

A functional group analysis of change in the abundance and distribution of 207 plant species across 115 years in north-central North America

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Abstract Identifying declining species is essential for conservation planning. This research assessed abundance and distribution changes of 207 plant species in north-central North America and evaluated the importance of a suite of functional characteristics in predicting their persistence over 115 years (1895–2009). Functional characteristics included native versus introduced origin, pollination syndrome, symbiosis and habitat requirements, and phenological responsiveness to temperature change. Plant specimens from Ohio State University’s Herbarium were used to assess abundance and distribution changes. The partial Solow equation and the sighting rate model were used to calculate the average probability that a species had declined over the study interval. Rarefaction analysis was used to calculate the percent change in distribution as measured by county occurrences from historic (1895–1970) to modern (1971–2009) time periods. Twenty-seven percent of the 207 species decreased in abundance from 1895 to 2009 and 68 % showed distribution contraction. Native species were seven times more likely to decline in abundance and showed a two-fold greater distribution contraction compared to introduced species. Introduced species that strongly advanced flowering with warming showed greater distribution expansion than those with weak phenological responsiveness. Species that require a symbiont for growth or development were twice as likely to decrease in abundance as those without symbiont requirements. This analysis indicates non-random patterns of threat to species diversity among plant functional groups. With climate warming, highly responsive introduced species may become more widespread. Thus, climate warming may exacerbate

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the already substantial impacts of land-use change, symbiont loss, and non-native species invasion on species persistence.

Keywords Functional trait · Abundance · Distribution · Climate change · Phenology · Invasive species

Introduction

Efforts to monitor and identify declining species and groups of species are of increasing importance given the ubiquity of alteration to natural systems, the decline of suitable habitat, and anthropogenic climate change. As assessment of every species in a given region is not possible, functional characteristics may provide key information for predicting which species are most likely to experience declines in abundance and geographic distribution. Identification of characteristics that predispose species to decline would allow conservation efforts to target groups of species most likely to be threatened in absence of extensive data on the occurrence and distribution of these species, which often does not exist (Farnsworth and Ogurcak 2008). For example, insect-pollinated species in New England, USA had significantly greater range contraction than species not reliant on an insect pollinator (Farnsworth and Ogurcak 2008) and plant species in Ontario, Canada able to reproduce clonally or with relatively high seed production were less rare relative to those without these traits (Cadotte and Lovett-Doust 2002).

Plant phenological responses to climate warming present conservation concerns because species with phenological responses less well suited to the warming environment may show non-random patterns of decline (Willis et al. 2008). Shifts in flowering phenology with increased temperature (phenological responsiveness, *sensu* Calinger et al. (2013) have been observed globally (Parmesan and Yohe 2003) and suggest that climate change may already be impacting community-level functions and interactions (CaraDonna et al. 2014; Menzel et al. 2006; Rosenzweig et al. 2008). Further, the extent to which species shift flowering with increased temperature is highly variable (Abu-Asab et al. 2001; Fitter and Fitter 2002; Iler et al. 2013a, b). In a study of 141 species of flowering plants in north-central North America, Calinger et al. (2013) found flowering shifts ranging from 13.5 days earlier to 7.3 days later per degree C temperature increase. Coupled with the 0.9 °C springtime temperature increase over the past century across Ohio and locally greater temperature increases of up to 2 °C, these results suggest climate change is already significantly altering the timing of seasonal events across broad spatial scales. The differential performance of plants with varying phenological responsiveness to increased temperature has already been observed in a handful of studies. In a meta-analysis of 57 species, Cleland et al. (2012) found that those species that were able to “track” warming by advancing their flowering or leaf phenology showed enhanced performance in a variety of metrics including number of flowers and biomass production while those with weaker phenological responses experienced performance declines. Further, in the northeastern U.S., species with weak flowering advancement in response to higher temperatures (in other words, flowering time is not shifted significantly earlier with higher temperatures) have shown significantly greater declines in abundance over the past 150 years relative to those with stronger flowering advancement (Willis et al. 2008).

Climate change raises further conservation concerns as non-native species may use shifting phenology with temperature increase to create windows of opportunity for invasion (Wolkovich and Cleland 2011). With higher temperatures, introduced species may shift flowering times to currently unoccupied niches, before or after the typical native growing season, to take advantage of higher light availability and lower competition for pollinators (vacant phenological niche hypothesis, Wolkovich and Cleland 2011). Also, successful introduced species may be better able to track climate change than less responsive native species through phenotypic plasticity, adaptation to the climatic conditions of their invaded ranges, or some combination of the two (phenological flexibility hypothesis, Wolkovich et al. 2013). Willis et al. (2010) found that invasive species advanced flowering approximately 9 days more than non-invasive introduced species and other studies have shown greater flowering shift among non-native species compared to native species (Calinger et al. 2013; Wolkovich et al. 2013) suggesting a link between high phenological responsiveness and invasiveness. Thus, phenological responsiveness could potentially become a valuable conservation metric for identifying introduced species likely to become invasive with further warming. However, the relationship between phenological responsiveness and long-term abundance and distribution shifts of native versus non-native species remains largely untested at the community level or above (but see Wolkovich et al. 2013).

A single functional trait like phenological responsiveness or invasive status is unlikely to be diagnostic for decline (Cadotte and Lovett-Doust 2002). Assessing the effects of multiple functional traits on species persistence is critical for predicting species decline and for conservation planning. Functional traits that are affected by anthropogenic alteration of the landscape are likely to be highly predictive of decline as these alterations are major drivers of species loss. For instance, pollination syndrome, wetland requirements, flowering responses to temperature, and symbiosis requirements may be impacted by pollinator declines and competition with invasive species, wetland drainage and deforestation, climate warming and extreme temperature variation, and pollution, respectively. However, assessments of functional trait impacts on species decline are often limited by insufficient data (Newbold 2010). Thus, development and implementation of methods that allow for investigation of decline in many species covering multiple functional traits across varied regions is essential.

Specimens stored in museums represent the most complete record describing both occurrence and distribution for most of the 1.5 million described species (Burgman et al. 1995; Ponder et al. 2001; Solow and Roberts 2003). As a result, a variety of methods have been developed to estimate abundance decline and extinction (Burgman et al. 1995; McCarthy 1998; McInerney et al. 2006; Solow 1993; Solow and Roberts 2003) and distribution shifts (Solow and Roberts 2006) using museum specimens. These methods have been used successfully to assess changing abundance in a diversity of taxonomic groups including plants (Duffy et al. 2009; Farnsworth and Ogurcak 2006; McInerney et al. 2006), amphibians and reptiles (Akmentins et al. 2012; Hamer and McDonnell 2010), mammals (van der Ree and McCarthy 2005), insects (Carpaneto et al. 2007), and fish (Luiz and Edwards 2011). Application of museum-based methods to a large number of species paired with functional group characterizations is an invaluable tool for conservation planning, not only to identify currently threatened species, but also to target species with traits that may predispose them to decline.

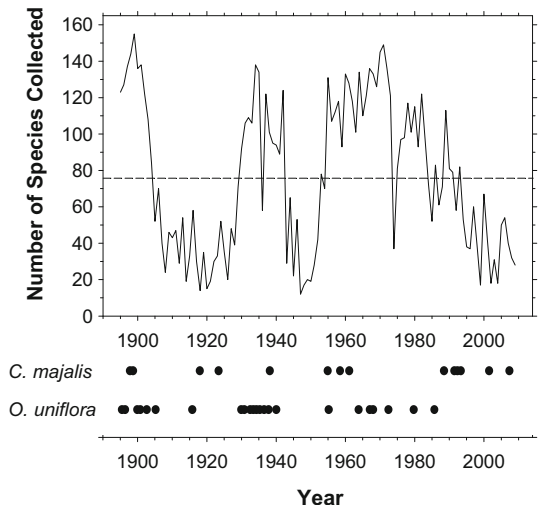
Using museum-based techniques coupled with a functional trait analysis, I tested the following hypotheses regarding functional trait impacts on abundance and distribution shifts in 207 plant species found in north-central North America. (1) Species with high

phenological responsiveness (flowering shift with temperature increase) will experience less abundance and distribution decline than those with weak phenological responsiveness as these species will be able to take advantage of longer windows of favorable temperatures and will be more likely to maintain mutualisms. (2) Species incapable of vegetative reproduction will display greater abundance and distribution decline because those species with some capacity for asexual reproduction are less likely to be negatively impacted by competition for pollination services or pollinator mismatches. (3) Habitat specialists for wetland or upland areas will also show greater abundance and distribution declines relative to habitat generalists as dispersal for specialists is limited to specific habitat types. (4) Species with reproductive obligate mutualisms will experience greater decreases in abundance and distribution than those without these mutualisms. Specifically, wind-pollinated species will experience the lowest threat as these species do not require pollinators for reproductive success. (5) Species that require mutualists for growth and establishment including mycorrhizae and nodulating bacteria or parasitic species will show greater declines in abundance and distribution than those without such relationships as symbiotic relationships may be interrupted by pollution or distribution declines of the symbiont (Farnsworth and Ogurcak 2008) (6) Introduced species will not experience decreased abundance and distribution. Further, high phenological responsiveness in introduced species will be linked with greater distribution expansion and therefore invasiveness.

Methods

I evaluated species-specific and functional group-level shifts in both abundance and distribution using herbarium specimens from the Ohio State University herbarium (OS) collected in the U.S. state of Ohio (approximately 116,000 km², between 38°24' and 42°19' North and 80°31' and 84°49' West). The data set included a total of 20,742 specimens from 207 species collected between 1895 and 2009 with species sample sizes ranging from 11 to 352. Specimens of the same species that had identical collection locations, dates, and collectors were treated as a single data point to avoid non-independence of samples.

Fig. 1 Collection effort from 1895–2009 and example data for abundance shift calculations of *Convallaria majalis* and *Orobanchae uniflora*. The solid line indicates the number of species from the 207 species data set collected in a given year while the dashed line shows the overall average number of species collected per year. Each point represents a collection in a given year from 1895 until 2009 for *C. majalis* and *O. uniflora*. The mean *P*-value from the partial Solow equation and the Sighting Rate Model was 0.837 and 0.019 for *C. majalis* and *O. uniflora*, respectively



Calculating abundance declines

The partial Solow equation (McCarthy 1998) and the Sighting Rate Model (McInerny et al. 2006) were used to identify species likely to be declining in abundance over the 1895–2009 study period. The partial Solow equation is derived from the Solow equation (Solow 1993, modified by Burgman et al. 1995) which estimates the probability of a period of absences in collection at the end of a sampling period if a population is still extant. However, because collection effort over time is rarely constant, McCarthy (1998) derived the partial Solow equation to account for collection absences due to sampling bias. The partial Solow equation gives the probability (P) that a taxon is still extant in a given collection area as:

$$P = \left(\frac{\sum_{i=1}^t e_i}{\sum_{i=1}^T e_i} \right)^n$$

where e_i is an index of yearly collection effort (the yearly probability a given taxon will be collected expressed as the number of species collected in a single given year divided by the total number of species collected across all years in the study period, Fig. 1), t is the time of the last collection of the taxon of interest, T is the last year of the collection period, and n is the number of times the taxon has been recorded between the first year of the collection period and time t .

If the taxon was collected in the final year of the collection period, $P = 1$ as there is 100 % certainty the taxon was extant at the end of the collection interval. In contrast, small p values suggest a low probability that the observed run of collection absences would be present if the population was still extant and thus indicates a significant probability that the taxon has declined in abundance (McCarthy 1998; Ungricht et al. 2005). Thus, the partial Solow equation predicts how “overdue” a taxon is for collection relative to prior collection patterns.

To illustrate, in Ohio collection effort varied substantially over the 115 year study period (Fig. 1). On average, 76 of the 207 species were collected each year with the lowest collection effort in 1947 (12 species collected) and the highest in 1899 (155 species collected). *Orobancha uniflora* was collected $n = 23$ times from the beginning of the collection period in 1895, with its last collection in $t = 1986$ (Fig. 1). The absence of collection for *O. uniflora* from 1986 until $T = 2009$, the last year of the collection period, indicates a significant probability of decline ($P = 0.037$, Online Resource 1). In contrast, *Convallaria majalis* was collected $n = 14$ times from 1895 until $t = 2007$. Because *C. majalis* was last collected shortly before $T = 2009$, there is a low probability of decline ($P = 0.907$, Online Resource 1).

The Sighting Rate Model (McInerny et al. 2006), uses the previous sighting rate of a taxon and the time since the last observation to calculate the probability that another sighting of that taxon will occur as follows:

$$P = \left(1 - \frac{n-1}{t_n} \right)^{T_n - t_n}$$

where n is the number of sightings as above, t_n is the number of years between the initial and final sighting of a given taxon, and T_n is the number of years from the initial sighting until the end of the collection period. For example, the first and last collection dates for *O. uniflora* are 1896 and 1986, respectively, with the collection period ending in 2009 (Fig. 1). Thus, $t_n = 91$ and $T_n = 114$ for this species and with $n = 23$, these data indicate

a significant probability of abundance decline ($P = 0.002$, Online Resource 1). Similarly, *C. majalis* was first and last collected in 1898 and 2007, respectively, producing $t_n = 110$ and $T_n = 112$ which indicates a low probability of decline for this species ($P = 0.778$, Online Resource 1).

Both methods estimate the probability (P) that a species has declined over a given time period. Based on the average probability of decline \bar{P} from both methods (McCarthy 1998), species were assigned to two categories for abundance change, declining $\bar{P} \leq 0.1$ or no change $\bar{P} > 0.1$. This somewhat less conservative probability value was selected given that the central research focus was to identify functional traits that predispose species to decline. For research focused on identifying and targeting specific declining species for conservation planning, a stricter probability value requirement may be appropriate.

Calculating distribution shifts

Species geographic distributions within Ohio were compared between two periods; 1895–1970 (historic) and 1971–2009 (modern). The timing of the two periods was selected because climate warming began to accelerate in the 1970s and because major land-use changes likely to affect species persistence based on functional traits occurred at least several decades prior to 1970. Rarefaction analysis was used to calculate the expected number of county occurrences (E) for a given species, x , in the historic (E_{Hx}) and modern (E_{Mx}) periods while controlling for sampling effort (Duffy et al. 2009, Solow and Roberts 2006). Rarefaction is commonly used to estimate species richness when comparing between locations to control for differences in sampling intensity at study sites (as in Gotelli and Colwell 2001). Solow and Roberts (2006) were the first to apply this method to control for varying sampling intensities while estimating differences in species distributions.

The vegan package in R (Oksanen et al. 2013; R Development Core Team 2008, version 3.0.2) was used to calculate E_{Hx} and E_{Mx} as follows:

$$E_x(L(n)) = k - \sum_{j=1}^k \binom{m - m_j}{n} / \binom{m}{n}$$

where k is the number of locations in which each species was collected, m_j is the number of collections from location j ($j = 1, 2, \dots, k$), m is the total number of collections for a species $m = \sum_{j=1}^k m_j$ and $E(L(n))$ is the expected number of locations in a random sample n of the collections where $n \leq m$ (Solow and Roberts 2006).

Distribution shifts over time for each species (ΔD_x) were calculated as:

$$\Delta D_x = (E_{Mx}/E_{Hx} - 1) * 100$$

ΔD_x therefore is the percent change in the expected number of county occurrences from the historic to modern period for each species. A negative ΔD_x indicates distribution contraction while a positive ΔD_x indicates expansion. Species with non-overlapping standard errors (calculated in vegan according to Heck et al. 1975) between E_{Hx} and E_{Mx} were considered to have changing distributions (similar to Comita et al. 2010 assessing diversity differences among plots and DeVries et al. 1997 comparing butterfly species richness among different canopy layers). Thus, species with overlapping standard errors between E_{Hx} and E_{Mx} experienced no distribution shift ($\Delta D_x = 0\%$). A minimum of 3 specimens were required for both the historic and modern time periods (thus, a minimum of six total

specimens) to calculate ΔD_x , which excluded seven species from this analysis (Online Resource 1).

To illustrate, in the modern period, *Castilleja coccinea* was collected six times ($m = 6$) in two counties, Adams and Scioto ($k = 2$), with five collections in Adams Co. ($m_j = 5$) and one collection in Scioto Co. ($m_j = 1$, Fig. 2a). In contrast, in the historic period *C. coccinea* was collected 35 times ($m = 35$) in fifteen counties ($k = 15$) with m_j values ranging from $m_j = 10$ (Adams Co.) to $m_j = 1$ in eight different counties. *Ranunculus hispidus* (Fig. 2b) was collected 31 times in the modern period ($m = 31$) from 18 counties ($k = 18$) with m_j values ranging from $m_j = 6$ in Franklin Co. to $m_j = 1$ in ten different counties. In the historic period, *R. hispidus* was collected 29 times ($m = 29$) in 14 counties ($k = 14$) with m_j ranging from 1 to 4.

Functional group classifications

Species were classified based on the following functional traits: origin (native vs. introduced), phenological responsiveness, reliance on a symbiont, pollination syndrome, habitat requirements (wetland vs. upland specialists), and ability to reproduce vegetatively (Online Resource 1).

All species were classified with regard to origin as native ($n = 183$) or introduced ($n = 24$) using the USDA Plants Database (<http://plants.usda.gov/java/>). Introduced species are those non-native to North America.

Reliance on a species-specific symbiont was determined by a literature search and included those species that rely on an obligate symbiont for establishment and survival ($n = 38$) and those that do not ($n = 58$; as in Farnsworth and Ogurcak 2008). Obligate mutualisms included mycorrhizal relationships, hemiparasitic relationships with host plants, and nodulating bacteria and were found primarily in Orchidaceae, Fabaceae, Ericaceae, and Orobanchaceae.

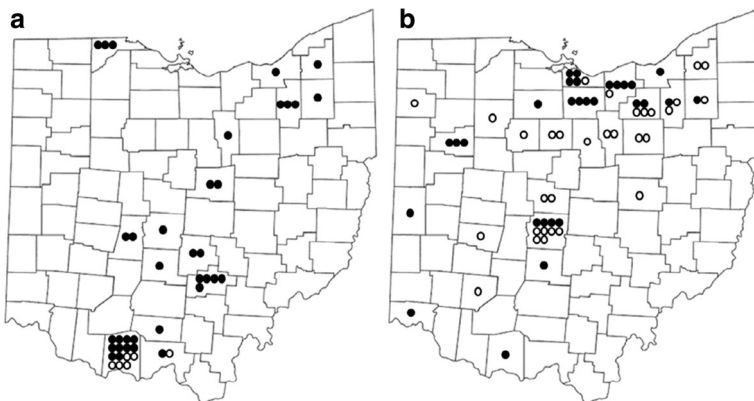


Fig. 2 Historic (filled symbols) and modern (open symbols) occurrences for **a** *Castilleja coccinea* and **b** *Ranunculus hispidus*. Each point represents a county-level occurrence taken from a herbarium specimen. The expected number of counties for each time period was used to calculate the change in county occurrence (%) from the historic to modern period. *C. coccinea* shows a significant decrease in its distribution ($\Delta D_x = -58\%$, $E_{Mx} = 2$, $E_{Hx} = 4.7$) while *R. hispidus* has increased its distribution throughout Ohio ($\Delta D_x = 24\%$, $E_{Mx} = 17.3$, $E_{Hx} = 14$)

Species were classified as animal- ($n = 124$) or wind-pollinated ($n = 13$) via an extensive literature search and the USDA Tree Atlas (as in Calinger et al. 2013; Prasad et al. 2007; http://www.nrs.fs.fed.us/atlas/tree/tree_atlas.html). I further categorized animal-pollinated species as facultative or obligate out-crossers ($n = 68$ and $n = 56$, respectively). Obligate out-crossing species are those with complete self-incompatibility while facultative out-crossing species are capable of selfing.

Habitat requirements were determined from the 2012 National Wetland Plant List (Lichvar 2013) and include 5 categories; obligate ($n = 17$) and facultative ($n = 25$) wetland specialists, generalists that occur without preference in wetlands or uplands ($n = 29$), and obligate ($n = 5$) and facultative ($n = 74$) upland species.

Vegetative reproduction ability was assigned to one of three character states (as in Farnsworth and Ogurcak 2008) based on an extensive literature search. Among species that are capable of vegetative reproduction, I grouped species that reproduce via stolons or rhizomes ($n = 91$) as having “high” capacity for vegetative reproduction and those that reproduce with short vegetative buds ($n = 26$) as having “medium” capacity. The third group included those species that reproduce solely sexually with no ability to reproduce vegetatively (“none,” $n = 61$).

To determine phenological responsiveness (days flowering shifted/ $^{\circ}$ C, temperatures calculated as the average temperature for each species’ month of flowering and the 3 months prior), herbarium specimens were paired with long-term temperature data from the U.S. Historical Climatology Network (see Calinger et al. 2013 for further details, Menne et al. 2010 for climate data). Briefly, herbarium specimens were visually examined and only those with at least 50 % of flower buds in anthesis were included in the analysis. The flowering date, F_{xi} , and collection location were taken from the collection label attached to each specimen. Specimens were then assigned to one of ten climate divisions in Ohio determined by the National Oceanic and Atmospheric Administration (Online Resource 2). To determine phenological responsiveness to temperature, the flowering date, F_{xi} , of specimen i in species x , was regressed against the average temperature of the species’ month of flowering and the 3 months prior \bar{T}_{4i} for that specimen’s collection year and climate division such that:

$$F_{xi} = b_x + \rho_x(\bar{T}_{4i})$$

where ρ_x is the slope, or the phenological responsiveness of flowering to temperature. Calinger et al. (2013) found a strong correlation between F_{xi} and the average temperatures of F_{xi} and the 3 months prior and thus \bar{T}_{4i} was used in the models of phenological responsiveness. Phenological responsiveness values were calculated for all 207 species.

Statistical analysis of abundance and distribution shifts

I evaluated differences within functional groups using both linear and generalized linear models through the lme4 package of the statistical software R (Bates et al. 2012) with significance assessed at $p \leq 0.1$. For abundance shifts, the generalized linear models used a binomial error structure (1 = decreased abundance, 0 = no change) and a logit link function to produce average probabilities of decline for each functional group. For distribution shifts, the linear models used a Gaussian error structure and provided the average percent change in distribution for each functional group. The lme4 program calculated p -values based on z - or t test statistics for models using binomial or Gaussian error structures, respectively. Both models use maximum likelihood methods for coefficient calculation.

Similarly, I used logistic regression to determine the relationship between phenological responsiveness and abundance declines. The slope of this regression provides the change in the probability a species will decline in abundance versus phenological responsiveness. For example, a positive slope from this regression indicates that species with high phenological responsiveness (significant advancement of flowering time with temperature increase) are less likely to decline in abundance than species with weak phenological responsiveness. The relationship between phenological responsiveness and distribution shifts was determined by linear regression. The slope of this line provides the percent change in distribution versus phenological responsiveness. A negative slope indicates that species with high phenological responsiveness have expanded their distributions more than species with weak phenological responsiveness. Given strong seasonal differences in patterns of phenological responsiveness, I also separately analyzed the relationships between phenological responsiveness and abundance and distribution shifts for spring (April and May), early summer (June and July), and late summer (August and later) flowering species (Calinger et al. 2013).

Phylogenetic analysis

Closely related species are likely to be more similar than species more distantly related because of their shared evolutionary history. This phylogenetic similarity can result in non-independence of data, and if this autocorrelation is not accounted for in models, it violates the assumptions of statistical tests in comparative analyses (Revell et al. 2008). To assess phylogenetic autocorrelation in both abundance and distribution shifts, a phylogenetic tree of the 207 study species was first generated using the software Phylomatic (Online

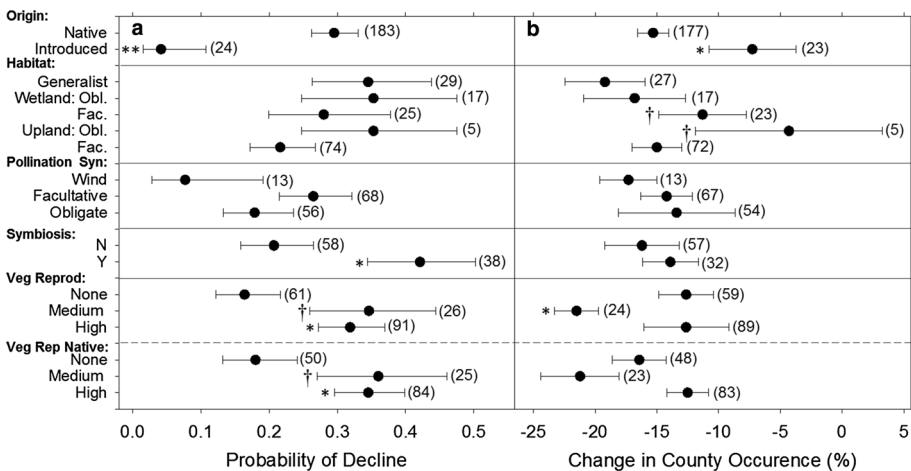


Fig. 3 Functional group patterns of abundance (a) and distribution (b) shifts. For abundance shifts, each point represents the average probability of decline for a given functional group. Higher probabilities indicate a greater likelihood that a species in that group will have decreased in abundance over time. For distribution shifts, points indicate the average percent change in county occurrence from the historic to modern time period for a functional group. Negative and positive changes in county occurrence indicate distribution contraction and expansion, respectively. The Veg Rep Native group indicates results for vegetative reproduction capacity in the native species only analysis. Differences from the reference group (uppermost group for each functional category) are indicated by † $p \leq 0.1$, * $p \leq 0.05$, ** $p \leq 0.001$, error bars indicate ± 1 SE, and species sample sizes are given in parentheses

Resource 3, Stevens 2004; Webb and Donoghue 2005). The effects of phylogenetic similarity on abundance and distribution shifts were tested by including the phylogenetic covariance matrix in generalized least squares models of abundance (0 = no change, 1 = declining abundance) and distribution shifts (ΔD_x). This phylogenetic covariance structure was multiplied by a phylogenetic signal value (λ), with values from 0 (no phylogenetic autocorrelation) to 1 (maximum phylogenetic autocorrelation), and the log-likelihood of each run was recorded. Using the likelihood surface generated from each run, a maximum likelihood phylogenetic signal value of λ was determined (Freckleton et al. 2002; Pagel 1999). Approximate confidence intervals were calculated for λ via likelihood ratio tests (Freckleton et al. 2002) on values from the likelihood surface. To model the likelihood profile for λ for both abundance and distribution shifts, the maximum likelihood method ‘ppls.profile’ function in the R package caper was used (Orme et al. 2012).

Results

Changes in abundance

Fifty-five of the 207 species significantly declined in abundance over the past 115 years with significant differences among functional groups in the probability of decline (Fig. 3a, Online Resource 1). Native species were seven times more likely to have declined in abundance than introduced species ($p < 0.001$, $df = 205, 206$, $z = 2.19$). Only one introduced species (*Anthemis arvensis*) significantly decreased in abundance. Further, those species that rely on a symbiont were twice as likely to decrease in abundance as those without symbiont requirements ($p = 0.02$, $df = 94, 95$, $z = 2.22$). Species with a high or moderate capacity for vegetative reproduction were roughly twice as likely to decrease in abundance relative to those that exclusively reproduce sexually ($p = 0.03$ and 0.06 , respectively, $df = 175, 177$, $z = 2.11$ and 1.85 , respectively) although these results may be conflated with species origin. I found no significant differences in the probability of decline among wetland specialists *versus* generalists and among different pollination syndromes. As origin significantly impacted abundance declines, I separately analyzed all functional

Table 1 Probability of decline as a function of phenological responsiveness for species flowering during different seasons (spring = April and May, early summer = June and July, late summer = August and later)

Season	All origins			Natives only		
	Probability of decline (unitless)/phenological responsiveness (days/°C)	Std. error	p	Probability of decline (unitless)/phenological responsiveness (days/°C)	Std. error	p
All seasons	0.005	0.06	0.92	−0.327	0.62	0.60
Spring	0.130	0.12	0.26	0.108	0.11	0.35
Early summer	0.001	0.10	0.99	0.010	0.12	0.93
Late summer	−0.031	0.12	0.79	−0.196	0.18	0.28

Values are the slope of the logistic regression of abundance decline versus phenological responsiveness and associated standard error and significance of the slope. A positive slope indicates that species that advance flowering with increased temperature have a lower probability of decline. A negative slope indicates that species with no flowering advancement or a delay of flowering with higher temperatures have a lower probability of decline

group effects on abundance changes including species of all origins (both native and introduced species) as well as in native species only. The all-origin models and native-only models produced statistically indistinguishable results for all functional groups.

Abundance declines were insensitive to phenological responsiveness in models including species of all origins as well as in the native species only models (Table 1). The insensitivity of abundance decline to phenological responsiveness was found in the models including all flowering seasons and in models including only spring, early-summer, or late-summer flowering species.

Changes in distribution

Across 200 species, I found an average 14 % reduction in distribution (ΔD) from the historic to modern time period (Fig. 4, Online Resource 1). Among those species exhibiting negative ΔD ($n = 136$), average distribution declined by 23 %. Distribution contractions ranged from 66 % (*Cypripedium candidum*, $E_{Mx} = 1$, $E_{Hx} = 2.9$) to 7 % (*Quercus rubra*, $E_{Mx} = 32$, $E_{Hx} = 34.6$, Fig. 4, Online Resource 1). Only twelve species expanded their distributions between the time periods and among these species, distributions increased by 26 % on average. Distribution expansions in the modern period ranged from 10 % (*Maianthemum stellatum*, $E_{Mx} = 17$, $E_{Hx} = 15.4$) to 51 % (*Asclepias sullivantii*, $E_{Mx} = 12$, $E_{Hx} = 8$, Fig. 4, Online Resource 1). The remaining 52 species showed no change in distribution.

Native species exhibited a two-fold greater decline in distribution compared to introduced species ($p = 0.03$, $df = 198, 199$, $t = 2.14$, Fig. 3b). Given the significant effects of origin on distribution shifts, I separately analyzed all functional group effects on distribution shift including species of all origins (both native and introduced species) as well as in native species alone. These all-origins versus native-only models produced statistically similar results for all functional groups except capacity for vegetative reproduction. The model results discussed here were produced using the all origins dataset unless otherwise specified.

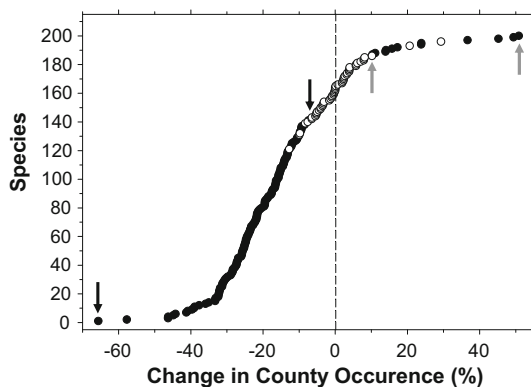


Fig. 4 Changes in distribution (ΔD_x) as measured by county occurrence from the historic to modern time periods for 200 Ohio plant species. Closed circles represent significant changes in county occurrence between time periods ($n = 148$) while shifts indicated with open circles are not significant ($n = 52$). Black arrows indicate the species with the highest and lowest distribution contraction (*Cypripedium candidum* and *Quercus rubra*, respectively). Grey arrows show the species with the highest and lowest distribution expansion (*Asclepias sullivantii* and *Maianthemum stellatum*, respectively)

Upland species and facultative wetland species experienced significantly less decline in distribution than habitat generalists ($p = 0.07$ and $p = 0.1$, respectively, $df = 139, 143$, $t = 1.82$ and 1.64 , respectively, Fig. 3b). Obligate wetland and facultative upland species show no significant difference in distribution shift from habitat generalist species. I found no significant effects of pollination syndrome or symbiosis requirement on distribution shift ($p > 0.1$).

Species with a moderate capacity for vegetative reproduction showed a significantly greater distribution decline than species that reproduce exclusively sexually ($p = 0.03$, $df = 169, 171$, $t = 2.17$, Fig. 3). I found no differences between sexually reproducing species and species with a high capacity for vegetative reproduction. However, the analysis in which only native species were included revealed no significant differences between groups with varying capacities for vegetative reproduction suggesting the effects of capacity for vegetative reproduction are conflated with origin effects.

Introduced species that advance flowering more strongly with increased temperatures have significantly increased distributions from the historic to modern periods compared with introduced species that show weak flowering advancement or delay of flowering ($p = 0.056$, $df = 21, 22$, Fig. 5a). This trend is primarily driven by introduced species that flower in the early summer (June and July; $p = 0.006$, $df = 9, 10$, Fig. 5b). For these species, distributions in the modern period increased by roughly 4 % per day of flowering advancement associated with a 1 °C temperature increase. For example, an early summer flowering introduced species that advances flowering by 10 days/°C would show a 20 % increase in its distribution while a species in this group that advances flowering only by 2 days/°C would show a 14 % decrease in distribution. I found no significant relationship between distribution shifts and phenological responsiveness for spring flowering introduced species (April and May, $p > 0.1$, $df = 8, 9$, Fig. 5c) or for native species. As only two introduced species in the dataset flowered in the late summer (August and later), this relationship could not be tested in that season.

Importantly, there was no significant phylogenetic signal in the abundance or distribution shift data (Online Resources 3 and 4). Thus, the impacts of functional groups on these variables can be interpreted independently from phylogenetic signal.

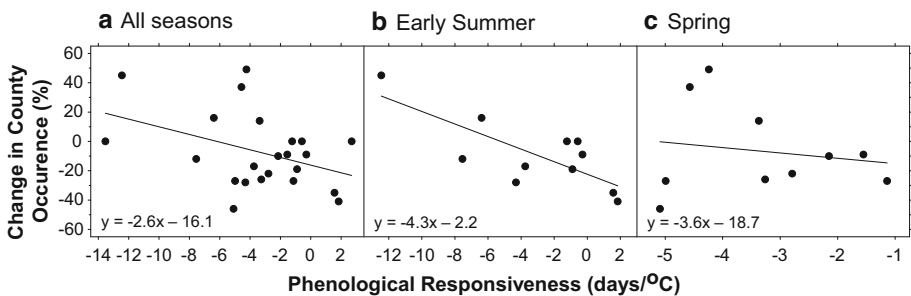


Fig. 5 Distribution shifts of introduced species with varying phenological responsiveness and flowering season. Each point indicates a single species that flowers during **a** all seasons, **b** early summer only (June and July), and **c** spring only (April and May)

Discussion

These results suggest a wide range of species in Ohio are at risk of increased rarity or local extirpation, with 27 % of the species assessed showing significant abundance declines and 68 % experiencing distribution contraction. This large-scale study of species performance assessed both species-specific responses and functional group level patterns of threat. Many of the functional traits that predispose species to decline are directly related to performance under a variety of anthropogenic stresses such as land-use change, non-native species invasion, pollution, and climate warming. Thus, this study allows inferences about a suite of anthropogenic impacts on species performance and therefore biodiversity. These results add to the few studies world-wide that have assessed the link between phenological responsiveness to temperature and performance of introduced species (Wolkovich et al. 2013; Willis et al. 2010).

I found that native species experienced significantly greater threat than introduced species as indicated by their greater average declines in both abundance and distribution compared with non-native species. Certain functional traits that are more prevalent among native species than non-natives and are associated with greater declines in abundance may predispose native species to decline. For instance, 33 species of the 78 (42 %) native species classified with regard to symbiosis requirements required a symbiont while only 5 of 18 non-native species classified for this trait required a symbiont (27 %). Further, unlike introduced species, native species that track climate warming by advancing flowering phenology seem to gain no performance benefits.

My results suggest that introduced species with high phenological responsiveness, particularly those that flower in early summer, may become more widespread with climate warming. The range of phenological responsiveness values for early summer flowering introduced species from (−12.4 to 1.8 days/°C) was far broader than for those flowering in the spring (−5.1 to −1.1 days/°C, Online Resource 1). Thus, the spring flowering introduced species sampled may not have included adequate variation in phenological responsiveness to detect a relationship with distribution shift. Alternatively, the narrower range of phenological responsiveness may reflect selection for moderate temperature sensitivity of flowering for spring flowering species to limit damage from spring frosts and possible pollinator mismatches (Thomson 2010; Inouye 2008). This selection would not allow exploitation of vacant niches before the native growing season as some natives in the spring advanced flowering more with temperature increase than introduced species (Online Resource 1). A handful of community-scale studies have assessed the vacant niche hypothesis (Gerlach and Rice 2003; Pearson et al. 2012) and the phenological flexibility hypothesis (Wolkovich et al. 2013; Hulme 2011) although the link between vacant niche exploitation or phenological flexibility and enhanced performance of introduced species remains unclear. My results provide additional support for the phenological flexibility hypothesis with important seasonal effects and add to the limited number of studies to address the link between phenological responsiveness and non-native species invasion.

Early summer flowering introduced species with high phenological sensitivities may be favored with climate warming as they are able to shift reproduction before summer temperatures exceed their temperature optimum. Sherry et al. (2007) found significant advancement of flowering and fruiting in early summer flowering grassland species in response to experimental warming and significant delay of these phenological events in late summer flowering species resulting in a phenological gap mid-summer corresponding to peak high temperatures. Early summer flowering introduced species that do not advance

flowering may experience temperatures beyond the optimum for flowering and fruiting (Sherry et al. 2007) potentially leading to lowered reproductive success. Further, warmer temperature have been linked to shorter flowering durations as a result of accelerated water loss through floral structures (Iler et al. 2013a, b). In contrast, those introduced species capable of shifting reproduction before peak summer temperatures may maintain or increase their reproductive success and therefore increase their invasiveness.

Seasonal differences in phenological responsiveness among introduced and native species likely explain the differing effects of high phenological responsiveness on distribution expansion between these groups. Previous research indicated that introduced species advanced flowering more, on average, than native species across the study area (Calinger et al. 2013). Further, the stronger average advancement of flowering with temperature increase among introduced species resulted primarily from high temperature responsiveness of introduced species in the summer while native summer-flowering species showed very weak temperature responses. High phenological responsiveness in the spring was not related to distribution expansion in either native or non-native species. In contrast, significant advancement of flowering with warming in the summer resulted in substantial performance benefits for non-natives. Thus, as high phenological responsiveness is not common among summer-flowering native species, native species did not experience the same performance benefits as highly responsive summer-flowering introduced species.

Species that require a symbiont for growth and development were significantly more likely to decline in abundance than those without symbiosis requirements. The majority of species that required a symbiosis were members of Orchidaceae (23 of 38 species) and twelve of the 23 orchid species assessed had significantly declined in abundance. Among the other families in the symbiosis requirement group, two of the nine species of Fabaceae and one of the two species of Orobanchaceae had decreased in abundance (Online Resource 1). As all orchids require mycorrhizal symbionts during their non-photosynthetic phase of development, disruptions of these symbioses as a result of declining mycorrhizal abundance may cause decreased survival and recruitment (McCormick et al. 2004; Rasmussen and Whigham 2002). Lower mycorrhizal species diversity and abundance is associated with a variety of air pollutants such as SO₂, NO_x, and ozone (Arnolds 1991). Further, invasive species typically have weak mycorrhizal associations which may cause declines in mycorrhizal communities as invasive species outcompete the native mycorrhizal hosts (Vogelsang and Bever 2009).

Proportionally, introduced species were overrepresented in the group of species incapable of vegetative reproduction compared with the moderate and high capacity for vegetative reproduction groups. Introduced species comprised 19.7 % of species with no vegetative reproduction (12 of 61 species), while they make up only 7.7 and 3.8 % of high and medium capacity vegetative reproducing species (7 of 91 species and 1 of 26 species, respectively, Online Resource 1). This overrepresentation of introduced species likely drove differences between the vegetative reproduction groups. Species with a medium or high capacity for vegetative reproduction had a greater probability of declining abundance than species incapable of vegetative reproduction and the medium capacity group had greater distribution reduction than exclusively sexually reproducing species. The functional group effects on distribution are not found when analyzing only native species, suggesting these results are conflated with species origin. Conversely, the vegetative reproduction group effects on abundance shifts are unchanged in the native only analysis. The differing effects of removing introduced species between the abundance and distribution shift analyses are likely a result of the differing sensitivities of these two analyses. A species must pass a given threshold of collection decline to be recognized by the

abundance equations as decreasing in abundance. These equations are relatively insensitive to moderate decreases in abundance if an adequately long period of collection absence is not met. Further, if a declining species is collected in the final year of the collection period, it is categorized as having unchanged abundance, irrespective of collection reductions prior to the last year of collection. Some native species without the capacity for vegetative reproduction that were classified as having stable abundances were likely experiencing moderate declines that weren't detected by the abundance equations. In contrast, the distribution shift analysis assesses continuous changes in county occurrence and thus is sensitive to moderate declines. Thus, the lower ability of the abundance shift equations to detect changes relative to the distribution equations likely mask the effects of species origin on changes in abundance predicted by vegetative reproduction strategies.

I found no significant effects of pollination syndrome on abundance or distribution changes. In contrast, (Farnsworth and Ogurcak 2008) found greater declines in range size and number of populations among rare species for animal-pollinated species compared with wind-pollinated species or species capable of selfing. Reduction in population sizes and ranges of animal-pollinated and obligate out-crossing species are attributed to a variety of factors including declining pollinator populations (Biesmeijer et al. 2006), habitat loss and fragmentation (Honnay et al. 2005) and loss of pollination services as a result of non-native species introduction (Traveset and Richardson 2006). Among the 56 species categorized as obligate outcrossing species, 33 had some capacity for vegetative reproduction. Thus, the impacts of disrupted pollinator mutualisms or population isolation on these species may be reduced.

I hypothesized that obligate wetland species would display greater declines in abundance and distribution given the dramatic declines in wetland habitats in the contiguous U.S. over the past 200 years (Dahl 1990). Habitat requirements showed no effects on abundance declines while upland and facultative wetland species experienced less distribution contraction than habitat generalists. Declines in abundance and distribution of wetland specialists were not observed likely because they occurred before the 1895 start date of the study period. Drainage of Ohio's wetlands began in the mid 1830s (Dahl and Allord 1996) suggesting that wetland specialists would have experienced their greatest period of decline in the mid-19th century. The gradual reforestation in Ohio over the past 70 years from a low of 12 % cover in the 1940s to 30 % cover by the 1990s (Medley et al. 1995) may have contributed to the relatively stable distribution of upland specialists. Further, only five upland specialists were able to be included in the dataset and thus the distribution shift estimate for this group may not be representative of a broader sample of upland species. The distribution shift of facultative wetland species was not significantly different from any habitat requirement group except generalists. Given the roughly uniform probabilities of abundance decline among the varying habitat requirements and the limited differences in distribution shifts among facultative wetland and upland species, habitat requirements had relatively little impact on species performance.

Collection effort across the 115 year sampling interval was variable, with notable declines from ~1910–1930 and the mid-1940s to 1950s roughly corresponding to World Wars I and II. On average, 76 of the 207 focal species were collected per year (Fig. 1). Sampling intensity did not consistently fall below average until 1994, showing a brief period of sampling decline at the end of the test period. The predictions of decline using the partial Solow method and the Sighting Rate Model were highly correlated (Spearman's $\rho = 0.99$, $R^2 = 0.81$, $p < 0.001$, Online Resource 5). The partial Solow method was more conservative than the Sighting Rate Method with predicted declines in 34 and 79 species, respectively. Both methods were in agreement for all 34 species the partial Solow equation

showed as declining. Predictions from the Sighting Rate Model are highly correlated with IUCN Red List Categories of threat providing additional support for these methods (McInerney et al. 2006). Rarefaction analysis was used to control for varying sampling intensity in the analysis of distribution shifts. Further, I analyzed individual species that exhibited extreme distribution contraction or expansion to determine if changes in county sampling intensity over time could disproportionately affect species distribution shift calculations. Collections of *Asclepias sullivantii*, which increased its distribution by 51 %, were more common during the modern collection period in five counties. Four of those counties experienced decreased collection rates suggesting that the increased frequency of *A. sullivantii* collection in the modern period was unlikely affected by declining sampling rates. Similarly, *Castilleja coccinea*, which experienced a 58 % distribution contraction, was found more often in the historic collection period in 14 counties. Half of these counties experienced increased sampling rates while the other half experienced sampling declines, again suggesting the declining collections of *C. coccinea* are unlikely affected by changes in overall sampling rate.

An additional concern when analyzing museum data is the possible effects of bias as a result of changing interest in certain species or groups of species among collectors. Evidence for changes in abundance and distribution might then result from changes in collector behavior rather than actual changes in population dynamics for these species. Collecting at any time is always done by a diverse group of people who may be seeking certain species or who may be interested in general collecting. The most likely biases would be (1) against collecting weedy, invasive species or (2) increasing interest in a particular group of native species (J. Freudenstein, pers comm). My results are not consistent with collector bias against non-native species (introduced species were not decreasing in abundance and many have experienced increased distribution) nor do they reflect systematic changes in collector interest in certain native groups (23 families were represented among the 55 species which experienced abundance decline). Thus, it seems very unlikely that collector bias substantially affected my analyses.

I used multiple methods with different underlying assumptions and differing sensitivities to various aspects of the collection to calculate abundance change in order to increase the probability of correctly identifying threatened species (McCarthy 1998). Generally, models of abundance change are grouped into three classes based on their assumptions regarding sampling distributions over time (Rivadeneira et al. 2009). Class 1 models assume a constant probability of collection over time with a rapid decline at the end of the sampling interval (i.e. Sighting Rate Model and the Solow equation). These models may be prone to mis-categorizing a species as in decline if sampling effort has shown large decreases over the study period (Type I error, Rivadeneira et al. 2009). Class 2 models account for changes in sampling effort over time by incorporating an index of collection effort (i.e. the partial Solow method). Finally, class 3 models make no assumptions regarding sampling distribution (i.e. the non-parametric Solow and Roberts equation, Solow and Roberts 2003). In class 3 models, the run of absences in collection at the end of the collection period must be proportionally larger to result in a prediction of decline when compared to the other two method classes (Rivadeneira et al. 2009). Thus, when sampling effort has remained constant or not declined significantly over time, class 3 methods are more likely to misidentify declining species as not declining (Type II errors). The use of class 1 and 2 models in this analysis reflects a balance between Type I and Type II errors appropriate for the relatively low decline in collection at the end of the sampling interval.

Conclusions

Ecosystems face numerous anthropogenic threats such as climate change, loss of mutualists, and invasion by non-native species that may cause non-random declines in both native species' performance and diversity. Understanding species-specific and functional group patterns of threat along with the complex impacts of climate change on ecosystem function is crucial for efficient conservation planning. This study suggests that climate change may act on native species diversity by favoring highly phenologically responsive introduced species while highly responsive native species gain no performance benefits with warming. These analyses of abundance and distribution shifts indicate significant threat to species diversity that may be aggravated by continued climate warming.

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