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Evidence of deterministic assembly according to flowering time in an old-field plant community

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Summary

1. Theory has produced contrasting predictions related to flowering time overlap among coexisting plant species largely because of the diversity of potential influences on flowering time. In this study, we use a trait-based null modelling approach to test for evidence of deterministic assembly of species according to flowering time in an old-field plant community.

2. Plant species coexisting in one-metre-square plots overlapped in flowering time significantly more than expected. This flowering synchrony was more pronounced when analyses focused on bee-pollinated species. Flowering synchrony was also observed for wind-pollinated species, although for only one of our two null model tests, highlighting the sensitivity of some results to different randomization methods. In general, these patterns suggest that relationships between pollinators and plants can influence community assembly processes.

3. Because our study community is composed of approximately 43% native plant species and 57% exotic species, and because the arrival of new species may complicate plant–pollinator interactions, we tested whether flowering time overlap was altered by introduced species. Flowering synchrony was greater in plots with a higher proportion of introduced species. This pattern held for both null model tests, but was slightly stronger when analyses focused on bee-pollinated species. These results indicate that introduced species alter community flowering distributions and in so doing will inevitably affect pollinator–plant interactions.

4. Finally, we tested whether our results were influenced by variation among study plots in above-ground biomass production, which some theory predicts will be related to the importance of competition. Our results were not influenced by this variation, suggesting that resource variation among our plots did not contribute to observed patterns.

5. *Synthesis:* Our results provide support for predictions that coexisting species should display flowering synchrony, and provide no support for species coexistence via temporal niche partitioning at this scale in this study community. Our results also indicate that introduced species significantly alter the community assembly process such that flowering synchrony is more pronounced in plots with a greater proportion of introduced plant species.

Key-words: coexistence, community assembly rules, competition, flowering synchrony, introduced species, limiting similarity, niche overlap, null model, overdispersion, underdispersion

Introduction

A central goal in ecology is to identify and quantify the mechanisms driving the organization of species within and among communities (i.e. community assembly rules) (e.g. Diamond 1975; Weiher & Keddy 1999). Species organization can be viewed as a 'filtering' process that determines species membership at a given scale, with reference to the pool of species available in the larger surrounding area that have the potential to colonize (Keddy 1992; Weiher & Keddy 1999). This filtering process may be driven by competition, disturbance, environmental adversity (e.g. Grime 1979) or other factors and will constrain community composition at a particular site by selecting for certain species or for particular traits (e.g. Weiher, Paul Clarke & Keddy 1998; Stubbs & Wilson 2004; Schamp, Chau & Aarssen 2008). A number of specific predictions have been made concerning how competition will drive the deterministic assembly of plant communities according to specific traits (e.g. Weiher & Keddy 1995, 1999; Grime 2006). Several of these predictions remain untested or insufficiently explored.

One prediction concerning how interspecific trait variation may influence the diversity and organization of species

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within and among plant communities is that coexisting species will differ strongly with respect to traits for which variation may contribute to the use of different resources, and thus the avoidance of competition (i.e. reduced niche overlap/limiting similarity; MacArthur & Levins 1967; Roughgarden 1974; Weiher & Keddy 1995; Stubbs & Wilson 2004). One way that plant species can avoid or reduce interspecific competition, and therefore spatially coexist, is to grow and/or reproduce at different times (i.e. temporal niche separation; e.g. Cody 1968; Veresoglou & Fitter 1984; Fargione & Tilman 2005). Species with different phenological schedules should compete less, and therefore have an increased potential to coexist. Based on this premise, coexisting plant species should differ in flowering time (Pleasants 1980), although species may also differ in other traits that contribute to reduced niche overlap (e.g. Stubbs & Wilson 2004). Flowering time as we use it here refers to the timing of development and maintenance of traits associated with reproduction. Flowering time varies across species (Pleasants 1980; Cole 1981; Fleming & Partridge 1984; Rathcke 1988) and may be an indicator of timing of maximum resource requirement for many herbaceous plant species, which typically reproduce towards the pinnacle of yearly growth. Accordingly, interspecific overlap in flowering time among neighbouring herbaceous plants can lead to intense competition for soil and light resources or for pollinators (e.g. Rotenberry 1990). While expectations under limiting similarity would be that coexisting plant species will overlap less with respect to flowering time (i.e. reduced niche overlap; Weiher *et al.* 1999), other work suggests that coexisting plant species that share pollinators may benefit from flowering synchrony, which may increase the likelihood of pollination/reproduction (Thomson 1978; Ghazoul 2006), and increase the frequency of outcrossing (Rathcke & Lacey 1985). Thus, contrasting predictions have been made regarding expected patterns of plant organization within communities with respect to flowering time.

Several studies have investigated overlap in flowering time among plant species (e.g. Snow 1965; Mosquin 1971; Gentry 1974; Heithaus 1974; Heinrich 1976; , Anderson & Schelfhout 1980; Pleasants 1980, 1990; Schemske 1981; Fleming & Partridge 1984; Rathcke & Lacey 1985), although predictions, mechanisms, methods and findings vary from study to study. Some researchers have predicted reduced overlap (divergence/overdispersion) in flowering time in response to competition for either soil resources or pollinators (e.g. Mosquin 1971; Pojar 1974; Pleasants 1980; Fleming & Partridge 1984), to prevent or minimize heterospecific pollen transfer (Waser 1978a,b; Waser & Fugate 1986; McLernon, Murphy & Aarssen 1996; Brown & Mitchell 2001; Morales & Traveset 2008) or to avoid the spread of pollinator transmitted diseases (Elzinga *et al.* 2007). Other researchers have predicted convergence (underdispersion) in flowering time related to ensuring pollinator visitation (e.g. Corner 1940; Augspurger 1981; Schemske 1981; Ims 1990), reducing flower damage by seed predators (Janzen 1971; Stephenson 1981; Mittelbach & Gross 1984), satiating granivores (e.g. Smythe 1970; Janzen 1971; Beattie, Breedlove & Ehrlich 1973; Augspurger 1981) or ensuring fruit consumption by dispersing animals (Poulin *et al.* 1999).

Previous studies have focused on testing whether overlap in flowering time among species within a community differs from what would be expected if flowering times were randomly assigned from a uniform distribution (e.g. Pleasants 1980; Cole 1981; Fleming & Partridge 1984; Ashton, Givnish & Appanah 1988; Rathcke 1988). Importantly, none of these studies have compared actual flowering time overlap patterns with a null distribution defined by the flowering times of species in the larger species pool, a method commonly used in other trait-based assembly investigations (e.g. Stubbs & Wilson 2004; Schamp, Chau & Aarssen 2008; Schamp, Horsak & Hajek 2010).

A number of researchers have noted that exotic plant species may alter the pollination dynamics within a natural community (e.g. Bjerknes *et al.* 2007; Bartomeus, Bosch & Vilà 2008; Cariveau & Norton 2009), although particular expectations vary. There are predictions, for example, suggesting that introduced plant species may suffer more pollen limitation (Parker 1997), but there are also predictions that introduced species may be less pollen limited because they would experience reduced competition with native plants for pollinators (Brown & Mitchell 2001; Rambuda & Johnson 2004; Dietzsche, Stanley & Stout 2011). These studies have not produced specific predictions related to flowering time overlap among coexisting species; however, it is logical to expect that under pollen limitation, plants could benefit from synchronous flowering. It is unclear at this time how the inclusion of introduced plant species may affect flowering time overlap within plant communities; however, some authors have predicted that exotics will have greater success in communities when they differ from other species with respect to important functional traits (Moles, Gruber & Bonser 2008). This prediction is supported by the findings of Cleland *et al.* (2011) that native and introduced plant species differed significantly with respect to suites of functional traits. It is not known whether the addition of introduced plant species alters the degree of flowering time overlap within a plant community, or whether introduced species are more likely to be found in plant associations where they differ strongly in flowering time (e.g. Case 1990).

In this study, we tested three predictions related to the ecological filtering of plant species according to flowering time: (i) plant species coexisting at the local neighbourhood scale (within 1-m^2 plots) in an old-field plant community will overlap in flowering time significantly more or less than expected under our null model, signifying ecological filtering or limiting similarity, respectively; (ii) patterns related to ecological filtering or limiting similarity with respect to flowering time will be more pronounced for bee-pollinated plant species than when analysis includes all plant species, as these species potentially compete directly for pollinators in addition to soil nutrients and sunlight;

(iii) evidence of ecological filtering or limiting similarity based on flowering time will be more pronounced in plots containing a greater proportion of introduced plant species, which theory predicts may succeed in new communities by differing from other resident species in important ways that reflect reduced niche overlap (i.e. flowering time) (Moles, Gruber & Bonser 2008).

Materials and methods

STUDY SITE

This research was conducted in an old-field plant community from May to October 2009 at the Queen's University Biological Station, Chaffey's Locks, Ontario, Canada (44°34′N, 76°20′W). The field is relatively homogeneous topographically and hosts 37 plant species known to differ considerably with respect to multiple functional traits (Schamp, Chau & Aarssen 2008) including flowering time (Fig. 1). The study field has not been ploughed or tilled for more than 40 years, but in most years since then it has been mown for hay once per year. Vegetation in this community is dominated by perennial plant species, the most common of which include *Poa pratensis, Phleum pratense, Cerastium arvense, Potentilla recta, Vicia cracca* and *Rumex acetosella.*

DATA COLLECTION

A 50 × 50 m study area near the centre of the field was chosen to reduce any edge effects from the surrounding forest, and 50 1 × 1 m plots were randomly located within a 20 × 20 grid of possible plots. This plot size was chosen to reflect a scale at which plant species interactions, particularly negative interactions between neighbouring plants, are likely to be relevant. All 50 plots were surveyed early in the season (15 May 2009) to determine species composition and surveyed three additional times throughout the growing season (29 May, 17 July, and 9 October) to ensure that plot censuses were complete and accurate. Above-ground biomass from each plot was harvested in October 2009, dried at 60°C for 3 days and then weighed. Also, 25 individual plants (i.e. ramets) of each species were located in the field, and marked at the base using a labelled aluminium tag (925 tagged plants). All tagged plants were located outside of the 50 study plots, but within the study field. Tagged individuals of each species were monitored once weekly from the start of May to the end of October in 2009 (24 weeks) to produce species-specific flowering time distributions; not all individuals of a particular species were flowering in each week. Flowering was considered started when the first flower was observed to be open on an individual plant (Pleasants 1980), and flowering was considered terminated when the plant no longer possessed any flowers with anthers. All study species flowered within the 24 weeks of monitoring (Fig. S1, Supporting information). At the time monitoring began, some individuals of six species had already begun flowering. We ran sensitivity analyses, extending the flowering distribution start times for these species backwards up to 4 weeks based on information from published floras (Gleason & Cronquist 1991; Fitter & Peat 1994), to test whether missing the start of the flowering period for these species influenced the results.

DATA ANALYSIS

To calculate flowering time overlap within our plots, we used the number of flowering plants per species per week for each species (i.e. species-specific flowering distribution), which was based on our collection of flowering time data for 25 individuals of each species within the study community (but not within plots). We calculated overlap in flowering time (Overlap) for each plot using an index of niche overlap (Schoener 1970; Pleasants 1980). This index is calculated as:

$$1 - \frac{1}{2}\sum_{k=1}^{n} |p_{ik} - p_{jk}|,$$

with p_{ik} and p_{jk} representing the proportion of individuals flowering of species i and species j in the kth week (for each of the 24 weeks plants were monitored). An average of pair-wise overlap in flowering time across all species pairs in a given plot was used as a measure of plot-level overlap in flowering time (Pleasants 1980), and the average across all plots was used as a community score, the first of two test statistics. We also calculated, for each plot, the standard deviation in overlap between each species and its nearest neighbour with respect to flowering time overlap. This is a measure of how regularly spaced coexisting species are with respect to flowering time (SDNN used by Kraft and Ackerly 2010). Assembly processes may drive coexisting species to overlap more strongly in flowering time, but still be more evenly spaced with respect to this trait. Such a pattern has been interpreted as the product of both competitive and ecological filtering. The mean of this value across plots was used as our second test statistic. Because flowering time was not assessed for each species in each plot, species-specific flowering time distributions were applied to each species observed in plots that were observed to flower in that plot within the year of study. This method assumes that flowering times for species in plots are adequately represented by our collected distribution data, analogous to the application of species-level trait data in general (Weiher, Paul Clarke & Keddy 1998; Stubbs & Wilson 2004; Schamp, Chau & Aarssen 2008; Schamp & Aarssen 2009; Schamp, Horsak & Hajek 2010; Schamp, Hettenbergerová & Hájek 2011; Wilson & Stubbs 2012). Using flowering time distribution data, as we do here, takes advantage of more detailed information on intraspecific variation than simple means or maxima, which ignore intraspecific variation (e.g. Schamp, Chau & Aarssen 2008).

To test for evidence that coexisting plant species overlap in flowering time more or less than would be expected in the absence of ecological filtering or limiting similarity, we used an established null model (Stubbs & Wilson 2004; Schamp, Chau & Aarssen 2008; Schamp & Aarssen 2009, Schamp, Horsak & Hajek 2010). This null model uses the community presence–absence matrix (species x plot) in conjunction with a matrix of flowering time data for each species (species × number of individuals out of 25 flowering per week over the 24 week period) to test whether, on average, flowering time overlap among coexisting species differs from what is expected when flowering time data are randomized (see below). Average flowering time overlap among plots, the community test statistic (Weiher, Paul Clarke & Keddy 1998; Stubbs & Wilson 2004; Schamp, Chau & Aarssen 2008), is then compared to a distribution of test statistics generated by (i) applying a randomization to the trait matrix (or presence–absence matrix; see below for details), (ii) recalculating the test statistic using the randomized data, (iii) repeating steps 1–2 many times (5000 times here; Schamp, Chau & Aarssen 2008; Schamp, Horsak & Hajek 2010). With this null model, flowering time overlap can either be greater or less than expected (i.e. flowering synchrony or limiting similarity respectively) and consequently all tests are presented using two-tailed P-values, calculated as follows:

$$P = \mathrm{MIN}[2S/(5000), 2L/(5000)]$$

where S and L are the number of randomized test statistics greater than or equal to, or less than or equal to the measured test statistic, respectively (Bersier & Sugihara 1997). All tests were performed using Matlab code developed by B. Schamp. Although we use presence–absence matrices to calculate overlap, abundance matrices can also be used (e.g. Stubbs & Wilson 2004). However, evidence suggests that this approach, at least as it has been previously implemented (e.g. Schamp, Chau & Aarssen 2008), may be overly conservative (Schamp, Hettenbergerová & Hájek 2011). Also, previous work has shown that the combination of fixed plot sizes and abundance-weighted analysis may be influenced by variation in plant density due to species size differences (Schamp, Chau & Aarssen 2008), an issue that is exacerbated when abundance is quantified using per cent cover.

In consideration of recent discussion in the literature (e.g. Wilson & Stubbs 2012), we completed all null model tests using two different randomization procedures (step 1 above). The first randomization procedure has been common in the literature (Stubbs & Wilson 2004; Schamp, Chau & Aarssen 2008; Schamp & Aarssen 2009; Schamp, Horsak & Hajek 2010; Schamp, Hettenbergerová & Hájek 2011). Using this randomization method, here called the Abundance-Independent Trait Shuffling approach (AITS), the null model asks whether overlap in flowering time among coexisting species differs from what is expected if flowering time distributions are shuffled among species within the community randomly (without replacement). This method allows the flowering time distributions of rare species to be shuffled in such a way that they can become common, something that may inappropriately inflate the influence of transient species on the results (Wilson & Stubbs 2012). It is possible that this null model confounds the processes that govern abundance with those that govern trait distributions among coexisting species. Essentially, this method assumes that the trait in question is not limiting any species from being abundant in the community (i.e. no correlation between trait and abundance). In most cases, the truth of this assumption is unknown. In the current case, there is no significant correlation between mean flowering time and abundance, measured here as the number of plots each species was found in (Pearson Correlation: $n = 37$, $P = 0{\cdot}556$).

The second null model randomization technique we used, which we call Abundance-Weighted Trait Shuffling (AWTS), addresses these concerns by separating the processes governing abundance from those governing trait distributions. To accomplish this, we randomly assign flowering time distributions from the species pool to each plot; however, the probability of assigning a given flowering time distribution is weighted by the abundance of the species with that flowering schedule across our study plots (i.e. the number of plots that a species/flowering time distribution is found in). Thus, if five species are found in a plot, five flowering time distributions are assigned randomly to this plot (again without replacement), but the likelihood of a given flowering time distribution being assigned is weighted by its abundance in the actual community. The AWTS randomization method ensures that trait–abundance relationships remain relatively stable in the system, with common trait values remaining relatively common while rare traits remain relatively rare. This second null model therefore asks whether overlap in flowering time among coexisting species differs from what is expected if traits are shuffled, but flowering time–abundance relationships are kept relatively stable. This is therefore a slightly different question than asked with AITS. Both randomization methods conserve species richness patterns in the community and avoid potentially problematic issues that arise when the presence–absence matrix is randomized (e.g. Weiher, Paul Clarke & Keddy 1998; Mouillot, Mason & Wilson 2007). We include both models because it is not clear at this time that one is more correct than the other; this depends on whether the mechanisms that determine abundance and trait combinations are in fact distinct. We believe the inclusion of both models is a careful approach that allows us to determine how sensitive our results are to the assumptions of the null model, and can be taken as a test of whether the first of the null models (AITS), which has been more commonly used, is likely to produce different results than the second (AWTS).

Predictions related to flowering time overlap range in focus from all coexisting species, if flowering time overlap is used as a general proxy for temporal overlap in demand on many resources, to a guild of plant species potentially competing for pollinators in addition to soil and light resources (e.g. bee-pollinated species; Pleasants 1980). Therefore, we first used our null model analyses to test for evidence of deterministic patterns of flowering time overlap for all 37 plant species. Then, given the potential for patterns of species organization related to flowering time to differ among wind- and animal-pollinated species (wind-pollinated species do not compete for pollinators), we also carried out these analyses for only wind-pollinated species (11 species) and for only plants pollinated by bees (26 species; sources for pollinator data in Table S1, Supporting information).

To test whether introduced species contribute to observed patterns of plant species organization in relation to flowering phenology, we took advantage of the fact that our study plots naturally varied in the proportion of native and introduced species (native status in Ontario, USDA 2010; Table S1, Supporting information). We tested whether standardized effect sizes for each of our study plots, obtained from our null model analyses of all species (18 introduced plant species, 19 native species) and of bee-pollinated species (15 introduced; 11 native), are related to the proportion of native species within vegetation plots, using linear regression. Standardized effect sizes (i.e. z-scores) were calculated for each plot as (O-M)/S, where O is the observed flowering time overlap for that plot, and M and S are the mean and standard deviation in flowering time overlap for that plot across 5000 iterations of the null model randomization procedure (Schamp & Aarssen 2009; Schamp, Horsak & Hajek 2010). This test addresses (i) whether the presence of more introduced species in plots alters flowering time distributions and (ii) whether plots containing more introduced species are characterized by more or less niche overlap (with respect to flowering time) than expected if flowering times are randomized without regard to native status. This test also addresses predictions that introduced species succeed in new communities by being sufficiently different from other resident species (Moles, Gruber & Bonser 2008), although only with respect to variation in flowering time. Six plots were excluded from the analysis of bee pollinated species as they did not contain more than one bee-pollinated species, which does not allow for the calculation of a standardized effect size (i.e. overlap cannot change with trait randomization).

Finally, to test whether our results are influenced by variation in abiotic conditions among plots within our study site, we tested whether plot-level standardized effect sizes of our tests were related to plot-level variation in above-ground biomass production.

Results

COMMUNITY ASSEMBLY AND FLOWERING TIME

When all plant species in the community were considered (37 species), locally coexisting plant species overlapped in flowering time significantly more than expected under both null model randomization schemes (AITS: $P = 0{\cdot}0188$; AWTS: $P = 0{\cdot}0164$; Table 1). These results provide support for ecological filtering of species with coexisting species overlapping in flowering time more than expected (i.e. flowering synchrony). Additionally, we found no evidence that coexisting species were more evenly spaced with respect to overlap in flowering time among nearest neighbours (SDNN Overlap: AITS: $P = 0{\cdot}5348$; AWTS: $P = 0{\cdot}1024$). Collectively, these results provide no support for predictions that coexisting species will differ significantly with respect to flowering time. When we extended the start of flowering backward for a few early-flowering species, results were unchanged (Table S2, Supporting information), indicating that missing the beginning of the flowering period for these species did not impact our results.

OVERLAP IN FLOWERING TIME FOR PARTICULAR POLLINATION GUILDS

Wind-pollinated species (11 plant species) overlapped in flowering time more than expected; however, this was confined to one of our two null model tests (AITS: $P = 0{\cdot}2428$; AWTS: $P = 0{\cdot}0008$; Table 1). When we only considered bee-pollinated plant species in the analysis (26 plant species), species overlapped in flowering time significantly more than expected (AITS: $P = 0{\cdot}0032$; AWTS: $P = 0{\cdot}0096$; Table 1).

NATIVE VS. INTRODUCED SPECIES

To examine the impact of introduced species on observed patterns of interspecific overlap in flowering time, we tested whether the proportion of introduced species in plots were significant predictors of plot-level effect sizes of our tests. This test was conducted for all species and for bee-pollinated species separately. For both null model tests, overlap in flowering time relative to what was expected under our null model (i.e. standardized effect size) was significantly higher in plots with a higher proportion of introduced plant species. This was the case when all species were considered together (AITS: $n = 50$; slope=4·097; $R^2 = 0{\cdot}14$, $P = 0{\cdot}008$; Fig. 2a; AWTS: $n = 50$; slope=4·664; $R^2 = 0{\cdot}27$; $P < 0{\cdot}001$) and when only bee-pollinated species were considered (AITS; $n = 44$; slope=3·36; $R^2 = 0{\cdot}18$, $P = 0{\cdot}005$; Fig. 2a; AWTS: $n = 44$; slope=3·49; $R^2 = 0{\cdot}28$; $P < 0{\cdot}001$; Fig. 2b). The proportion of introduced species in plots explained more variation in plot-level overlap for bee-pollinated species (Fig. 2).

To control for the potential impact of variation in plot-level species richness, we tested for the impact of both variation in plot-level richness and the proportion of introduced species on plot-level overlap effect sizes using multiple linear regression. Significant flowering synchrony is generally more pronounced in more species rich plots (3 of four tests); however, the proportion of introduced species has a consistently significant influence on flowering synchrony across our study plots. This was true for all species (AITS: $n = 44$, $R^2 = 0{\cdot}29$, richness: $P = 0{\cdot}004$, proportion invasive: $P < 0{\cdot}001$; AWTS: $n = 44$, $R^2 = 0{\cdot}36$, richness: $P = 0{\cdot}101$, proportion invasive: $P < 0{\cdot}001$), as well as for bee species (AITS: $n = 44$, $R^2 = 0{\cdot}48$, $P < 0{\cdot}001$ for both variables; AWTS: $n = 44$, $R^2 = 0{\cdot}43$, richness: $P = 0{\cdot}002$, proportion invasive: $P < 0{\cdot}001$). Interestingly, the proportion of introduced species is a better predictor of overlap for bee-pollinated species than for all species.

EFFECTS OF PLOT-LEVEL BIOMASS VARIATION

Plot-level standardized effect sizes were not significantly related to above-ground dry biomass production of plots for all species (AITS: $n = 50$ plots, $P = 0{\cdot}92$; AWTS: $n = 50$, $P = 0{\cdot}86$) or for bee-pollinated species (AITS: $n = 44$ plots, $P = 0{\cdot}65$; AWTS: $n = 40$, $P = 0{\cdot}53$). These results provide no support for our observed results being driven by differences in annual biomass production among plots.

Discussion

OVERLAP IN FLOWERING TIME AMONG COEXISTING SPECIES

When all plant species were analysed together, our results indicated that plant species coexisting in 1 × 1 m square plots within our study community overlap in flowering

Table 1. Results from two different null model tests for nonrandom species organization (AITS, abundance-independent trait shuffling; AWTS, abundance-weighted trait shuffling) according to mean overlap in species flowering phenology, and variation (SDNN) in nearest neighbour overlap in flowering time for: (i) all flowering plant species (37 species), (ii) wind-pollinated species (11 species) and (iii) bee-pollinated species (26 species). Significantly lower mean overlap in flowering time than expected is consistent with limiting similarity predictions (Obs < Exp), while higher overlap than expected is consistent with theory predicting flowering synchrony (Obs > Exp). High variability in pair-wise overlap in flowering time among coexisting species (SDNN Overlap: Obs > Exp) is considered consistent with limiting similarity predictions. Values for Obs > Exp and Obs < Exp are *P*-values; bold values are significant at $\alpha = 0{\cdot}025$

Randomization method	Species guild	Mean overlap		SDNN overlap	
		Obs < Exp	Obs > Exp	Obs < Exp	Obs > Exp
AITS	All species		**0·0188**	0·5348	
	Wind-pollinated	0·2428		0·9228	
	Bee-pollinated		**0·0032**		0·6272
AWTS	All species		**0·0164**		0·1024
	Wind-pollinated		**0·0008**	0·9360	
	Bee-pollinated		**0·0096**		0·2548

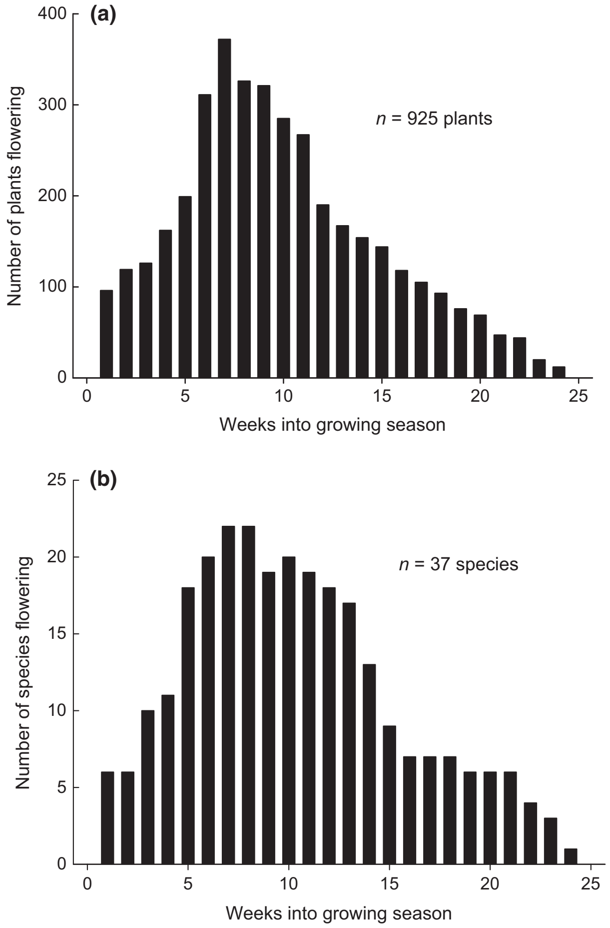

Fig. 1. A frequency histograms showing the distribution of flowering time for 925 tagged plants belonging to 37 species over the growing season at the Queen's University Biological Station, Ontario, Canada (a). Panel (b) is a frequency histogram showing how many species (n = 37 species) are flowering each week over the growing season. The flowering season commenced on 15 May 2009 and ended by 22 October 2009 (24 weeks). The onset of flowering occurred once a flower in a given plant opened (Pleasants 1980). Flowering was considered to be terminated when species no longer possessed anthers.

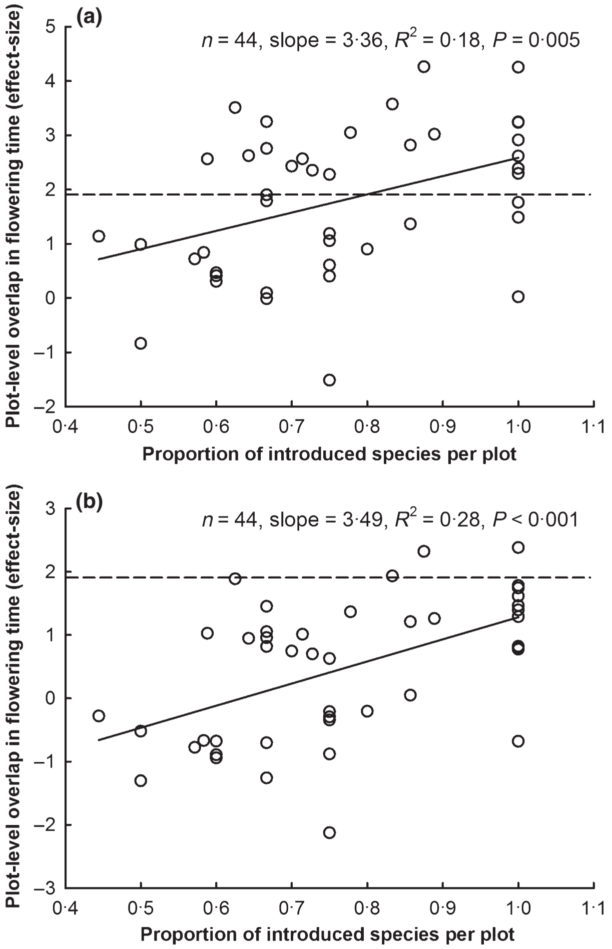

Fig. 2. Linear regressions showing that flowering time overlap among coexisting plant species pollinated by bees is significantly higher than expected under the null model (measured as the plot-level standardized effect size) when plots contain a higher proportion of introduced plant species. This pattern is observed when (a) traits are shuffled among species without regard to trait–abundance relationships (AITS) and (b) traits are assigned randomly to plots but weighted by trait abundance such that trait–abundance relationships are more closely maintained (AWTS).

time significantly more than expected (i.e. synchronous flowering; Table 1). These results were not affected by extending backwards the start of flowering for six species that had representatives already flowering at the start of our census (Table S2, Supporting information). This observed flowering synchrony, clear evidence of ecological filtering of species according to flowering time, may result from a combination of improved pollination and therefore seed production under locally synchronous flowering, in combination with relatively local dispersal. This amounts to a form of interspecific facilitation in terms of pollinator attraction. Under such circumstances, species that flower at very different times than near neighbours may achieve lower local seed dispersal compared with synchronously flowering heterospecifics, resulting in the eventual loss of asynchronously flowering species from the neighbourhood (i.e. plot). This mechanism is analogous to that theorized by Grime (2006) to remove less competitive ends of a trait gradient among species, resulting in a contracted/convergent set of trait values left among coexisting species. This pattern may be more pronounced for relatively rare species, or newly arriving species, for which flowering synchrony may be more important, although our data cannot be used to test this. Alternatively, flowering synchrony may result from local resource availability peaking within a relatively narrow timeframe, such that species that do not peak in resource use around this focal time are eventually locally excluded; however, this possibility is perhaps less likely given the relatively homogeneous nature of the community. Our results provide no support for the prediction that coexisting plant species will differ significantly with respect to flowering time as a possible mechanism for reducing overlap among species in timing of maximal resource requirement (i.e. limiting similarity; Table 1).

Reduced flowering time overlap may still contribute to species coexistence in combination with other differences among coexisting species; however, we find no evidence of the reduced overlap in flowering time that has been predicted previously (e.g. Pleasants 1980).

OVERLAP IN FLOWERING TIME FOR PARTICULAR POLLINATION GUILDS

When our analyses concentrated on those plant species known to be pollinated by bees, we again found evidence of ecological filtering of species according to flowering time (i.e. flowering synchrony). Coexisting bee-pollinated species overlap significantly in flowering time, independently of which randomization method was used (Table 1). We analysed bee-pollinated species separately to focus on a group of plant species competing for pollinators, presumably in addition to other resources, and to allow us to compare our results with previous work (e.g. Pleasants 1980; Augspurger 1981). Additionally, this approach acknowledges that flowering time may differently impact the fitness of distinct pollination guilds. This approach was validated by the fact that we found evidence of consistent, significant overlap in flowering time (i.e. flowering synchrony) among coexisting bee-pollinated species, but only inconsistently among wind-pollinated species (Table 1). We are aware of no theory predicting flowering synchrony among coexisting wind-pollinated species. This finding, which also highlights the potential for these two null model tests to produce different results, warrants future attention. In general, however, these results suggest that patterns observed for all species are likely driven by these more pronounced and consistent patterns of flowering time synchrony among bee-pollinated species.

Evidence suggests that pollen limitation may be a reality for as much as 60% of plant species (Ashman *et al.* 2004; Knight *et al.* 2005), suggesting that pollen limitation is likely for at least some of the species in this community. Therefore, competition among plant species for pollinators may be contributing to our observed patterns. Consequently, our results add to the existing body of theory suggesting that a synchronous flowering schedule contributes to reproductive success, possibly as a result of greater pollinator exposure (e.g. Ims 1990). It is also possible that flowering synchrony contributes to reduced seed predation (Janzen 1971; Stephenson 1981; Mittelbach & Gross 1984). For example, Augspurger (1981) experimentally demonstrated that synchronously flowering populations of a single species achieved greater seed production through increased pollination and suffered less seed predation. Synchronized pollination may also contribute to seed-predator satiation, improving fitness for synchronously flowering and seeding species (Smythe 1970; Beattie, Breedlove & Ehrlich 1973).

These results differ from previous work identifying reduced flowering time overlap (i.e. flowering asynchrony) in plant communities (Mosquin 1971; Heinrich 1976; Stiles 1977; Anderson & Schelfhout 1980; Pleasants 1980; Ashton, Givnish & Appanah 1988) and from studies identifying random patterns of assembly according to flowering phenology (Rabinowitz *et al.* 1981; Wheelwright 1985), but are in agreement with other studies that have observed convergence in flowering time among coexisting plant species (Parrish & Bazzaz 1979; Schemske 1981; Rathcke 1988). Our results also depart from predictions that plant species in communities characterized by the presence of introduced species should have a relatively random assorting of flowering periods (Heinrich 1976). These results also suggest that the negative effects of heterospecific pollen transfer (Waser 1978a,b; Waser & Fugate 1986; McLernon, Murphy & Aarssen 1996; Brown & Mitchell 2001; Morales & Traveset 2008) are not strong enough to contribute to reduced patterns of overlap in flowering time in this community, in spite of the clear effects on fitness that this can have. At least one study suggests that heterospecific pollen transfer may not necessarily occur among coflowering species (Bartomeus, Bosch & Vilà 2008).

The degree to which our results can be directly compared to those from studies listed above is limited by important differences in approach. We believe that our approach is an improvement on some aspects of previous approaches that have compared the observed flowering time overlap among species to distributions of overlap generated from a uniform distribution (e.g. Pleasants 1980; Rathcke 1988). Such approaches discount the general tendency for flowering distributions across species to show a mid-domain effect within the growing season (Morales, Dodge & Inouye 2005). The current approach avoids this problem by generating null expectations from the existing flowering time distributions of all species within the community; thus, any mid-domain effect is built into the null expectations. Additionally, we believe our approach more appropriately tests for differences between observed and theoretical overlap. We tested how extreme observed overlap is relative to our null distributions, in contrast to a variety of earlier approaches, which include comparing observed overlap to the grand mean of overlap in the null distribution using a t-test (Pleasants 1980), an approach that appears to discount the breadth of the null distribution. These differences, along with the relatively high contribution of introduced species within our study community and the focus on small plots (i.e. local neighbourhoods) within our study community, may also account for the difference between our findings and some of those mentioned above.

NATIVE VS. INTRODUCED SPECIES

Recent research suggests that introduced species may disrupt plant–pollinator interactions (Bjerknes *et al.* 2007; Bartomeus, Bosch & Vilà 2008). In our study community, introduced species have a pronounced effect on the degree of flowering time overlap (i.e. synchrony) observed among all coexisting species, as well as coexisting bee-pollinated species; overlap in flowering time is accentuated in plots that have a higher proportion of introduced species, independent of which randomization method is used with our null models (Fig. 2). While it is clear that introduced species can affect pollination (Bjerknes *et al.* 2007; Cariveau & Norton 2009), the impact of introduced species on the organization of species has received less attention. Evidence suggests that introduced species that are less related to resident species may become invasive with greater probability than more closely related exotics (Strauss, Webb & Salamin 2006), and another study has indicated that introduced species can increase phylogenetic diversity (Valiente-Banuet & Verdú 2007). Finally, Cleland *et al.* (2011) found evidence that exotic and native species differed significantly with respect to suites of functional traits. The underlying suggestion in these studies is that introduced species may succeed by avoiding competition through reduced overlap in new communities. Our results do not support this view as plots with more introduced species were characterized by increased flowering time overlap (increased temporal niche overlap) relative to null model expectations. Indeed, the association between the proportion of introduced species and plots with high flowering time overlap suggests that introduced species may reap some benefit from flowering synchrony. Our results are the first we are aware of that demonstrate how introduced species alter local flowering distributions (Fig. 2), and to suggest that introduced species may benefit from flowering at the same time as nearby species.

Flowering synchrony may improve pollination across species, and this may have contributed to our results if asynchronously flowering species in our plots achieve lower fitness due to pollen limitation. Contrasting predictions have been set out concerning whether introduced species should suffer more or less pollen limitation. Parker (1997), for example, has proposed that introduced species may suffer more pollen limitation because they lack effective pollinators, implying that they may benefit from flowering synchrony. Others have suggested that introduced species may be less pollen limited due to reduced competition for pollinators (Brown & Mitchell 2001; Dietzsche, Stanley & Stout 2011) or by augmenting pollinator populations by providing more floral resources (Bjerknes *et al.* 2007). Finally, Rambuda & Johnson (2004) have suggested that introduced species may suffer less pollen limitation as they generally have higher frequencies of autogamy in introduced species; if this is the case, these species would not necessarily benefit from flowering at the same time as other species. While our results do not test these predictions directly, they do indicate that flowering synchrony is increased in plots with more introduced species, which is consistent with the predictions of Parker (1997), and the notion that introduced species may augment pollination in general by providing more floral resources to flower visitors (Bjerknes *et al.* 2007). We explored the possibility that increased flowering synchrony in plots with a greater proportion of introduced species resulted from introduced species simply having longer flowering times. However, *post hoc* tests indicate that for all species, or for bee-pollinated species, introduced species do not flower for a significantly shorter or longer period than native species (All Species: Mann–Whitney rank sum test: $P = 0{\cdot}998$; Bee Species: Mann–Whitney rank sum test: $P = 0{\cdot}657$). Newly arriving species within a community, which will inevitably be rare at first, may be more successful in gaining a foothold by overlapping more greatly in flowering time with residents. Our results do not support theory and findings that introduced species can gain a foothold in new communities by being sufficiently different from other species with respect to flowering time (e.g. Case 1990; Moles, Gruber & Bonser 2008), a measure of temporal niche differentiation, as flowering synchrony among coexisting species clearly increases with the addition of introduced species (Fig. 2).

EFFECTS OF PLOT-LEVEL BIOMASS VARIATION

Finally, we explored the possibility that abiotic differences among plots may have contributed to our results, and found no evidence that variation in productivity among plots contributed to the observed overlap in flowering time. It is possible that other abiotic differences between plots may have contributed, but this analysis reduces the likelihood of resource differences contributing to our observed patterns.

SUMMARY

Our study community is deterministically organized with respect to species flowering times within local neighbourhoods. While this applies to all species, our results, considered altogether, suggest that this is likely a function of strong flowering synchrony among plant species that are pollinated by bees (Table 1). One possible explanation for our results is that pollen limitation incurred by a species that differs in flowering time from other species that it shares pollinators with may impose greater fitness costs than competition incurred through greater phenological overlap or from heterospecific pollen transfer. These results suggest that interspecific variation in flowering time within plant communities is less likely a broad mechanism for resource partitioning than a mechanism contributing to greater pollination. Additionally, we found evidence that flowering synchrony is greater in plots with a larger number of introduced species, suggesting that newly arriving species may succeed more readily by overlapping in flowering time with other species.

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Supporting Information

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

Fig S1. Frequency histograms showing the distribution of flowering time over the growing season for 25 individuals (ramets) of each species (n = 37 species) at the Queen's University Biological Station.

Table S1. A list of plant species from this community highlighting whether species are native or introduced, and what pollinators are associated with all animal pollinated species.

Table S2. Results from a sensitivity test intended to assess the potential impact of missing the start of the flowering distribution for six of our study species.