

The importance of phylogeny to the study of phenological response to global climate change

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Climate change has resulted in major changes in the phenology—i.e. the timing of seasonal activities, such as flowering and bird migration—of some species but not others. These differential responses have been shown to result in ecological mismatches that can have negative fitness consequences. However, the ways in which climate change has shaped changes in biodiversity within and across communities are not well understood. Here, we build on our previous results that established a link between plant species' phenological response to climate change and a phylogenetic bias in species' decline in the eastern United States. We extend a similar approach to plant and bird communities in the United States and the UK that further demonstrates that climate change has differentially impacted species based on their phylogenetic relatedness and shared phenological responses. In plants, phenological responses to climate change are often shared among closely related species (i.e. clades), even between geographically disjunct communities. And in some cases, this has resulted in a phylogenetically biased pattern of non-native species success. In birds, the pattern of decline is phylogenetically biased but is not solely explained by phenological response, which suggests that other traits may better explain this pattern. These results illustrate the ways in which phylogenetic thinking can aid in making generalizations of practical importance and enhance efforts to predict species' responses to future climate change.

Keywords: climate change; community ecology; extinction; phenology; phylogeny; invasive species

1. INTRODUCTION

Climate change has had demonstrable effects on plant and animal communities around the world, and poses one of the most significant threats to biodiversity in the coming decades (Walther *et al.* 2002; Root *et al.* 2003; Parmesan 2006). Despite the relevance of phylogeny to numerous areas of ecology (Webb *et al.* 2002; Cavender-Bares *et al.* 2009; Vamosi *et al.* 2009)—e.g. patterns of community assembly (Ackerly 2004; Cavender-Bares *et al.* 2004, 2006), pathogen–host interactions (Gilbert & Webb 2007) and ecosystem function (Cadotte *et al.* 2008)—it remains underused for studying the impacts of climate change on biodiversity (Edwards *et al.* 2007; Willis *et al.* 2008). In particular, analyses of community-wide phenological datasets that demonstrate species' long-term

responses to climate change (Visser 2008) have lacked a phylogenetic framework (e.g. Sparks & Carey 1995; Bradley *et al.* 1999; Fitter & Fitter 2002; Butler 2003; Parmesan & Yohe 2003; Root *et al.* 2003; Mills 2005; Macmynowski *et al.* 2007; Parmesan 2007; Miller-Rushing *et al.* 2008; Miller-Rushing & Primack 2008). **This is problematic because species' traits, such as phenological response, may exhibit a phylogenetic pattern whereby closely related species share similar traits** (Lord *et al.* 1995; Wright & Calderon 1995; Prinzing *et al.* 2001; Ackerly 2004; Kang & Jang 2004; Wiens & Graham 2005; Cavender-Bares *et al.* 2006, 2009; Donoghue 2008; Losos 2008). **We refer to this pattern as phylogenetic signal (*sensu* Losos (2008)), but the terms phylogenetic trait conservatism or phylogenetic niche conservatism have also been applied in this context.**

The rationale for including phylogeny in phenological studies of climate change is twofold. First, closely related species are not statistically independent owing to their shared evolutionary history (Felsenstein 1985; Harvey & Pagel 1991; Fisher & Owens 2004). The non-independence of species can bias

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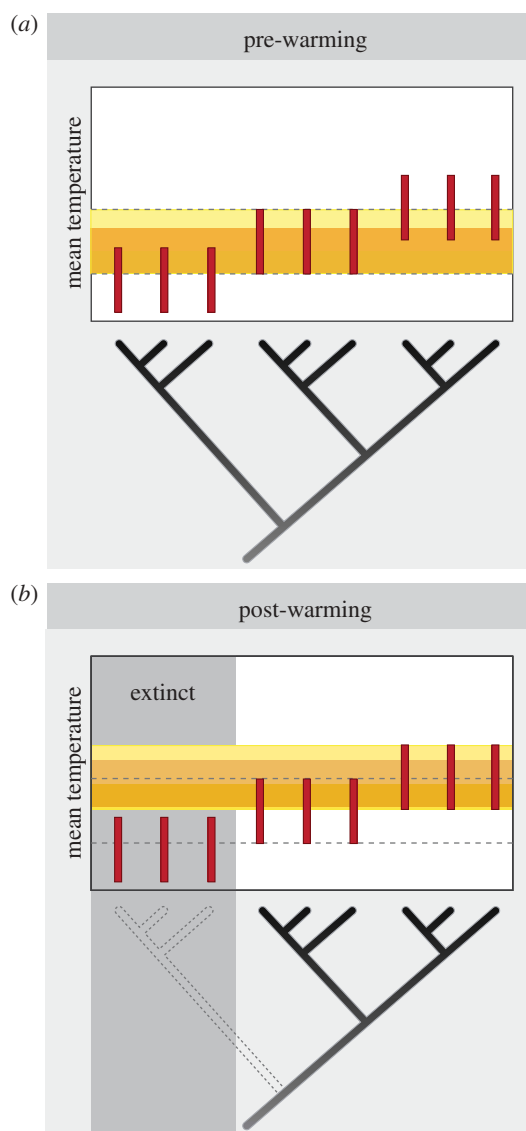


Figure 1. Phylogenetic bias in the pattern of species decline owing to climate change. A hypothetical phylogeny of organisms is depicted during pre- and post-warming intervals. The red vertical bars over each species represent a climatically relevant trait that is linked to species success (e.g. 'species thermal tolerance'). This trait exhibits phylogenetic signal—i.e. closely related species share similar thermal tolerances. An environmental temperature regime, mean annual temperature, is depicted by the yellow shading in the background. Following warming, some clades of species remain within their thermal tolerance range, whereas other clades are now well outside their range and become locally extirpated. This results in a phylogenetically biased pattern of species loss (i.e. phylogenetic selectivity).

comparative analyses of trait correlations, particularly if the traits in question exhibit phylogenetic signal. Second, knowledge of the phylogenetic distribution of species' traits can provide a better way to assess the impact of climate change on biodiversity. For instance, if closely related species share traits that have made them more susceptible to climate change (Wright & Calderon 1995; Dukes & Mooney 1999; Kang & Jang 2004), species decline may not be random or uniform, but rather biased against certain clades (i.e. phylogenetic selectivity, Cardillo *et al.* 2008; McKinney 1997; Purvis 2008) (figure 1). This

is especially relevant because climate change has greatly altered the phenology of some species but not others, which has been shown to result in ecological mismatches that can have negative fitness consequences (Stenseth & Mysterud 2002; Stenseth *et al.* 2002; Visser & Both 2005; Both *et al.* 2006). Under these circumstances, not only is the inclusion of phylogeny an important analytical tool for more properly assessing statistical trait correlations, but it is vital for understanding the pattern of differential species' response to climate change.

Willis *et al.* (2008, 2009) recently demonstrated the value of applying a phylogenetic approach to examine the impacts of climate change using a long-term phenological dataset from Concord, MA (USA) that was initiated by the naturalist and conservationist Henry David Thoreau (Miller-Rushing & Primack 2008; Primack *et al.* 2009). They analysed these floristic data using statistical methods that incorporate phylogenetic history and discovered that clades that have been less able to respond to climate change by adjusting their flowering time have significantly declined in abundance. These results can help predict which species face a greater risk of regional extinction as climate change is exacerbated. For example, they indicate that we should be particularly concerned about the continued regional loss of species in the Liliaceae and Orchidaceae clades, but perhaps less so of species in the Brassicaceae and Fabaceae. The latter two clades contain species that have been far better able to adjust their phenology to climate change, and contain fewer species that have declined in abundance. However, the extent to which these regional results are more broadly applicable to other geographically disjunct plant communities, or to other groups of species in the Tree of Life, remains unexamined. In particular, do closely related species in different geographical regions, and in different parts of the Tree of Life, share similar phenological responses to climate change? And is phenological response similarly associated with changes in species' abundance?

To address these questions, we extend the approach of Willis *et al.* (2008) to test for similar trends in plant and bird communities in the United States and the UK. First, we compare the phylogenetic distribution of phenological response traits between the geographically disjunct temperate plant communities of Concord, USA and Chinnor, UK. Second, we examine how phenological response traits contribute to the phylogenetic pattern of non-native plant species' success within each of these communities. And third, we test for the influence of climate change on the pattern of phylogenetic selectivity of species loss in a European bird community.

2. DATA AND METHODS

(a) Study sites for plant data: Concord, Massachusetts (MA), USA and Chinnor, Oxfordshire, UK

Concord, MA, USA (42°27'38" N; 71°20'54" W) is a township encompassing approximately 67 km². Although the town has undergone extensive development since the time of Thoreau (*ca* 1850),

approximately 60 per cent of Concord remains undeveloped or has been well protected through the efforts of numerous land-trusts and national, state, local and private parks (Primack *et al.* 2009).

Chinnor (Oxfordshire, UK) (51°42' N; 0°42' W) is a large rural area that has remained relatively undeveloped over the past half century (Fitter & Fitter 2002).

(b) *Plant trait data*

Change in flowering time was calculated from the Concord dataset as two separate traits (described in more detail by Willis *et al.* (2008) and Miller-Rushing & Primack (2008)). *Flowering time shift* was calculated as the difference in the mean first flowering day between 1851–2006 and 1900–2006. *Flowering time tracking* was calculated as the correlation between first flowering day and inter-annual temperature variation from 1888 to 1902. These traits represent two distinct measures of phenological response, one long-term (flowering time shift) and the other short-term (flowering time tracking). While it is possible that these two traits are linked, it is also possible that different mechanisms underlie these separate phenological response traits. For example, flowering time tracking might reflect species plasticity to annual temperature variation, whereas flowering time shift might reflect a longer term evolutionary response to climate change. **Using independent contrasts, we find that the two traits are not correlated in Concord ($R^2 = 0.01$, $p = 0.1389$). In Chinnor (see also below), they are correlated, such that species that are better trackers have shifted more, but the association is weak ($R^2 = 0.08$, $p < .001$). For this reason, we treat these two traits independently.**

Change in abundance was calculated from observations of the Concord community. For convenience, we apply the term 'community' here to indicate a large regional assemblage of species. **Flowering time tracking was calculated as the correlation between first flowering day and mean monthly temperature in January, April and May.** This aggregate temperature has been found to be the best predictor of first flowering day in Concord (Miller-Rushing & Primack 2008), and similar measures have been used in several other temperate floras (Sparks *et al.* 2000; Fitter & Fitter 2002; Miller-Rushing & Primack 2008). In previous analyses, we examined several additional ecologically relevant traits to determine the most likely explanation for the pattern of species' change in abundance (Willis *et al.* 2008, 2010). The inclusion of these traits in our multiple regression analyses presented here did not affect the relationship between climate change response and change in species' abundance.

Flowering time traits for Chinnor were obtained from Fitter & Fitter (2002). Flowering time shift was calculated as the difference in mean first flowering day between 1954–1990 and 1991–2000. Flowering time tracking was calculated as the correlation between first flowering day and 'spring temperature' (Fitter & Fitter 2002) from 1954 to 2000. Spring temperature was calculated as the mean monthly temperature during January, February and March. This aggregate

temperature was found to be the best predictor of first flowering day for most species in this community (median correlation coefficient = 0.40; see also Fitter & Fitter (2002)). For our main analyses, we excluded members of the Poales clade (i.e. grasses and their allies) for a more direct comparison between Chinnor and Concord—the Concord dataset does not contain phenological data for Poales. We did, however, compare our main results from Chinnor with results when Poales were included (see §3).

(c) *Temperature information for plant data*

Mean monthly temperature data were obtained from the Blue Hills Observatory, MA, USA (<http://www.bluehill.org/>) and the Central UK Temperature database (<http://badc.nerc.ac.uk/data/cet/>).

(d) *Plant non-native and invasive species status*

Non-native species status for Concord was obtained from the United States Department of Agriculture PLANTS online Database (<http://plants.usda.gov>; see also Willis *et al.* 2010). Species were scored as 'native' if they occurred in the continental United States or Canada at the time of Columbus (*ca* 1492) and 'non-native' if they arrived from other regions since that time. Concord non-natives were further categorized as 'non-invasive' (here as non-native non-invasive) and 'invasive' using the Invasive Plant Atlas of New England (IPANE) (Mehrhoff *et al.* 2003). Importantly, our data 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 (see Willis *et al.* 2010).

Non-native species status for Chinnor was obtained from the Botanical Society of the British Isles online database (<http://www.bsbi.org.uk/>). Invasive species status was obtained from the Invasive Alien Project for the UK (R. Marrs 2010, personal communication). The invasive status of these species was further corroborated by the Global Invasive Species Database (<http://www.issg.org/database/>) and by the Great Britain Non-native Species Secretariat (<http://www.nonnativespecies.org/>).

(e) *Bird trait data*

In addition to the plant examples above, the study of climate change and its impact on other branches of the Tree of Life can also benefit from a phylogenetic approach. Birds are particularly amenable for such studies because the phenology and abundance of bird communities have been intensively studied. Møller *et al.* (2008) recently analysed a dataset including information on changes in spring migratory arrival date and population trends for 100 European bird species spanning two time intervals (1970–1990 and 1990–2000). They found that **species that were less responsive to climate change in terms of their spring migratory arrival dates exhibited greater declines in abundance.** However, this relationship was not uniformly distributed across time. Instead, climate change-influenced losses were only detectable for the

Table 1. Phylogenetic signal of phenological response traits for Concord, USA and Chinnor, UK. Phenological response includes two traits: *flowering time tracking* (i.e. the correlation between annual first flowering day and seasonal temperature variation) and *flowering time shift* (i.e. the change in mean first flowering day over multiple decades; see §2). Phylogenetic signal was tested by comparing the rank of the observed mean standard deviation (observed rank) across all nodes in the community phylogeny to a null distribution of mean standard deviations based on 9999 iterations of trait values arranged randomly across the phylogeny tips. These analyses were conducted with branch lengths adjusted for estimated divergence times (observed rank_{bladj}) and with branch lengths set to unity (observed rank_{BL1}). These results were also examined for the effects of phylogenetic uncertainty (electronic supplementary material, table S1). A high observed rank indicates that closely related species are more dissimilar than expected by chance (i.e. trait overdispersion). A low observed rank indicates that closely related species are more similar than expected by chance (i.e. phylogenetic signal). Significance of observed rank based on a two-tail test: significant observed rank less than 250, greater than 9750 = *P*, 0.05; marginally significant observed rank less than 500, greater than 9500 = *P*, 0.10.

trait	<i>n</i>	observed rank _{bladj}	<i>p</i> -value	observed rank _{BL1}	<i>p</i> -value
Concord, USA					
flowering time tracking	167	351	0.0702	667	0.1334
flowering time shift (1900–2006)	342	3497	0.6994	9525	0.0950
Chinnor, UK					
flowering time tracking	323	181	0.0362	38	0.0076
flowering time shift (1954–2000)	323	9145	0.1710	8229	0.3542

more recent time interval (1990–2000). During this time period, change in migration date was the only variable that predicted population trends. In contrast, the best predictors of population trends during the earlier time interval (1970–1990), were body mass, breeding habitat type, over-wintering grounds and northern-most breeding latitude—smaller bird species that over-wintered in Africa, had summer ranges that extended into more northern latitudes, and bred in farmlands exhibited far greater declines in abundance. These findings suggest that phenological shifts related to climate change have become greatly exacerbated in recent years.

Møller *et al.* (2008) corrected for phylogeny in their statistical analyses, but did not directly focus on the phylogenetic distribution of the traits they investigated. As has been argued above, we feel that in overlooking this aspect, important associations related to the pattern of species change may have been missed. We re-analysed their data to determine (i) if the pattern of species abundance change has been phylogenetically biased, and (ii) if that pattern is also correlated with the phylogenetic pattern of phenological response (i.e. change in migration date).

(f) Composite phylogenies

We constructed an initial composite phylogeny for the Concord and Chinnor floras using PHYLOMATIC (Webb & Donoghue 2005). These phylogenies were further resolved above the generic level based on the literature (see Willis *et al.* (2008) for additional details on phylogeny construction). Divergence time estimates for these phylogenies were calculated using the 'bladj' function in PHYLOCOM (Webb *et al.* 2008) based on Wikström *et al.* (2001). To test for branch length sensitivity, we performed our analyses with branch lengths adjusted for time and with branch lengths set to unity. The phylogeny used to analyse the European bird dataset was taken from Møller *et al.* (2008). The bird phylogeny was not easily adjustable for divergence

time information, and thus all branch lengths were set to unity.

(g) Analyses of phylogenetic signal

Phylogenetic signal was tested using the 'aotf' module in PHYLOCOM 4.01 (Webb *et al.* 2008), which compares the rank of the observed mean variance of the trait of interest across all nodes to a null distribution generated from 9999 random iterations of the observed trait values across the composite phylogeny. The observed rank is compared with the null distribution in a two-tail test of significance (Webb *et al.* 2008). For the Concord and Chinnor datasets, phylogenetic signal was tested for the following traits: flowering time tracking, flowering time shift, non-native species status and invasive species status.

In general, results from Concord and Chinnor were not sensitive to phylogenetic uncertainty (electronic supplementary material, table S1) or branch length (see observed rank_{BL1} in tables 1 and 2). The inclusion of Poales, however, did affect the phylogenetic signal of traits in Chinnor (electronic supplementary material, table S2). For the European bird dataset, phylogenetic signal was tested for change in abundance from 1970–1990 to 1990–2000, and for the following traits for each time interval: body mass, sexual dichromatism, population size, migration distance, number of broods, over-wintering in Africa, natal dispersal, northernmost latitude, thermal maximum, change in migration date, habitat specificity and farmland habitat. Sensitivity analyses of phylogenetic uncertainty were not performed on the European bird dataset because the phylogeny was fully resolved.

(h) Analyses of trait correlations

To correct for phylogenetic non-independence, we used the method of generalized estimating equations (GEE; Paradis & Claude 2002), as implemented in APE v. 2.1–3 (Bolker *et al.* 2007). GEE incorporates

Table 2. Phylogenetic signal of non-native and invasive species status for Concord, USA and Chinnor, UK. Phylogenetic signal was tested by comparing the rank of the observed mean standard deviation (observed rank) calculated across all nodes in the community phylogeny to a null distribution of mean standard deviations based on 9999 iterations of trait values arranged randomly across the phylogeny tips. These analyses were conducted with branch lengths adjusted for estimated divergence times (observed rank_{bl_{dj}}) and with branch lengths set to unity (observed rank_{BL1}). A high observed rank indicates that closely related species are more dissimilar than expected by chance (i.e. trait overdispersion). A low observed rank indicates that closely related species are more similar than expected by chance (i.e. phylogenetic signal). Significance of observed rank based on a two-tail test: significant observed rank less than 250, greater than 9750 = *P*, 0.05; marginally significant observed rank less than 500, greater than 9500 = *P*, 0.10. See the electronic supplementary material, table S8 for corresponding tests of phylogenetic uncertainty.

trait	<i>n</i>	observed rank _{bl_{dj}}	<i>p</i> -value	observed rank _{BL1}	<i>p</i> -value
Concord, MA					
non-native status	587	1	0.0002	1	0.0002
invasive status	587	519	0.1038	5551	0.8898
Chinnor, UK					
non-native status	323	2997	0.5994	526	0.1052
invasive status	323	9417	0.1166	9916	0.0168

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 (Willis *et al.* 2008). The *estimate* describes the direction and magnitude of the difference of interest (e.g. the directional difference, or slope, in shift response between native and non-native species).

To test if phenological response differed within non-native species' classes we compared species' traits in Concord and Chinnor in three ways using univariate regression: non-native versus native species, invasive versus native species and non-invasive non-native versus native species. Results for Chinnor presented in the main text were largely similar with the inclusion of Poales (electronic supplementary material, table S3). Additionally, our statistical analyses for Concord and Chinnor were not sensitive to phylogenetic uncertainty (electronic supplementary material, table S4) or branch-length variation (electronic supplementary material, table S5).

For the European bird dataset, we analysed the effect of several traits on change in abundance using multivariate regression implemented in GEE. These traits include: body mass, sexual dichromatism, migration distance, number of broods, over-wintering in Africa, natal dispersal, northernmost latitude, change in migration date and farmland habitat. The two traits 'migration distance' and 'over-wintering in Africa' were highly correlated. For this reason, we excluded migration distance from the final multiple regression model presented in the main text. Including migration distance and excluding over-wintering in Africa did not alter our conclusions (results not shown). We also performed univariate regression of each trait on change in abundance (electronic supplementary material, table S6). Finally, we performed a second multiple regression on change in abundance that included the phenological response trait 'change in migration date' plus two traits that were sampled across a smaller subset of species (i.e. thermal maximum, and habitat specificity; electronic supplementary material, table S7).

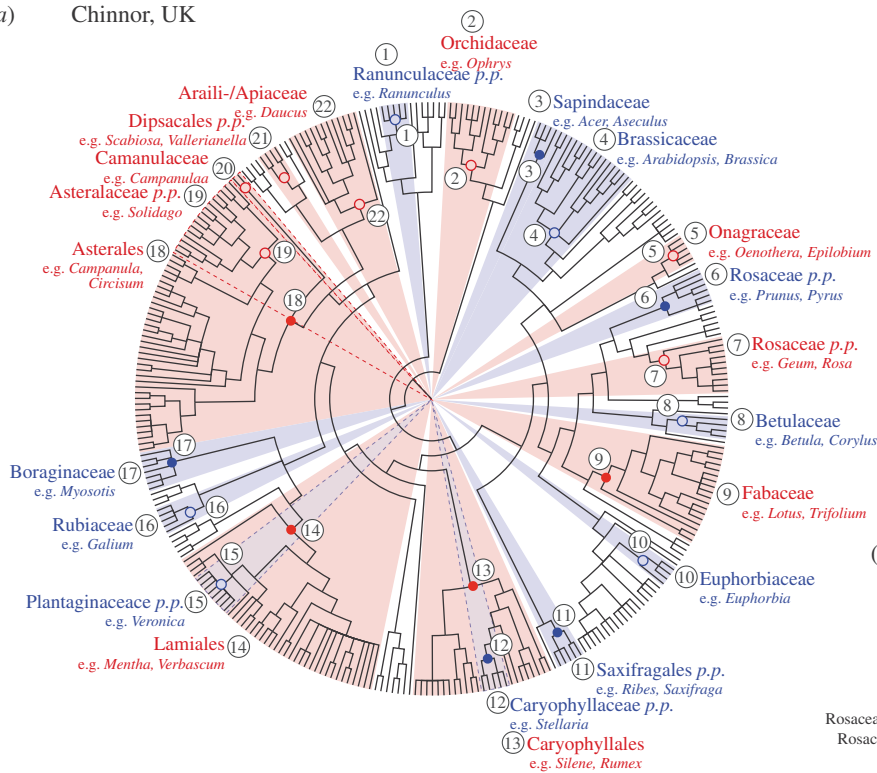
3. RESULTS AND DISCUSSION

(a) *Phylogenetic signal and phenological response in two geographically disjunct temperate floras: Concord, USA and Chinnor, UK*

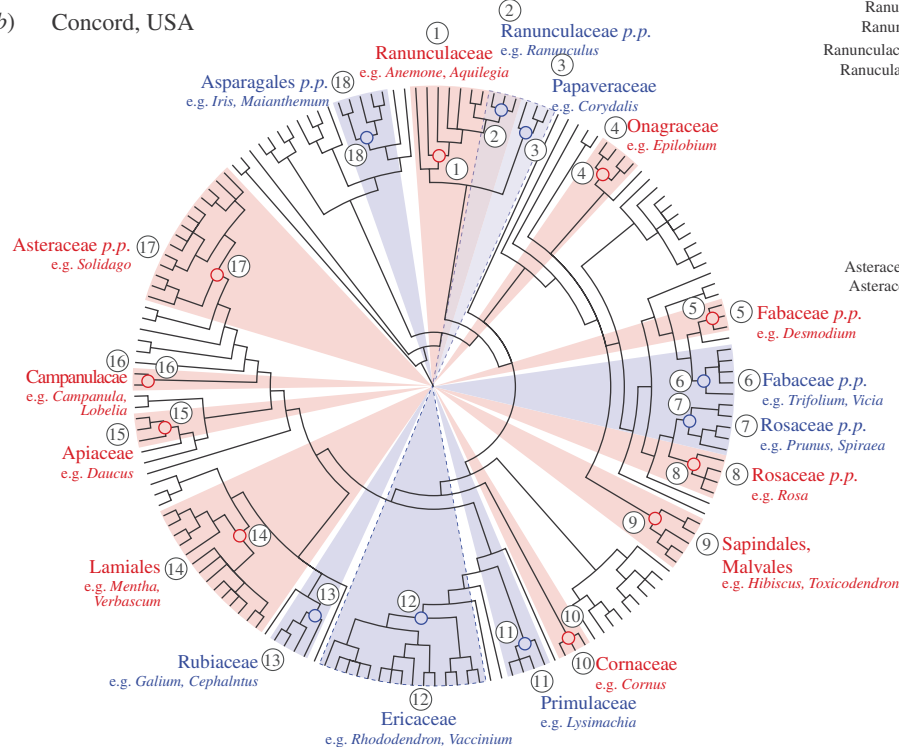
Our results demonstrate striking similarities in the pattern of phenological response traits between Concord and Chinnor. **In both communities flowering time tracking, but not flowering time shift, exhibit phylogenetic signal (table 1; figure 2). This indicates that there is a high degree of phylogenetic signal in flowering time tracking across similar clades despite the geographical isolation of these floras (figure 2 and the electronic supplementary material, table S8).** For example, the Apiales, Asteraceae *pro parte* (*p.p.*), Campanulaceae, Lamiales and Onagraceae were identified as poor tracking clades in Concord and Chinnor when compared with the community means of this trait. Similarly, *Ranunculus*, Rubiaceae, and Rosaceae *p.p.* were identified as good tracking clades.

To our knowledge, these analyses are the first to identify similar phylogenetic patterns in phenological response across geographically disjunct communities. **Moreover, they provide preliminary evidence that flowering time tracking may be phylogenetically conserved across major clades of flowering plants.** One explanation for this pattern is that the developmental pathways that regulate flowering time response to temperature are conserved within major clades. For example, *FLC*-like genes have been shown to be involved in regulating flowering time response to temperature in Brassicaceae and appear to be highly conserved in this clade. This is indicated by the fact that two widely diverged Brassicaceae species, *Arabidopsis thaliana* and *Brassica rapa*, exhibit nearly identical developmental pathways (Johanson *et al.* 2000; Sheldon *et al.* 2000; Michaels & Amasino 2001; Tadege *et al.* 2001). Our results further support this assertion because Brassicaceae in Concord and Chinnor exhibit very similar tracking abilities (phylogenetically corrected mean with s.d.: $n = 2$, -0.41 ± 0.28 and $n = 15$, -0.49 ± 0.09 , respectively). The extent to which this genetic pathway has been similarly recruited in other clades,

(a) Chinnor, UK



(b) Concord, USA



(c) Chinnor versus Concord

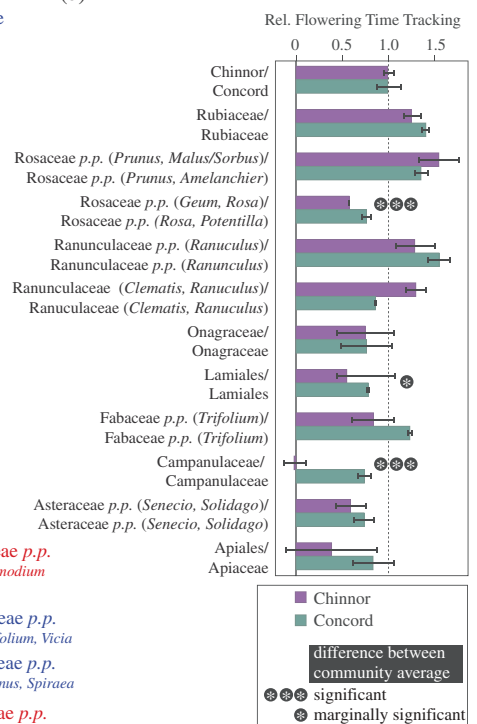


Figure 2. Composite phylogenies of 167 and 323 flowering plant species from (a) Chinnor, UK and (b) Concord, USA. Red and blue dots at nodes represent less and more phenologically responsive clades, respectively, based on their ability to track their flowering times to seasonal temperature variation. Solid-coloured dots indicate those clades that have demonstrated a significant tracking response. A null distribution of mean flowering time tracking for each node in the phylogeny was generated by 9999 randomizations ('node.mn' in PHYLOCOM). Observed clade values that ranked less than or equal to 250 ($p \leq 0.05$) indicated significantly strong trackers while values that ranked greater than or equal to 9750 ($p \leq 0.05$) indicated significantly weak trackers. Open dots indicate marginally significant tracking clades ($p \leq 0.10$). Each of the clades exhibiting these tracking responses is further highlighted in pink and blue and referenced numerically to its clade name. Subclades of interest are labelled with the more familiar, and more inclusive, clade to which they belong followed by *pro parte* (*p.p.*). See the electronic supplementary material, figure S1 for full taxon labels. Bar graphs (c) depict phylogenetically corrected mean differences between tracking and non-tracking clades between Chinnor and Concord. These results are normalized against the community mean of flowering time tracking for each flora, which is the uppermost pair of bars (see the electronic supplementary material, table S8).

or different pathways have evolved and been maintained independently, is an important area for future investigation.

It is interesting to consider why certain clades are poor trackers. What might explain this lack of response across clades? We hypothesize that these species probably evolved to flower in response to other environmental cues, such as precipitation or photoperiod, instead of temperature. One explanation for why a clade might respond to different cues is that they originated in environments where precipitation or photoperiod was a more reliable signal for flowering. For example, species that belong to poor-tracking clades may have evolved in more xeric environments, such as deserts, where precipitation is the most important cue (Beatley 1974). Also, in many tropical regions, neither photoperiod nor temperature exhibits a great deal of seasonal variation, and many species instead use decreasing light intensity (i.e. increasing cloud cover) as an indicator of the advent of the rainy season (van Schaik *et al.* 1993).

Despite the striking similarity of tracking response between these two floras, however, there is not complete clade overlap in phenological response. In particular, species' tracking response differs in several clades: Asparagales, Fabaceae (e.g. *Trifolium*) and Malpighiales were poor trackers in Chinnor, but good trackers in Concord (figure 2). Such differences could be attributable to small taxon sample size. For example, in Concord some clades are represented by only a few species, which could bias estimates of mean tracking ability for the larger clade to which these species belong. In this case, poor taxon representation could artificially underestimate or inflate the apparent clade similarity between regions. This is confounded by the fact that in some instances closely related species in different regions will exhibit very different trait responses as a result of their unique environmental and evolutionary histories. For example, the poor tracking ability of *Trifolium* (Fabaceae) in Chinnor differs sharply from that of their closest relatives in Concord. This may be due to the fact that seasonal temperature variability in Chinnor has not been as intense historically as it was in Concord, resulting in these regional trait differences. In support of this hypothesis, we find that overall tracking ability across the entire community is lower in Chinnor than in Concord (phylogenetically corrected mean with s.d.: -0.416 ± 0.049 and -0.472 ± 0.126 , respectively).

These results provide preliminary evidence that the results from Concord (Willis *et al.* 2008) reflect a more global phylogenetic pattern of species' phenological response to climate change. In particular, Concord and Chinnor show remarkable overlap in the pattern of non-tracking clades. This is significant because the inability to match flowering time to seasonal temperature is strongly associated with species' decline in Concord. Although the mechanism linking species' abilities to adjust their flowering phenology and species' success is not completely understood, it may be that species' success is directly linked to flowering time. For example, species that fail to appropriately adjust their flowering time response to climate change could suffer from a lack of pollinators

(Bierzychudek 1981; Memmott *et al.* 2007). Alternatively, species' success could be indirectly linked to flowering time. For instance, changes in flowering time are known to be correlated with timing of leafing out, a character that is often linked to competitive ability and physiological adaptation (Knight *et al.* 2007; Sola & Ehrlén 2007; Xu *et al.* 2007). A species that starts its growing cycle earlier in warmer years will likely have a competitive advantage in terms of nutrient acquisition and light availability. As a result, it may be more likely to complete its life cycle under more optimal 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.

But is it reasonable to assume that the overlapping pattern of phenological response between these two floras indicates that the pattern of species decline in Concord has been the same in Chinnor? The answer to this question depends on the regional conditions resulting from climate change. If regional selective pressures in Chinnor have been historically similar to Concord, then non-tracking clades are liable to have been similarly lost to climate change. Unfortunately, we cannot make these comparisons directly because abundance data are lacking from Chinnor. However, given what we know about the recent climatic history of Chinnor, this scenario seems unlikely. The selective pressures that would influence flowering time tracking appear to be very different between these two regions. Although the mean temperature has increased significantly in both Concord and Chinnor over the past 30 years (mean annual temperature versus time: estimate = 0.022, $r = 0.40$, $p < 0.001$; estimate = 0.033, $r = 0.63$, $p < 0.001$, respectively), inter-annual temperature variation in the months correlated with first flowering day has increased much more dramatically in Concord than in Chinnor (estimate = 0.047, $r = 0.37$, $p = 0.023$; estimate = 0.002, $r = 0.12$, $p = 0.480$, respectively). Thus, the inability to track seasonal temperature is likely to have been more disadvantageous in Concord than in Chinnor. Nevertheless, the shared phenological responses identified between these two floras justify further study, and indicate that we should be concerned about the potential global impact of climate change in shaping the phylogenetically non-random pattern of plant species loss.

(b) Climate change response and non-native species success: an empirical example from Concord, USA and Chinnor, UK

Willis *et al.* (2010) recently demonstrated that non-native species introduced to Concord have shown a greater ability to adjust their flowering phenology to climate change than have native species: non-native species in general are far better trackers than native species, and invasive species in particular have shifted their flowering to be significantly earlier than have either native or non-native non-invasive species during the past 100 years. Although climate change

Table 3. Phylogenetic correlations of two phenological response traits across non-native and native species' classes in Concord, USA and Chinnor, UK. Phylogenetic branch lengths have been adjusted for time (see the electronic supplementary materials, tables S4 and S5 for tests of phylogenetic uncertainty and branch-length sensitivity, respectively). Phenological response traits examined include *flowering time tracking* (i.e. the correlation between annual first flowering day and seasonal temperature variation) and *flowering time shift* (i.e. the change in mean first flowering day over multiple decades; see §2). Trait comparisons were made between native and non-native species and between natives and the two subclasses of non-native species, invasive and non-native non-invasive. Trait correlations between these species' classes were tested with generalized estimating equations (see §2). The 'estimate' (i.e. slope) describes the direction and magnitude of the trait difference between the first and second species' class in our comparisons. For example, the first comparison describes the trait difference between non-native and native species. Thus, for flowering time tracking, non-natives track seasonal temperature better than natives in Concord because they exhibit a greater negative correlation between flowering time and seasonal temperature variation. For flowering time shift, a positive estimate indicates that the first class has shifted its flowering time to be earlier than the second class (e.g. in Concord, invasives have shifted their flowering time earlier by approx. 11 days relative to natives). n = species sample size within each class: (1) natives, (2) non-native non-invasives and (3) invasives.

traits	n_1	n_2	n_3	non-native versus native			invasive versus native			non-invasive non-native versus native		
				estimate	t	p -value	estimate	t	p -value	estimate	t	p -value
Concord, USA												
flowering time shift (1900–2006)	259	72	11	0.57	0.64	0.5223	11.09	4.97	0	−0.65	−0.70	0.4837
flowering time tracking	134	28	5	−0.09	−3.43	0.0012	−0.17	−2.64	0.0113	−0.08	−3.05	0.0038
Chinnor, UK												
flowering time shift (1954–2000)	271	41	11	−0.27	−0.52	0.6024	−5.21	−5.51	0	1.04	1.89	0.0062
flowering time tracking	271	41	11	−0.09	−4.67	0	0.01	0.28	0.7778	−0.12	−5.62	0

has been hypothesized to facilitate non-native species' naturalization and further increase the likelihood of these species becoming invasive (Dukes & Mooney 1999; Simberloff 2000; Walther 2003; Thuiller *et al.* 2007; Vilá *et al.* 2007), this was the first study to document this pattern across a community.

The phenological response of non-natives in Chinnor and Concord was similar, but the response of invasives was markedly different between the two regions (table 3). In both Chinnor and Concord, non-native species have been significantly better able to track seasonal temperature variation than native species, but they did not differ from the native flora in their flowering time shift response. In contrast, while invasive species in Concord tended to be better trackers than native species, the reverse was observed in Chinnor. Invasives have exhibited a dramatic, but different, flowering time shift in Concord and Chinnor. In Concord, invasive species have significantly shifted their flowering time earlier since 1900 relative to native and non-native non-invasive species, whereas in Chinnor, invasive species have significantly shifted their flowering time to be later.

The phylogenetic pattern of non-native species status and their associated traits has offered important insights into the mechanisms underlying non-native species success (Strauss *et al.* 2006; Lambdon 2008; Cadotte *et al.* 2009). However, the extent to which the phylogenetic distribution of non-native species success can be explained by climate change response has not been tested. This is relevant because a better understanding of such patterns can shed light on the utility of phylogeny as a tool for assessing the likelihood of future naturalizations and invasions (Fisher & Owens 2004; Strauss *et al.* 2006; Proches *et al.* 2008). For

example, if non-native species status and favourable phenological response to climate change exhibit phylogenetic signal and are correlated, then the phylogenetic placement of newly introduced species can inform their likely phenological response, and thus their potential of future success in light of continued climate change. If, on the other hand, non-native species status and phenological response traits are correlated, but one or both traits do not exhibit phylogenetic signal, then the species trait, and not its phylogenetic placement, becomes the more important factor in predicting its future success.

We find a significant phylogenetic signal in non-native species status in Concord (table 2). As noted in the previous section, there is significant phylogenetic signal in flowering time tracking, but not flowering time shift in both communities (table 1). Together with the correlations above (table 3), these results indicate that clades of non-native species that share the ability to track seasonal temperature have tended to become naturalized in Concord. In contrast, although non-native species in Chinnor exhibit a greater ability to track seasonal temperature, there is no phylogenetic signal in non-native species status (table 2). Thus, the greater ability of non-native species to track seasonal temperature in Chinnor does not correlate to a phylogenetic signal in non-native species status. Finally, there is no phylogenetic signal in invasive species status in either community.

These results collectively indicate that climate change has likely played a significant role in shaping non-native species success in these two communities. A greater ability to track seasonal temperature variation corresponds to a higher rate of non-native species naturalization in both Concord and Chinnor

(i.e. non-natives are better trackers in both communities). This suggests that there may have been strong historical filters that favoured the establishment of trackers over non-trackers, which may be due to the fact that trackers can more easily acclimate to the seasonality of their introduced range. However, they also demonstrate striking regional differences in *how* climate change has influenced non-native species success. In Concord, tracking response and non-native species status exhibit phylogenetic signal. Thus, tracking response may explain the phylogenetic patterning of non-native species establishment in this community. In Chinnor, however, tracking response exhibits phylogenetic signal, but non-native species status does not. Why we observe this discrepancy is unclear. One explanation is that the two floras have experienced different climatic histories whereby selection on the ability to track seasonal temperature has been far greater in Concord than in Chinnor. Modern climatic data lend some support to this hypothesis because average inter-annual variation has been much higher in Concord than in Chinnor during the past 150 years (mean two-year variance with standard errors in annual temperature from 1840–2007 for Concord and Chinnor: 84.8 ± 0.06 and 23.3 ± 0.03 , respectively). This could heavily favour the establishment of trackers in Concord, which may in turn favour the establishment of closely related species. On the other hand, while tracking appears to be an important trait to non-native species establishment in Chinnor, additional traits that do not exhibit a phylogenetic signal may be more important in facilitating their establishment. This might dilute any phylogenetic pattern in non-native species status that might be due to tracking. Finally, it is important to note that these discrepancies may be strongly influenced by the source areas from which non-native species arise. For example, it may be that non-natives in Chinnor originate principally from Asia where tracking response may not exhibit a phylogenetic signal. If this were the case, a filter that favoured tracking in Chinnor would select for a phylogenetically random pattern of species, and thus non-native status would not exhibit a phylogenetic signal. To better examine such effects a more global assessment of non-native species status that includes information on species' centre of origin and tracking ability is necessary.

In contrast, the lack of phylogenetic signal in invasive species status in both communities may be due, in part, to recent evolutionary shifts in flowering time of non-natives that have become invasive (Lambdon 2008). Rapid trait evolution has been shown to be frequent among invasive species (Sakai *et al.* 2001; Maron *et al.* 2004). The lack of an apparent phylogenetic pattern may also be due to the relatively small number of invasive species within each community. Regardless of the mechanisms that best explain the patterns above, our results demonstrate that community phylogenies are useful for assessing the likelihood of future non-native species success in the face of continued climate change.

Finally, the distinct advantage of using phylogeny as a proxy for assessing non-native species' climate change response is that it provides a framework for

Table 4. Phylogenetic signal of traits implicated in changes in European bird species' abundance. Phylogenetic signal was tested by comparing the rank of the observed mean standard deviation (observed rank) calculated across all nodes in the community phylogeny to a null distribution of mean standard deviations based on 9999 iterations of trait values arranged randomly across the phylogeny tips. A high observed rank indicates that closely related species are more dissimilar than expected by chance (i.e. trait overdispersion). A low observed rank indicates that closely related species are more similar than expected by chance (i.e. phylogenetic signal). Significance of observed rank based on a two-tail test: significant observed rank less than 250, greater than 9750 = P , 0.05; marginally significant observed rank less than 500, greater than 9500 = P , 0.10.

trait	<i>n</i>	observed rank	<i>p</i> -value
change in abundance (1990–2000)	98	1	0.001
body mass	100	1	0.001
sexual dichromatism	100	1	0.001
European population size	100	1	0.001
migration distance	100	1	0.001
number of broods	100	1	0.001
over-winter in Africa	100	1	0.001
natal dispersal	44	45	0.009
northernmost latitude	100	150	0.030
change in abundance (1970–1990)	98	310	0.062
thermal maximum	38	590	0.118
change in migration date	100	780	0.156
habitat specificity	38	1340	0.268
farmland habitat	100	1675	0.335

inferring species' abilities to respond to climate change, which can be used to make predictions about the susceptibility of species to future climate change. In Concord, our results suggest that newly introduced species that clade with other phenologically responsive species (i.e. better trackers) may be more likely to become naturalized. The same cannot be said for Chinnor, however, owing to the lack of phylogenetic signal in non-native species status. In this case, a more trait-based approach with a focus on species' phenological tracking response, rather than its phylogenetic affinity, is necessary for predicting future naturalization. Phylogeny is similarly unhelpful for predicting the rise of non-native species to invasive status in both floras. Given the lack of phylogenetic signal of invasive species status and flowering time shift response, efforts to predict future invasives in Concord and Chinnor will again require a more trait-based approach that focuses on ascertaining species' phenological response to climate change (especially their long-term flowering time shift response), rather than phylogenetic affinity.

(c) Species decline and phylogenetic selectivity in a European bird community

Our analyses of the Møller *et al.* (2008) bird data reveal previously undetected insights into the phylogenetic pattern of species' changes in abundance (table 4). Species that have declined in abundance are more closely related to one another than is

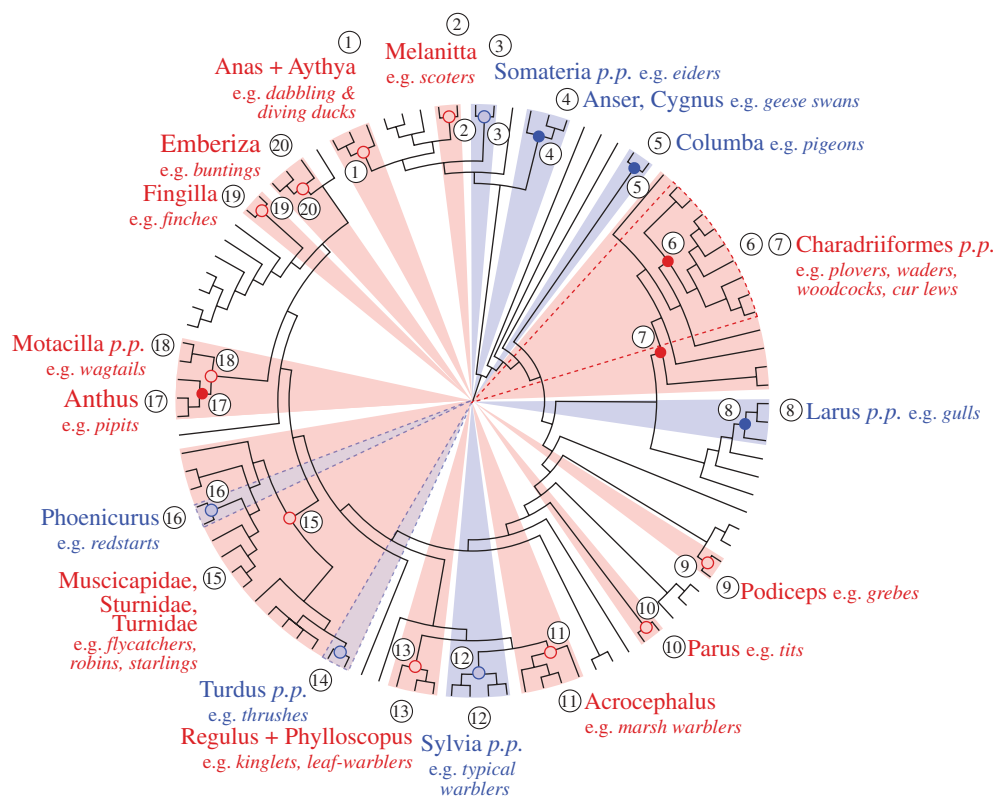


Figure 3. Composite phylogeny of 100 European bird species. Solid red dots indicate clades that have declined significantly from 1990 to 2000 (results were similar for the earlier interval, 1970–1990); solid blue dots indicate clades that have increased significantly. A null distribution of mean change in abundance for each clade in the phylogeny was generated by 9999 randomizations ('node.mn' in PHYLOCOM). Observed clade values that ranked less than or equal to 250 ($p \leq 0.05$) were considered to have significantly declined in abundance while values that ranked greater than or equal to 9750 ($p \leq 0.05$) were considered to have significantly increased in abundance. Open dots indicate marginally significant clades ($p \leq 0.10$). Each of these clades is further highlighted in pink or blue and referenced numerically to its clade name. Subclades of interest are labelled with the more familiar, and more inclusive, clade to which they belong followed by *pro parte* (*p.p.*). See the electronic supplementary material, figure S2 for full taxon labels.

Table 5. Multiple regression analyses of trait correlations with abundance change in European bird species. Regression analysis was performed using generalized estimating equation. All traits listed were included as covariates in the regression model. The multiple regression model was tested over two periods for which species' decline in abundance was available: 1970–1990 and 1990–2000. Estimates indicate the direction and magnitude of the correlation. n = species sample size. See the electronic supplementary material, table S6 for univariate regression analyses of trait correlations and the electronic supplementary material, table S7 for reduced multivariate regression analyses.

trait	change in abundance, 1970–1990				change in abundance, 1990–2000			
	n	estimate	t	p -value	n	estimate	t	p -value
body mass	98	0.81	0.20	0.0104	96	-0.53	-2.33	0.0839
change in migration date	98	-0.47	0.26	0.1360	96	-2.76	-9.35	0.0009
sexual dichromatism	98	0.11	0.13	0.4055	96	-0.08	-0.61	0.5769
European population size	98	0.16	0.10	0.1610	96	-0.17	-1.58	0.1929
farmland habitat	98	-0.67	0.15	0.0068	96	0.15	0.93	0.4096
northern most latitude	98	-0.06	0.01	0.0061	96	0.01	0.57	0.5987
number of broods	98	-0.09	0.07	0.2873	96	0.00	-0.03	0.9781
over-winter in Africa	98	-0.64	0.13	0.0056	96	-0.03	-0.20	0.8532
change in abundance (1970–1990)	—	—	—	—	96	0.17	3.56	0.0257

expected by chance. This is similar to the pattern of species' change in abundance that has been observed in Concord (summarized in §3a above). Moreover, these results apply to both time intervals, from 1970–1990 and 1990–2000. Those bird clades that have experienced dramatic declines in abundance include the buntings (*Emberiza*), dabbling and diving ducks (*Anas* and *Aythya*, respectively), grebes

(*Podiceps*), kinglets and leaf-warblers (*Regulus* and *Phylloscopus*, respectively), pipits (*Anthus*), and the waders, plovers, godwits, turnstones, woodcocks and curlews (*Charadriiformes p.p.*) (figure 3).

We have identified several traits that exhibit phylogenetic signal and are also correlated with the pattern of decline in abundance during the earlier interval, from 1970–1990 (table 5). **Clades of bird**

species that possess larger bodies, over-winter in Africa, and have more northerly ranges have declined more than other species during this time period. Two of these factors in particular—larger body size and migratory distance (here, represented by over-wintering in Africa, see §2)—have been repeatedly implicated in the pattern of bird decline from a variety of studies from Europe (reviewed by Reynolds 2003) and Japan (Amano & Yamaura 2007). Møller *et al.* (2008) identified similar trait correlations, but our analyses present a more comprehensive picture of the pattern of species loss. Specifically, we have identified those clades that have exhibited the most dramatic declines, and provided some likely explanations for this pattern.

The traits associated with decline during the more recent time interval (1990–2000), are much different than the earlier interval. Similar to what was observed by Møller *et al.* (2008), our results indicate that phenological response best explained the pattern of decline. The trait that is most strongly correlated with population trends from 1990 to 2000 is change in migratory arrival time. However, this trait does not exhibit strong phylogenetic signal. Thus, although the best explanation of change in abundance is phenological response to climate change, the pattern of phylogenetic selectivity in bird decline, we identified from 1990 to 2000 cannot be solely attributable to the lack of a favourable climate change response. If that were the case, we would expect change in migratory arrival time to also exhibit phylogenetic signal. This indicates that there are additional traits that may better explain the phylogenetic pattern of decline during this interval. In light of these results, we recommend gathering additional ecological trait data to assess why certain bird clades are at a greater risk than others (see also Bennett & Owens 1997).

4. CONCLUSIONS

Our analyses demonstrate the ways in which a phylogenetic perspective can provide important insights into phenological studies of climate change. For example, our results indicate that closely related plant species in Concord, USA and Chinnor, UK frequently share similar phenological responses to climate change. In Concord, those clades that have been less able to adjust their phenology to climate change have declined dramatically (Willis *et al.* 2008). Because phenological responses to climate change are similar across these geographically disjunct communities, the pattern of species decline observed in Concord may be more broadly applicable. However, the extent to which these shared responses have resulted, and may continue to result, in shaping global patterns of clade decline, is unclear. Answering this question will require: (i) more and better information on the geographical distribution of clades, (ii) a better understanding of the extent to which clade membership predicts climate change response and (iii) knowledge of the regional abiotic factors that influence clade vulnerability across communities and biomes.

These approaches also have broad applicability for predicting the naturalization of non-native plant species. Our results from Concord and Chinnor indicate that

non-native species naturalization, and the rise of non-natives to invasive species status, has been greatly influenced by a favourable climate change response exhibited by these species. This indicates that future climate change may greatly exacerbate non-native species success. In Concord, but not in Chinnor, the phylogeny will probably aid in predicting future non-native species naturalization because the relevant phenological response traits are strongly correlated with the phylogenetic pattern of non-native species status. Furthermore, in Concord and Chinnor, the phenological response traits, and not the phylogeny, will be most useful for predicting non-native species rise to invasive status.

Finally, our analyses of European bird species reveal previously unidentified patterns of phylogenetically non-random species decline, which cannot alone be explained by phenological response to climate change. These results point towards the need for additional ecological study to determine what traits may be influencing the phylogenetic pattern of bird decline identified here.

In all of the examples highlighted here, phylogenetic trees have revealed previously unidentified patterns that can help us to make practical decisions and set priorities for future conservation efforts. In the end, it is the predictive power of phylogenies that makes them useful in such a wide variety of ecological applications, including understanding and addressing climate change responses from phenological data. Although there have been few concrete practical applications to this problem so far, we see great potential in such approaches and an urgent need for more rapid integration of phylogenetic biology and climate change research. At the same time, our results indicate that in certain instances phylogeny will be less useful than direct knowledge of species' phenological response traits. For these reasons, it is critical that future efforts to model community response to climate change be more holistic in their approaches and incorporate data from phenology and phylogeny.

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REFERENCES

- Ackerly, D. D. 2004 Adaptation, niche conservatism, and convergence: comparative studies of leaf evolution in the California chaparral. *Am. Nat.* **163**, 654–671.
- Amano, T. & Yamaura, Y. 2007 Ecological and life-history traits related to range contractions among breeding birds in Japan. *Biol. Conserv.* **137**, 271–282. (doi:10.1016/j.biocon.2007.02.010)
- Beatley, J. C. 1974 Phenological events and their environmental triggers in Mojave desert ecosystems. *Ecology* **55**, 856–863. (doi:10.2307/1934421)
- Bennett, P. M. & Owens, I. P. F. 1997 Variation in extinction risk among birds: chance or evolutionary predisposition?

- Proc. R. Soc. Lond. B* **264**, 401–408. (doi:10.1098/rspb.1997.0057)
- Bierzychudek, P. 1981 Pollinator limitation of plant reproductive effort. *Am. Nat.* **117**, 838–840.
- Bolker, B. *et al.* 2007 *APE: analyses of phylogenetics and evolution*. v. 2.1-3. See <http://ape.mpl.ird.fr/>.
- Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006 Climate change and population declines in a long-distance migratory bird. *Nature* **441**, 81–83. (doi:10.1038/nature04539)
- Bradley, N. L., Leopold, A. C., Ross, J. & Wellington, H. 1999 Phenological changes reflect climate change in Wisconsin. *Proc. Natl Acad. Sci. USA* **96**, 9701–9704. (doi:10.1073/pnas.96.17.9701)
- Butler, C. J. 2003 The disproportionate effect of global warming on the arrival dates of short-distance migratory birds in North America. *Ibis* **145**, 484–495. (doi:10.1046/j.1474-919X.2003.00193.x)
- Cadotte, M. W., Cardinale, B. J. & Oakley, T. H. 2008 Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl Acad. Sci. USA* **105**, 17 012–17 017. (doi:10.1073/pnas.0805962105)
- Cadotte, M. W., Hamilton, M. A. & Murray, B. R. 2009 Phylogenetic relatedness and plant invader success across two spatial scales. *Divers. Distrib.* **15**, 481–488. (doi:10.1111/j.1472-4642.2009.00560.x)
- Cardillo, M., Mace, G. M., Gittleman, J. L., Jones, K. E., Bielby, J. & Purvis, A. 2008 The predictability of extinction: biological and external correlates of decline in mammals. *Proc. R. Soc. B* **275**, 1441–1448. (doi:10.1098/rspb.2008.0179)
- Cavender-Bares, J., Ackerly, D. D., Baum, D. A. & Bazzaz, F. A. 2004 Phylogenetic overdispersion in Floridian oak communities. *Am. Nat.* **163**, 823–843.
- Cavender-Bares, J., Keen, A. & Miles, B. 2006 Phylogenetic structure of floridian plant communities depends on taxonomic and spatial scale. *Ecology* **87**, S109–S122.
- Cavender-Bares, J., Kozak, K. H., Fine, P. V. A. & Kembel, S. W. 2009 The merging of community ecology and phylogenetic biology. *Ecol. Lett.* **12**, 693–715. (doi:10.1111/j.1461-0248.2009.01314.x)
- Donoghue, M. J. 2008 A phylogenetic perspective on the distribution of plant diversity. *Proc. Natl Acad. Sci. USA* **105**, 11 549–11 555. (doi:10.1073/pnas.0801962105)
- Dukes, J. S. & Mooney, H. A. 1999 Does global change increase the success of biological invaders? *Trends Ecol. Evol.* **14**, 135–139. (doi:10.1016/S0169-5347(98)01554-7)
- Edwards, E. J., Still, C. J. & Donoghue, M. J. 2007 The relevance of phylogeny to studies of global change. *Trends Ecol. Evol.* **22**, 243–249. (doi:10.1016/j.tree.2007.02.002)
- Felsenstein, J. 1985 Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.
- Fisher, D. O. & Owens, I. P. F. 2004 The comparative method in conservation biology. *Trends Ecol. Evol.* **19**, 391–398. (doi:10.1016/j.tree.2004.05.004)
- Fitter, A. H. & Fitter, R. S. R. 2002 Rapid changes in flowering time in British plants. *Science* **296**, 1689–1691. (doi:10.1126/science.1071617)
- Gilbert, G. S. & Webb, C. O. 2007 Phylogenetic signal in plant pathogen–host range. *Proc. Natl Acad. Sci. USA* **104**, 4979–4983. (doi:10.1073/pnas.0607968104)
- Harvey, P. H. & Pagel, M. D. 1991 *The comparative method in evolutionary biology*. Oxford, UK: Oxford University Press.
- Johanson, U., West, J., Lister, C., Michaels, S., Amasino, R. & Dean, C. 2000 Molecular analysis of *FRIGIDA*, a major determinant of natural variation in *Arabidopsis* flowering time. *Science* **290**, 344–347. (doi:10.1126/science.290.5490.344)
- Kang, H. & Jang, J. 2004 Flowering patterns among angiosperm species in Korea: diversity and constraints. *J. Plant Biol.* **47**, 348–355. (doi:10.1007/BF03030550)
- Knight, K. S., Kurylo, J. S., Endress, A. G., Stewart, J. R. & Reich, P. B. 2007 Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): a review. *Biol. Invas.* **9**, 925–937. (doi:10.1007/s10530-007-9091-3)
- Lambdon, P. W. 2008 Is invasiveness a legacy of evolution? Phylogenetic patterns in the alien flora of Mediterranean islands. *J. Ecol.* **96**, 46–57.
- Lord, J., Westoby, M. & Leishman, M. 1995 Seed size and phylogeny in six temperate floras: constraints, niche conservatism, and adaptation. *Am. Nat.* **146**, 349–364.
- Losos, J. B. 2008 Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. *Ecol. Lett.* **11**, 995–1003. (doi:10.1111/j.1461-0248.2008.01229.x)
- Macmynowski, D. P., Root, T. L., Ballard, G. & Geupel, G. R. 2007 Changes in spring arrival of Nearctic–Neotropical migrants attributed to multiscalar climate. *Global Change Biol.* **13**, 2239–2251. (doi:10.1111/j.1365-2486.2007.01448.x)
- Maron, J. L., Vila, M., Bommarco, R., Elmendorf, S. & Beardsley, P. 2004 Rapid evolution of an invasive plant. *Ecol. Monogr.* **74**, 261–280. (doi:10.1890/03-4027)
- McKinney, M. L. 1997 Extinction vulnerability and selectivity: combining ecological and paleontological views. *Annu. Rev. Ecol. Syst.* **28**, 495–516. (doi:10.1146/annurev.ecolsys.28.1.495)
- Mehrhoff, L. J., Silander, J. A., Leicht, S. A., Mosher, E. S. & Tabak, N. M. 2003 *IPANE: invasive plant atlas of New England*. Storrs, CT: Department of Ecology & Evolutionary Biology, University of Connecticut. See <http://www.ipane.org>.
- Memmott, J., Craze, P. G., Nickolas, M. W. & Price, M. V. 2007 Global warming and the disruption of plant–pollinator interactions. *Ecol. Lett.* **10**, 710–717. (doi:10.1111/j.1461-0248.2007.01061.x)
- Michaels, S. D. & Amasino, R. M. 2001 Loss of *FLOWERING LOCUS C* activity eliminates the late-flowering phenotype of *FRIGIDA* and autonomous pathway mutations but not responsiveness to vernalization. *Plant Cell* **13**, 935–941. (doi:10.1105/tpc.13.4.935)
- Miller-Rushing, A. J. & Primack, R. B. 2008 Global warming and flowering times in Thoreau’s Concord: a community perspective. *Ecology* **89**, 332–341. (doi:10.1890/07-0068.1)
- Miller-Rushing, A. J., Lloyd-Evans, T. L., Primack, R. B. & Satzing, P. 2008 Bird migration times, climate change, and changing population sizes. *Glob. Change Biol.* **14**, 1959–1972. (doi:10.1111/j.1365-2486.2008.01619.x)
- Mills, A. M. 2005 Changes in the timing of spring and autumn migration in North American migrant passerines during a period of global warming. *Ibis* **147**, 259–269. (doi:10.1111/j.1474-919X.2005.00380.x)
- Møller, A. P., Rubolini, D. & Lehikoinen, E. 2008 Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proc. Natl Acad. Sci. USA* **105**, 16 195–16 200. (doi:10.1073/pnas.0803825105)
- Paradis, E. & Claude, J. 2002 Analysis of comparative data using generalized estimating equations. *J. Theor. Biol.* **218**, 175–185. (doi:10.1006/jtbi.2002.3066)
- Parmesan, C. 2006 Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Syst.* **37**, 637–669. (doi:10.1146/annurev.ecolsys.37.091305.110100)
- Parmesan, C. 2007 Influences of species, latitudes and methodologies on estimates of phenological response to

- global warming. *Glob. Change Biol.* **13**, 1860–1872. (doi:10.1111/j.1365-2486.2007.01404.x)
- Parmesan, C. & Yohe, G. 2003 A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42. (doi:10.1038/nature01286)
- Primack, R. B., Miller-Rushing, A. J. & Dharaneeswaran, K. 2009 Changes in the flora of Thoreau's Concord. *Biol. Conserv.* **142**, 500–508. (doi:10.1016/j.biocon.2008.10.038)
- Prinzing, A., Durka, W., Klotz, S. & Brandl, R. 2001 The niche of higher plants: evidence for phylogenetic conservatism. *Proc. R. Soc. Lond. B* **268**, 2383–2389. (doi:10.1098/rspb.2001.1801)
- Proches, S., Wilson, J. R. U., Richardson, D. M. & Rejmánek, M. 2008 Searching for phylogenetic pattern in biological invasions. *Global Ecol. Biogeogr.* **17**, 5–10.
- Purvis, A. 2008 Phylogenetic approaches to the study of extinction. *Annu. Rev. Ecol. Syst.* **39**, 301–319. (doi:10.1146/annurev.ecolsys.063008.102010)
- Reynolds, J. D. 2003 Life histories and extinction risk. In *Macroecology: concepts and consequences* (eds T. M. Blackburn & K. J. Gaston), pp. 195–217. Cambridge, UK: Cambridge University Press.
- Root, T. L., Price, J. T., Hall, K. R., Schneider, S. H., Rosenzweig, C. & Pounds, J. A. 2003 Fingerprints of global warming on wild animals and plants. *Nature* **421**, 57–60. (doi:10.1038/nature01333)
- Sakai, A. K. *et al.* 2001 The population biology of invasive species. *Annu. Rev. Ecol. Syst.* **32**, 305–332. (doi:10.1146/annurev.ecolsys.32.081501.114037)
- Sheldon, C. C., Rouse, D. T., Finnegan, E. J., Peacock, W. J. & Dennis, E. S. 2000 The molecular basis of vernalization: the central role of *FLOWERING LOCUS C* (FLC). *Proc. Natl Acad. Sci. USA* **97**, 3753–3758. (doi:10.1073/pnas.060023597)
- Simberloff, D. 2000 Global climate change and introduced species in United States forests. *Sci. Total Environ.* **262**, 253–261. (doi:10.1016/S0048-9697(00)00527-1)
- Sola, A. J. & Ehrlén, J. 2007 Vegetative phenology constrains the onset of flowering in the perennial herb *Lathyrus vernus*. *J. Ecol.* **95**, 208–216. (doi:10.1111/j.1365-2745.2006.01191.x)
- Sparks, T. H. & Carey, P. D. 1995 The responses of species to climate over two centuries: an analyses of the Marsham phenological record, 1736–1947. *J. Ecol.* **83**, 321–329.
- Sparks, T. H., Jeffree, E. P. & Jeffree, C. E. 2000 An examination of the relationship between flowering times and temperature at the national scale using long-term phenological records from the UK. *Int. J. Biometeorol.* **44**, 82–87. (doi:10.1007/s004840000049)
- Stenseth, N. C. & Mysterud, A. 2002 Climate, changing phenology, and other life history and traits: nonlinearity and match-mismatch to the environment. *Proc. Natl Acad. Sci. USA* **99**, 13 379–13 381. (doi:10.1073/pnas.212519399)
- Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K. S. & Lima, M. 2002 Ecological effects of climate fluctuations. *Science* **297**, 1292–1296. (doi:10.1126/science.1071281)
- Strauss, S. Y., Webb, C. O. & Salamin, N. 2006 Exotic taxa less related to native species are more invasive. *Proc. Natl Acad. Sci. USA* **103**, 5841–5845. (doi:10.1073/pnas.0508073103)
- Tadege, M., Sheldon, C. C., Helliwell, C. A., Stoutjesdijk, P., Dennis, E. S. & Peacock, W. J. 2001 Control of flowering time by *FLC* orthologues in *Brassica napus*. *Plant J.* **28**, 545–553. (doi:10.1046/j.1365-313X.2001.01182.x)
- Thuiller, W., Richardson, D. M. & Midgley, G. F. 2007 Will climate change promote alien invasions? In *Biological invasions* (ed. W. Nentwig), pp. 197–211. Berlin, Germany: Springer.
- Vamosi, S. M., Heard, S. B., Vamosi, J. C. & Webb, C. O. 2009 Emerging patterns in the comparative analysis of phylogenetic community structure. *Mol. Ecol.* **18**, 572–592. (doi:10.1111/j.1365-294X.2008.04001.x)
- van Schaik, C. P., Terborgh, J. W. & Wright, S. J. 1993 The phenology of tropical forests: adaptive significance and consequences for primary consumers. *Annu. Rev. Ecol. Syst.* **24**, 353–377. (doi:10.1146/annurev.es.24.110193.002033)
- Vilá, M., Corbin, J. D., Dukes, J. S., Pino, J. & Smith, S. D. 2007 Linking plant invasions to global environmental change. In *Terrestrial ecosystems in a changing world* (eds J. Canadell, D. Pataki & L. Pitelka), pp. 93–102. New York, NY: Springer.
- Visser, M. E. 2008 Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proc. R. Soc. B* **275**, 649–659. (doi:10.1098/rspb.2007.0997)
- Visser, M. E. & Both, C. 2005 Shifts in phenology due to global climate change: the need for a yardstick. *Proc. R. Soc. B* **272**, 2561–2569. (doi:10.1098/rspb.2005.3356)
- Walther, G. R. 2003 Plants in a warmer world. *Perspect. Plant Ecol. Evol. Syst.* **6**, 169–185. (doi:10.1078/1433-8319-00076)
- Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M., Hoegh-Guldberg, O. & Bairlein, F. 2002 Ecological responses to recent climate change. *Nature* **416**, 389–395. (doi:10.1038/416389a)
- Webb, C. O. & Donoghue, M. J. 2005 PHYLOMATIC: tree assembly for applied phylogenetics. *Mol. Ecol. Notes* **5**, 181–183. (doi:10.1111/j.1471-8286.2004.00829.x)
- Webb, C. O., Ackerly, D. D., McPeck, M. A. & Donoghue, M. J. 2002 Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* **33**, 475–505. (doi:10.1146/annurev.ecolsys.33.010802.150448)
- Webb, C. O., Ackerly, D. D. & Kembel, S. W. 2008. PHYLACOM: software for the analysis of phylogenetic community structure and trait evolution. PHYLACOM. v. 3.41. See <http://www.phylodiversity.net/phylocom/>.
- Wiens, J. J. & Graham, C. H. 2005 Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst.* **36**, 519–539. (doi:10.1146/annurev.ecolsys.36.102803.095431)
- Wikström, N., Savolainen, V. & Chase, M. W. 2001 Evolution of the angiosperms: calibrating the family tree. *Proc. R. Soc. Lond. B* **268**, 2211–2220. (doi:10.1098/rspb.2001.1782)
- Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J. & Davis, C. C. 2008 Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proc. Natl Acad. Sci. USA* **105**, 17 029–17 033. (doi:10.1073/pnas.0806446105)
- Willis, C. G., Ruhfel, B., Primack, R. B., Miller-Rushing, A. J. & Davis, C. C. 2009 Reply to McDonald *et al.*: climate change, not deer herbivory, has shaped species decline in Concord, Massachusetts. *Proc. Natl Acad. Sci. USA* **106**, E29–E29. (doi:10.1073/pnas.0900170106)
- Willis, C. G., Ruhfel, B. R., Primack, R. B., Miller-Rushing, A. J., Losos, J. B. & Davis, C. C. 2010 Favourable climate change response explains non-native species' success in Thoreau's woods. *PLoS ONE* **5**, e8878. (doi:10.1371/journal.pone.0008878)
- Wright, S. J. & Calderon, O. 1995 Phylogenetic patterns among tropical flowering phenologies. *J. Ecol.* **83**, 937–948.
- Xu, C.-Y., Griffin, K. L. & Schuster, W. S. F. 2007 Leaf phenology and seasonal variation of photosynthesis of invasive *Berberis thunbergii* (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. *Oecologia* **154**, 11–21. (doi:10.1007/s00442-007-0807-y)