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REPLY TO ANGELO: CLIMATE CHANGE AND SPECIES LOSS IN THOREAU'S WOODS (CONCORD, MASSACHUSETTS, USA)

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Our research has identified that climate change has been responsible for shaping the pattern of species loss in Concord, Massachusetts, USA (Willis et al. 2008). In particular, we identified that closely related species (i.e., clades) that are less phenologically responsive to both long- and short-term changes in climate have declined in abundance. Phenological change has long been known to be a key indicator of species response to climate change (Fitter & Fitter 2002; Walther et al. 2002; Parmesan & Yohe 2003; Visser & Both 2005) and is believed to have important consequences for the success of species (Cleland et al. 2012; Cahill et al. 2013). In a recent critique of our work, Angelo (2014) called into question the main conclusion of our study on two grounds: i) our estimates of species loss in Concord are inaccurate, and ii) it is unlikely that climate change has significantly impacted species loss given the myriad of additional factors that effect species in suburban communities like Concord (e.g., reforestation, land-use change, non-native species, and increased deer herbivory). We believe that Angelo's critique of our study is based on a misunderstanding of our methods and conclusions. Here, we explicitly address his critique and reiterate that our results and conclusions are sound. Our response is focused specifically on the critique of Willis et al. (2008) because this is the study for which we performed the bulk of the analyses, interpretation, and writing.

To analyze the phylogenetic pattern of community-wide species loss in Concord, we utilized both historic and field observational data collected and compiled by Miller-Rushing and Primack (Willis et al. 2008; Primack et al. 2009). We reported that species that have been unable to respond to climate change by altering their flowering phenology have experienced significant declines in abundance over the last century. We based this conclusion on two findings. First, we found significant correlations between change in abundance over the past ~100 years and two metrics of flowering time response to temperature: *shift in flowering time* (i.e., mean difference in flowering time between 1900-2000 and 1850-2000), and *flowering time tracking* (i.e., ability of species to adjust their flowering time to inter-annual seasonal temperature changes). Secondly, we found that species loss has occurred disproportionally among particular clades—a pattern known as phylogenetic signal. We also found that one phenological response metric, *flowering time tracking*, also exhibited significant phylogenetic signal. On the basis of these findings we concluded that i) species phenological response to climate change is associated with species loss, and ii) climate change has played a role in *shaping* the phylogenetic pattern of species loss in Concord. To our knowledge, ours was the first study to identify a link between the phenological response of species to climate change and a phylogenetic bias in species loss.

Angelo raises two major criticisms of our study. First, he suggests that our estimates of species abundance change are problematic. As an initial point of clarification, we computed changes in abundance based on the observations beginning ~100 years ago from Hosmer (Hosmer 1903), not

Thoreau, as Angelo indicates. We used Hosmer's data because they included estimates of flowering time for over a decade, which allowed us to most accurately estimate our *flowering time tracking* metric. Angelo raises a valid point that the Hosmer surveys were not exclusive to the Concord area and therefore may bias estimates of species loss. As Primack et al. (2009) noted, however, similar patterns of species decline were observed in Concord when using both Thoreau's (mid-19th Century) and Eaton's (mid-20th Century) abundance estimates. Thus, we believe the broader patterns of species loss we identify would not significantly change if we were to use an alternative data source. More importantly, our analysis of species loss utilized relative, not absolute, estimates of abundance change (see Primack et al. [in review] for a more detailed response). To this end, we use "change in abundance" and "species loss" interchangeably because we were interested in factors underlying declines in abundances that have placed species at greater risk of local extinction. Finally, while Angelo focuses his discussion on Liliaceae and Orchidaceae, our metrics of abundance change included hundreds of additional species representing broad phylogenetic diversity (Willis et al. 2008). In addition to Liliaceae and Orchidaceae, several other flowering plant clades demonstrated similar patterns of dramatic decline, including Asterales, Cornaceae, Lamiaceae (in part), Lentibulariaceae, Malpighiales, Ranunculaceae (in part), and Saxifragales. Thus, targeting only Liliaceae and Orchidaceae is a biased comparison that is not reflective of the totality of our results. This is especially relevant because Angelo's dismissal of declines in Liliaceae and Orchidaceae is questionable (Primack et al., in review).

Angelo's second criticism is that climate change is not the best explanation for species loss in Concord. Although Angelo acknowledges that climate change has led to changes in flowering and leaf-out times in Concord, he dismisses these changes as important to species loss. This is surprising because it has been well documented that species phenological response to climate change can have significant consequences for plant success (Cleland et al. 2012; Cahill et al. 2013). For example, if a plant flowers too early it may be subject to late frost damage (Inouye 2008). Alternatively, changes in flowering time might expose species to greater competition and herbivory (Brooker 2006) or lead to ecological mismatches between plants and their pollinators (Kudo et al. 2008). Instead, he argues that other changes to the region are likely to have played a much more important role in species loss, including reforestation, land-use changes, increased deer herbivory, and the spread of non-natives.

We agree with Angelo that these additional factors have played a role in shaping species loss in Concord. Indeed, we acknowledged this much in our original paper, and our analyses corroborate this point. We used multivariate regression models (Paradis & Clausen 2002) that allowed us to account for as many potentially confounding factors as possible, including: habitat (a proxy for species affected by reforestation and land-use change), deer browse preference, native/introduced status, and latitudinal range. Not surprisingly, many of these factors were significantly associated with species loss. Habitat preference was strongly correlated with species loss: aquatic species have experienced significant declines, while roadside or ruderal species have increased in abundance. Species favored by deer have exhibited sharp declines (see McDonald et al. 2009; Willis et al. 2009). Non-natives have increased significantly in abundance over the last century, a trend that appears to be associated with their ability to respond phenologically to climate change (Willis et al. 2010). And finally, species with more southern distributions have increased in abundance, while species with more northern distributions have declined (Willis et al. 2008). This last point provides independent support for an effect of climate change on species loss in Concord and suggests that species are not only responding through phenological change but may be shifting their ranges northward as well.

Despite the significance of these additional factors, we still recovered a significant association between phenological response to climate change and species loss. Thus, while other factors have influenced species loss, there remains a significant signature of the impact of climate change on plant abundance in Concord. Furthermore, because one metric of species phenological

response, *flowering time tracking*, and species loss were significantly correlated and exhibit strong phylogenetic signal, we concluded that phenological response to climate change has contributed to a phylogenetically biased pattern of species loss. Herein lies the central point of our paper: that climate change has significantly contributed to the phylogenetic pattern of species loss in this community.

In conclusion, we acknowledge the limitations of correlative analyses such as ours to fully explain any complex ecological process, including species loss. We also agree that untangling the relative importance of these factors is difficult. Despite these challenges, however, these are deeply important questions that deserve investigation. By addressing such questions at a community level as we have done, we were able to identify general patterns underlying species loss that will provide fertile ground for future research. To this end, we believe that the association between phenological response to climate change and species loss in Concord is real and that future climate change not only poses continued threats to plant diversity in New England but possibly to other communities where similar phenological responses have been observed (Davis et al. 2010).

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