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Favorable Climate Change Response Explains Non-Native Species’ Success in Thoreau’s Woods

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Abstract
Invasive species have tremendous detrimental ecological and economic impacts. Climate change may exacerbate species invasions across communities if non-native species are better able to respond to climate changes than native species. Recent evidence indicates that species that respond to climate change by adjusting their phenology (i.e., the timing of seasonal activities, such as flowering) have historically increased in abundance. The extent to which non-native species success is similarly linked to a favorable climate change response, however, remains untested. We analyzed a dataset initiated by the conservationist Henry David Thoreau that documents the long-term phenological response of native and non-native plant species over the last 150 years from Concord, Massachusetts (USA). Our results demonstrate that non-native species, and invasive species in particular, have been far better able to respond to recent climate change by adjusting their flowering time. This demonstrates that climate change has likely played, and may continue to play, an important role in facilitating non-native species naturalization and invasion at the community level.

Introduction
Invasive species have significant negative effects on biodiversity, ecosystem function, agricultural productivity, and human health [1]. In the United States alone the estimated annual cost of invasive species exceeds $120 billion [2]. It has been hypothesized that climate change will exacerbate the impacts of non-native species naturalization and subsequent invasion across communities [3,4,5,6]. One important way in which non-native species could respond to climate change is by adjusting their phenology (i.e., the timing of seasonal activities, such as flowering time, leaf out time, germination and migration) [7,8]. Along these lines, the ability of species to appropriately adjust their phenology to climate change has been shown to have a significant impact on species success [9,10,11]. The extent to which phenological response is also linked to non-native species success, however, has not been examined, despite its potential relevance to conservation and management efforts in the face of continued climate change.

Here, we take advantage of a unique historical dataset from Concord, Massachusetts (USA) [12] to elucidate the role of climate change in shaping the patterns of non-native plant species’ naturalization and invasion [see Material and Methods]. Concord has experienced significant climate change in the last 150 years, during which time the mean annual temperature has increased 2.4°C [12]. The Concord dataset was initiated in 1851 by the American naturalist and conservationist Henry David Thoreau and continued by later observers, including the authors of this paper [12]. This dataset permits the calculation of two important phenological response traits: i) the ability of species to track seasonal temperature variation measured as the correlation between first flowering day and annual spring temperature from 1888–1902 [herein referred to as flowering time tracking] and ii) the change in mean first flowering day over two periods: 1851–2006 and 1900–2006 [herein referred to as flowering time shift, see Material and Methods].

We distinguished between native and non-native species using the United States Department of Agriculture (USDA) PLANTS Database [13]. We further distinguished non-native non-invasive and non-native invasive (i.e., herein referred to as invasive) species using the Invasive Plant Atlas of New England [14] (for complete definitions of non-native species status see Material and Methods).

To account for other factors that could also explain non-native species success, we examined several additional ecologically important traits that have been implicated in non-native species’ naturalization and invasion [15], including: habit, plant height at maturity, leaf mass per area, flower diameter, pollination syndrome, and seed weight.

We tested for significant differences in these traits between: i) natives and non-natives, ii) natives and non-native non-invasives, iii) natives and invasives, and iv) non-native non-invasives and

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indicated with an asterisk (p ≤ 0.05). Error bars indicate standard errors.

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Figure 1. Bar graphs depicting phylogenetically corrected mean differences between species groups for two climate change response traits: the correlation coefficient between first flowering day and annual spring temperature for the time period of 1888–1902 (A; i.e., flowering time tracking), and the shift in mean first flowering day during the period exhibiting the most dramatic increase in mean annual temperature, from 1900–2006 (B; i.e., flowering time shift). Trait differences significantly greater than zero are indicated with an asterisk (p ≤ 0.05). Error bars indicate standard errors.
species were considered ‘naturalized’ because they are thought to be established members of the Concord flora [27].

Non-native species were further categorized as ‘non-native non-invasive’ and ‘invasive’ using the Invasive Plant Atlas of New England (IPANE) [14]. IPANE defines a non-native species as ‘invasive’ if it meets all of the following criteria: 1) the species is or has the potential to become naturalized in New England, 2) the species is or has the potential to establish in minimally managed habitats, 3) the species does or has the potential to disperse rapidly and widely, 4) the species does or has the potential to establish large populations in minimally managed habitats, and 5) the species is classified as invasive in other areas outside of its native range. Importantly, our analyses, which include data on change in abundance [10], independently corroborate IPANE’s scoring of invasive species status. Invasive species, as classified by IPANE, have significantly increased in abundance in Concord relative to native and non-native non-invasive species over the past 100 years (Table S1).

Ecological Trait Data

Ecological trait data was collected from multiple sources. Shift in mean first flowering day (1851–2006), the correlation between flowering time and inter-annual temperature variation from 1888–1902 [i.e., flowering time tracking], and change in abundance were all calculated directly from observations of the Concord community [10,12]. Flowering time tracking was calculated as the correlation between first flowering day and mean monthly temperature in January, April, and May. This aggregate temperature was determined to be the best predictor flowering day in Concord [28,29]. We also obtained several additional ecologically relevant traits that have been implicated in non-native species success, including; leaf mass per area [30], plant height at maturity [13], seed weight [31], habit [32], flower diameter [32,33], and pollination syndrome [32,33]. Habit was coded as a binary trait (herbaceous vs. woody) using the Manual of the Vascular Plants of Northeastern United States and Adjacent Canada [32]. Pollination syndrome was coded as a binary trait (i.e., wind vs. insect pollinated) using refs [32, 33, 34]. Binary traits were treated as continuous in our correlation analyses and results should be interpreted as relative proportions. Leaf mass per area, plant height, seed weight, and flower diameter were log-transformed when necessary to meet the assumptions of normality. This study focuses on the ability of species to adjust their flowering phenology in response to climate change, an ability that has been shown to have important implications for species success [10]. Although poorly understood, a species’ ability to succeed might be linked with flowering time shifting if its fitness was directly dependent on when it flowered. For example, species that are unable to appropriately adjust their flowering time in response to climate change could suffer from a sudden lack of pollinators [22,35]. Alternatively, species’ fitness could be indirectly dependent on flowering time. For instance, changes in flowering time are generally correlated with the timing of leaf out, a character that is often linked to competitive ability and physiological adaptation [36,37,38]. A species that starts its growing cycle earlier in warmer years could have a competitive advantage in terms of nutrient acquisition and light availability. As a result, they may be more likely to complete their life cycle under favorable conditions (e.g., before the onset of warm and dry weather during the middle to late summer). Furthermore, a species that is able to leaf out earlier in warmer years could potentially shade out co-occurring species that are not responsive to temperature. Similarly, a species that puts out its leaves later in cold years might avoid late frosts that could damage its leaves.

Table 1. Trait correlations with non-native status.

| Traits | n1 | n2 | n3 | Non-native vs. Native | Invasive vs. Native | Non-native non-invasive vs. Native | Invasive vs. Non-native non-invasive |
|--------|----|----|----|-----------------------|-------------------|-----------------------------------|-----------------------------------|
| Change in abundance (1900–2006) | 260 | 69 | 15 | 1.26 ± 0.10*** | 2.39 ± 0.20*** | 1.03 ± 0.73*** | 1.56 ± 0.30*** |
| Flower diameter | 372 | 129 | 34 | 0.07 ± 0.02** | 0.02 ± 0.04 | 0.08 ± 0.02*** | −0.06 ± 0.04 |
| Flowering time shift (1851–2006) | 245 | 52 | 8 | −3.11 ± 1.01** | 9.98 ± 2.64*** | −4.12 ± 1.00*** | 10.89 ± 3.74** |
| Flowering time shift (1900–2006) | 245 | 65 | 11 | 0.60 ± 0.84 | 11.04 ± 2.04*** | −0.70 ± 0.87 | 9.07 ± 3.25* |
| Flowering time tracking | 126 | 25 | 5 | −0.11 ± 0.03*** | −0.18 ± 0.07** | −0.10 ± 0.03*** | −0.11 ± 0.07 |
| Habit (herbaceous vs. woody) | 256 | 97 | 23 | 0.004 ± 0.01 | 0.01 ± 0.02 | 0.003 ± 0.01 | 0.01 ± 0.01 |
| Height at maturity | 336 | 80 | 16 | −0.02 ± 0.03 | 0.08 ± 0.07 | −0.03 ± 0.03 | 0.09 ± 0.06 |
| Leaf mass per area | 53 | 39 | 11 | 0.01 ± 0.03 | 0.01 ± 0.03 | 0.07 ± 0.05 | 0.02 ± 0.04 |
| Seed weight | 275 | 123 | 31 | 0.10 ± 0.05 | 0.03 ± 0.10 | 0.11 ± 0.06* | −0.07 ± 0.09 |
| Syndrome (insect vs wind) | 385 | 136 | 35 | −0.01 ± 0.01 | 0.002 ± 0.02 | −0.01 ± 0.01 | 0.002 ± 0.02 |
| Non-native Status | 385 | 136 | 35 | − | − | − | − |
| Invasive Status | 385 | 136 | 35 | − | − | − | − |

Trait correlations between groups were tested using general estimator equations (GEE). Results shown here are robust to branch length estimates and phylogenetic uncertainty (see also Table S1). β-coefficients describe the direction and magnitude of the difference between groups. For example, a β-coefficient of −0.11 for flowering time tracking indicates that non-natives have a significantly greater negative correlation between flowering time and seasonal temperature variation than natives. Standard error of β-coefficients provided. n = sample size of 1) natives, 2) non-native non-invasives and 3) invasives. † P < 0.05, * P < 0.05; ** P < 0.01, *** P < 0.001. doi:10.1371/journal.pone.0008878.t001
correlations, we used the generalized estimating equations as implemented in APE [16,17]. GEE incorporates a phylogenetic distance matrix into the framework of a general linear model and permits the inclusion of multiple categorical and continuous traits as covariates in the same model [17]. This is similar to normal linear regression in that the β-coefficient describes the direction and magnitude of the difference between groups (e.g., the directional difference in shift response between native and non-native species). Our conclusions are drawn here from the results obtained from GEE analysis (Table S1), but correlation results were similar when using phylogenetic independent contrasts as implemented in the ‘aotf’ module in Phylocom [40].

Phylogeny Construction

We constructed an initial composite phylogeny of the Concord flora using Phylov [41] and further resolved relationships above the generic level based on the literature. For complete details of our construction of the phylogeny see Willis et al. [10]. Divergence time estimates were calculated using the ‘bladj’ function in Phylocom [40] based on Wikström et al. [42].

Sensitivity Analysis

Phylogenetic correlations can be biased by branch length estimates and phylogenetic resolution. We tested the sensitivity of our results to branch length estimates by setting all branch lengths equal to one. We tested the sensitivity of our results to phylogenetic uncertainty by performing our analyses on a set of 50 phylogenies where all polytomies, above and below the generic level, were randomly resolved using the ‘mutlidiv’ function in APE and ages were re-estimated using the ‘bladj’ function in Phylocom. Regression results were robust to both of these sensitivity analyses (Table S1).

Multivariate Analyses Including Abundance Data

Flowering time shift results remained similar when change in abundance [43] was included as an independent variable in the models we analyzed (flowering time shift 1831–2006). Non-native vs Native, β = -3.61, SE = 1.02, t = -3.54, p = 0.0007; Invasive vs Native, β = 8.28, SE = 2.67, t = 3.10, p = 0.0029; Non-native non-invasive vs Native, β = -4.51, SE = 1.01, t = -4.48, p < 0.0001; Invasive vs Non-native non-invasive β = 11.30, SE = 3.81, t = 2.96, p = 0.0090; flowering time shift 1900–2006: Non-native vs Native, β = -0.10, SE = 0.84, t = -0.12, p = 0.9015; Invasive vs Native, β = 9.30, SE = 2.05, t = 4.64, p < 0.0001; Non-native, non-invasive vs Native, β = -1.26, SE = 0.87, t = -1.46, p = 0.1498; Invasive vs Non-native, non-invasive, β = 7.99, SE = 3.23, t = 2.47, p = 0.0126.

Supporting Information

Table S1 Statistical tests of trait correlations. Found at: doi:10.1371/journal.pone.0008878.s001

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Author Contributions

Conceived and designed the experiments: CGW CD. Performed the experiments: CGW BRR RP AJMR JBL CD. Analyzed the data: CGW. Contributed reagents/materials/analysis tools: CD. Wrote the paper: CGW CD. Helped to revise the manuscript: RP AJMR JBL CD.

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