>Opuntia ficus-indica</i>	May	August	May	June	Cistaceae <i>Cistus albidus</i>	February	June
Caprifoliaceae							
<i>Lonicera japonica</i>	May	July	May	September	Ranunculaceae <i>Clematis vitalba</i>	June	August
Chenopodiaceae							
<i>Achyranthes sicula</i>	---	---	March	June	Lamiaceae <i>Marrubium vulgare</i>	March	July
<i>Amaranthus blitoides</i>	June	November	April	December	Chenopodiaceae <i>Chenopodium murale</i>	January	December
<i>Amaranthus hybridus</i>	---	---	May	December	Chenopodiaceae	April	October

<i>Amaranthus muricatus</i>	---	---	April	December	<i>Chenopodium vulvaria</i> Malvaceae <i>Malva parviflora</i>	March	August
<i>Amaranthus powelli</i>	June	December	June	November	Chenopodiaceae <i>Chenopodium opulifolium</i>	March	November
<i>Amaranthus retroflexus</i>	June	November	May	December	Chenopodiaceae <i>Chenopodium album</i>	May	November
<i>Amaranthus viridis</i>	June	August	April	December	Chenopodiaceae <i>Chenopodium chenopodioides</i>	July	October
<i>Atriplex semibaccata</i>	July	August	September	October	Chenopodiaceae <i>Atriplex postrata</i>	July	September
Commelinaceae							
<i>Tradescantia fluminensis</i>	---	---	March	September	Lamiaceae <i>Glechoma hederacea</i>	February	June
Convolvulaceae							
<i>Ipomoea acuminata</i>	June	August	June	November	Convolvulaceae <i>Calystegia sepium</i>	May	September
<i>Ipomoea purpurea</i>	June	August	June	November	Rubiaceae <i>Galium aparine</i>	March	July
<i>Ipomoea sagittata</i>	June	August	June	August	Ranunculaceae <i>Clematis flammula</i>	April	August
Cyperaceae							
<i>Cyperus alternifolius</i>	---	---	June	September	Cyperaceae <i>Scirpus lacustris</i>	May	July
Elaeagnaceae							
<i>Elaeagnus angustifolia</i>	April	May	May	July	Tamaricaceae <i>Tamarix canariensis</i>	April	November
Euphorbiaceae							
<i>Chamaesyce polygonifolia</i>	---	---	July	November	Fabaceae <i>Medicago littoralis</i>	February	November
<i>Ricinus communis</i>	---	---	May	December	Solanaceae <i>Lycium europaeum</i>	September	October

Fabaceae

<i>Acacia dealbata</i>	February	April	January	March
<i>Acacia longifolia</i>	December	April	March	June
<i>Acacia melanoxylon</i>	February	April	March	June
<i>Acacia saligna</i>	January	May	March	May
<i>Gleditsia triacanthos</i>	May	June	March	June
<i>Robinia pseudoacacia</i>	May	June	March	July
<i>Sophora japonica</i>	---	---	June	August

Hydrocharitaceae

<i>Elodea canadensis</i>	June	September	May	August
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Iridaceae

<i>Tritonia x crocosmiflora</i>	---	---	May	August
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Malvaceae

<i>Abutilon theophrasti</i>	May	October	August	September
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Myrtaceae

<i>Eucalyptus camaldulensis</i>	January	August	January	December
<i>Eucalyptus globulus</i>	November	January	October	January

Nyctaginaceae

<i>Mirabilis jalapa</i>	June	March	June	September
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Onagraceae

<i>Oenothera biennis</i>	July	October	June	September
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Betulaceae

<i>Betula alba</i>	April	May
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Rosaceae

<i>Pyrus cordata</i>	April	June
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Rosaceae

<i>Malus communis</i>	April	June
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Fabaceae

<i>Ceratonia siliqua</i>	September	January
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Salicaceae

<i>Populus alba</i>	February	April
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Ulmaceae

<i>Celtis australis</i>	April	May
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Ulmaceae

<i>Ulmus glabra</i>	February	April
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Potamogetonaceae

<i>Potamogeton densus</i>	July	July
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Primulaceae

<i>Lysimachia nemorum</i>	April	August
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Malvaceae

<i>Malva neglecta</i>	March	September
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Lauraceae

<i>Laurus nobilis</i>	February	April
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Tiliaceae

<i>Tilia platyphyllos</i>	June	September
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Malvaceae

<i>Malva sylvestris</i>	January	October
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Apiaceae

<i>Foeniculum vulgare</i>	June	November
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<i>Oenothera glazioviana</i>	July	October	June	September	<i>Daucus carota</i>	March	September
Oxalidaceae					Asteraceae		
<i>Oxalis pes-caprae</i>	December	June	September	May	<i>Cirsium arvense</i>	June	July
Papaveraceae					Papaveraceae		
<i>Eschscholzia californica</i>	February	September	May	October	<i>Papaver rhoeas</i>	February	September
Passifloraceae					Cannabaceae		
<i>Passiflora caerulea</i>	---	---	June	October	<i>Humulus lupulus</i>	June	September
Poaceae					Poaceae		
<i>Bromus willdenowi</i>	---	---	May	August	<i>Dactylis glomerata</i>	March	July
<i>Cenchrus incertus</i>	April	October	June	September	Poaceae	March	July
<i>Chloris gayana</i>	---	---	March	August	<i>Lagurus ovatus</i>		
<i>Echinochloa hispidula</i>	---	---	July	October	Poaceae	January	December
<i>Echinochloa oryzicola</i>	---	---	July	October	<i>Hyparrhenia hirta</i>		
<i>Echinochloa oryzoides</i>	---	---	July	October	Cyperaceae	June	November
<i>Eleusine indica</i>	---	---	July	October	<i>Cyperus difformis</i>	July	September
<i>Paspalum dilatatum</i>	January	December	July	October	Cyperaceae	May	August
<i>Paspalum paspalodes</i>	---	---	July	September	<i>Scirpus mucronatus</i>		
<i>Paspalum vaginatum</i>	---	---	July	September	Cyperaceae	May	August
<i>Sorghum halepense</i>	June	August	May	October	<i>Eleocharis palustris</i>		
<i>Spartina patens</i>	May	October	June	September	Poaceae	January	June
					<i>Poa annua</i>		
					Cyperaceae	May	November
					<i>Scirpus holoschoenus</i>		
					Poaceae	April	June
					<i>Polypogon viridis</i>		
					Cyperaceae	February	June
					<i>Carex divisa</i>		
					Poaceae	April	November
					<i>Piptatherum miliaceum</i>		
					Poaceae	May	July
					<i>Spartina Marchitima</i>		

<i>Stenotaphrum secundatum</i>	June	October	July	September	Poaceae <i>Cynodon dactylon</i>	January	December
Polygonaceae							
<i>Fallopia baldschuanica</i>	April	June	May	October	Caprifoliaceae <i>Lonicera peryclimenum</i>	May	August
<i>Reynoutria japonica</i>	June	September	August	September	Asteraceae <i>Eupatorium cannabinum</i>	July	September
Pontederiaceae					Nymphaeaceae		
<i>Eichhornia crassipes</i>	January	December	March	July	<i>Nymphaea alba</i>	March	October
Simaroubaceae					Ulmaceae		
<i>Ailanthus altissima</i>	April	May	May	July	<i>Ulmus minor</i>	February	April
Solanaceae					Boraginaceae		
<i>Datura innoxia</i>	September	November	May	September	<i>Heliotropium europaeum</i>	March	November
<i>Datura stramonium</i>	July	November	May	November	Solanaceae	January	May
<i>Nicotiana glauca</i>	---	---	April	October	<i>Hyoscyamus albus</i>	July	September
<i>Solanum bonariense</i>	---	---	April	July	Celastraceae <i>Maytenus senegalensis</i>	July	September
Tropaeolaceae					Solanaceae	July	September
<i>Tropaeolum majus</i>	---	---	May	September	<i>Solanum dulcamara</i>		
Verbenaceae					Urticaceae		
<i>Lippia filiformis</i>	---	---	June	September	<i>Urtica dioica</i>	April	September
Zygophyllaceae					Verbenaceae		
<i>Zygophyllum fabago</i>	May	September	June	August	<i>Verbena officinalis</i>	June	October
					Chenopodiaceae		
					<i>Atriplex rosea</i>	July	September