Decline in beetle abundance and diversity in an intact temperate forest linked to climate warming

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ABSTRACT

Insect abundances are declining in many areas around the world, but the causes of those declines are seldom clear. Here we report a dramatic decline in the abundance and diversity of Coleoptera (beetle) taxa in a large tract of intact northern hardwood forest during the last 45 years, and provide evidence supporting winter warming as the primary cause. Beetles were sampled using the same method (window traps) and in the same locations within the Hubbard Brook Experimental Forest, New Hampshire, in 1973–1977 and again in 2015–2017. The mean (± SE) number of beetles captured per 48-h fell from 23.2 (± 3.89) to 3.9 (± 1.19), a decline of 83% over this 45-year period. The number of beetle taxa captured decreased by 39%, with 19 beetle families disappearing entirely. Beetle capture rate was least when and where climate was warmest. Capture rate was significantly lower in the 2010s when mean daily temperature was about 1.8 °C warmer, and sampling during 2016–2017 at low, mid and high elevations (320, 540, and 810 m asl, respectively) revealed lowest beetle captures at low elevation where climate was warmest. Most importantly, beetle capture rate was significantly lower after winters with less snow cover during the previous winter, indicating that snow cover in northern hardwood forest is essential for sustaining the beetle community. These results imply that additional climate warming might further reduce the abundance and diversity of beetles and other arthropods inhabiting the forest-floor, potentially affecting critical ecosystem processes such as decomposition and carbon storage.

1. Introduction

Dramatic declines in insect abundance, biomass and diversity are being reported from multiple habitat types in the Neotropics, Europe and North America (e.g., Brooks et al., 2012; Hallmann et al., 2017; Gillespie et al., 2019; Homburg et al., 2019; Janzen and Hallwachs, 2019). Suggested causes of the declines reported include habitat loss, fragmentation and degradation, as well as pollution (e.g., from pesticides) and climate change (Sánchez-Bayo and Wyckhuys, 2019). However, no study to date has been able to isolate the cause(s) of the observed declines (Coyle et al., 2017), and some studies show no such losses in relatively undisturbed natural habitats (Sánchez-Bayo and Wyckhuys, 2019). Identifying causal mechanisms of change is urgently needed for assessing management and conservation options (Simmons et al., 2019), as is new information from relatively undisturbed habitats such as the forests of northeastern North America.

Change in forest insect abundance and diversity might best be revealed by examining the forest-floor "brown" food web, which sustains most of the animal diversity found in temperate forests (Decaëns,

2010). Tracking change in the brown food web can also provide insight into the processes that sustain forests and their biodiversity (Schowalter, 2017), because animals in this food web can affect key ecosystem processes such as decomposition (Ulyshen, 2016), nutrient cycling (Carrillo et al., 2011) and carbon storage (Wenk et al., 2016). Unfortunately, few long-term data document the composition and dynamics of the brown food web in the temperate deciduous forests of North America (Garrick et al., 2019; Adlam et al., 2017). Long-term studies are valuable because populations of forest-floor arthropods can be highly variable in space and time (Bentz et al., 2010) and because some factors affecting populations such as climate and vegetation change slowly, across decades rather than years.

Forest floor beetles (Coleoptera), in particular, can be sensitive indicators of long-term forest change and health (Hoekman et al., 2017) because they play multiple roles, ranging from decomposers (e.g., carrion beetles, Silphidae) to top predators (e.g., rove beetles, Staphylinidae). Consequently, the beetle community is likely to respond both to changes in resources (bottom up effects; e.g., Chen and Wise, 1999) and to shifts in predator-prey interactions (top down effects; e.g., Burtis

et al., 2015). In part for this reason, carabid beetles (Coleoptera: Carabidae) in particular have often been used as bioindicators of environmental change (Latty et al., 2006).

Beetle populations are sensitive to climatic conditions both during the growing season (Williams et al., 2014) and winter (Templer et al., 2012; Christenson et al., 2017). The abundance and richness of forest Carabidae in southeastern United States were reduced by long-term, experimentally created drought conditions (Williams et al., 2014). In northern forests, a shorter period of snow cover and experimentally reduced snow depth resulted in lower Coleoptera abundance during the following growing season (Templer et al., 2012). The response of arthropods to increasing temperature and a longer growing season is often expected to be positive, as higher temperatures increase metabolic rates and reproduction. This is often called the "warmer is better" hypothesis (Frazier et al., 2006). However, predicting the effects of climate change on arthropod communities is problematic, because it is uncertain whether the dominant drivers of change will be positive impacts on metabolism during the growing season or negative effects of changing precipitation and decreasing winter snow cover on survival (Groffman et al., 2012; Penczykowski et al., 2017).

In this study, we provide data on how Coleoptera have changed in a relatively undisturbed, unfragmented northern hardwood forest over a 45-year period, and we assess the possible causes of change. Using the window trap technique, we collected data on beetle abundance and diversity at one mid-elevation site (~540 m asl) during late May through early August in 1973–1977 and again at the same locations in 2015–2017. In the latter period, we expanded the sampling to both lower (~320 m) and higher (~810 m) elevations, which allowed us to assess the potential impact of differences in climate among elevations as well as over time on the Coleoptera community.

2. Methods

2.1. Field-site description

This study was conducted at the Hubbard Brook Experimental Forest (HBEF) in North Woodstock, New Hampshire, USA, a 3160-ha unfragmented tract of northern hardwood forest within the much larger White Mountains National Forest (WMNF) (317,478 ha). Dominant tree species within the HBEF are American beech (*Fagus grandifolia*), sugar maple (*Acer saccharum*), and yellow birch (*Betula alleghaniensis*), with the proportion of red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) increasing at higher elevations (Van Doorn et al., 2011). The forest was extensively harvested between 1906 and 1920 (Peart et al., 1992), but has remained unmanaged and been altered only infrequently by natural events such as hurricanes, ice storms, microbursts and by the invasion and expansion of Beech bark disease (BBD; Holmes and Likens, 2016, Cleavitt et al., 2008).

To assess the impact of shifting climate conditions over the study period, we used data from the Hubbard Brook Ecosystem Study website (hubbardbrook.org; Campbell, 2017a, 2017b, 2017c) for weather stations located < 1 km from the sites where Coleoptera were sampled. From 1973 to 2017, mean daily temperature increased significantly at all three elevations sampled (Linear regression, $F_{1,43} > 11.5$, $P < 0.01$) but by different amounts: about 1 °C at low elevation (~320 m) and 1.8 °C at both mid (~540 m) and high (~810 m) elevations. Mean daily precipitation showed no trend over this period, and it differed by < 2 mm among elevations (Appendix A, Fig. A1). Precipitation, however, was measured in clearings (Holmes and Likens, 2016) and it was likely higher than measured values under the canopy at the high elevation site due to cloudier conditions and canopy drip.

2.2. Sampling

Coleoptera were sampled by using window traps (Southwood and Henderson, 2009), which capture individuals as they fly above the forest-floor. Arthropods are trapped when they hit a sheet of clear plexiglass and fall into an underlying trough of soapy water (See Appendix A for details). This method compares well with others for sampling flying arthropods, but because of the diverse ecologies of beetles (e.g., different frequencies of flight), no method samples all families of Coleoptera equally (Bouget et al., 2008; Zou et al., 2012). Sampling began in late May and continued until early August in 1973–1977 and again in 2015–2017. In each period, three window traps were placed in a row ~200 apart in the same locations at a mid-elevation site (540 m asl) within the forest (Appendix A, Fig. A2 shows the specific weeks sampled in each year). In 2016–2017, sampling was expanded to include three elevations: 320 m, 540 m, 810 m asl., again with three traps in a row ~200 m apart at each elevation. We sampled in areas dominated by deciduous trees at each elevation. An approximately equal number of samples was collected in each period: 338 during 1973–1977 and 387 in 2015–2017. Sampling was done with three traps over five years during 1973–1977 and with up to nine traps during 2015–2017, with three traps at each of three elevation in 2016 and 2017. Because we used the same methods and collected an approximately equal number of samples in each sampling period, our results provide a credible measure of change in Coleoptera abundance over time. The 50 Coleoptera taxa identified in the samples included 4 super families, 42 families, and 4 subfamilies (Appendix A, Table A1). Individuals were counted in only one of these taxa. For example, Pselaphinae is a subfamily of Staphylinidae, but individuals of the subfamily Pselaphinae were not also counted as part of the family Staphylinidae.

2.3. Taxa accumulation curves

To assess whether sampling captured most of the taxa present during the two sampling periods, we constructed taxa-accumulation curves. Because differences in sampling intensity or duration can affect the number of taxa captured, and hence the shape of the curves, we used data from the two years within each period that were sampled completely between late May and early August: 1974–1975 and 2016–2017. We calculated accumulation curves with the R package 'vegan' and the 'specaccum' function. We used the 'random' method which selects sampling dates in random order and counts the number of taxa without replacement. Variation around the curve is based on 1000 permutations of the 'specaccum' function. The R^2 value for a log fit was 0.99 for each the 1970s and 2010s sampling periods. We used Chao's method (Chao et al., 2013) to determine the maximum predicted value and SE for the curves.

2.4. Statistical analyses

For statistical analyses, counts by taxon for all samples were adjusted to a 48-h collection period by simple linear interpolation. Variables were transformed as needed to meet the assumptions of parametric statistical tests, or analyses less sensitive to these constraints were used, e.g., nonparametric analysis (see below). To account for the effect of autocorrelation among sampling dates, we analyzed the weekly means of the three traps and two to three 48-h counts per week at each elevation. Autocorrelation among these weekly means occurred rarely (Appendix A, Table A2). We used Week as a continuous variable in statistical models to account for repeated sampling during the season. We defined weeks (Week) as week of the calendar year with the count beginning on 1 January (e.g., the beginning of week 21 was 21 May).

To test for differences in beetle capture rate between the 1973–1977 and 2015–2017 sampling periods (Period), we used Generalized Regression (SAS Institute Inc., 2015) with Period and Week as main effects and Period*Week their interaction. The dependent variable was the log-transformed weekly mean of samples of beetles captured per 48-h. We applied the adaptive elastic net technique (e.g., Park and Mazer,

2018) to aid with reducing model dimensionality (See Appendix A, Supplemental Methods for additional details).

To test whether winter weather conditions, particularly snow cover duration and depth, affected beetle abundance in the following growing season, we used a snow-depth data set collected across elevations within the HBEF and measured weekly (Campbell et al., 2010). The sites sampled for snow depth were within 1 km of our beetle sampling locations at each elevation. We used simple linear regression to test the relationship between mean beetle capture rate (Log10[weekly mean of captures per 48-h]) in summer months and two measures of snow from the preceding winter: median daily snow depth, and the number of days with snow cover. Days with snow cover began with the first non-zero measurement of snow depth and ended one week after the last recorded snow cover. Daily snow depth was determined by linear interpolation between snow depth measurements (Campbell et al., 2010). Because the number of days with snow cover included many zeros, a normal distribution of this variable could not be achieved for analysis; hence, we used Spearman's rank correlation to test the relationship between the number of days with snow cover and beetle capture rate the following summer.

To examine further the effect that climate might have on beetle capture rate, we tested for a difference in beetle captures across a climate (elevation) gradient sampled in 2016 and 2017. Because abundances were low, numerous zeros occurred in this data set and capture rate of beetles varied widely across the late May through early August sampling period (Appendix A, Fig. A3), we divided the season into three 4-week sections (21 May–17 June [weeks 21–24], 18 June–15 July [weeks 25–28], and 16 July–12 August [weeks 29–32]) and used the nonparametric Wilcoxon tests to contrast the capture of beetles across the three elevations sampled. We used the same method to test for differences across elevation among the seven taxa that were common enough to allow this test (Appendix A, Fig. A4).

3. Results

Beetle capture rate declined 83% between the mid-1970s and 2015–2017, from a mean of 23.2 (SE $\pm$ 4.19) to 3.9 ($\pm$ 1.19) beetles captured per 48-h (Generalized Regression, df = 1, Wald Chi-square = 39.73, $P < 0.001$, model R^2 = 0.40). Of the model's main effects, Period and Week, the main effect, Week, was not significant and was removed from the final model. However, the Period by Week interaction was significant and was retained (Wald Chi-square = 7.00, $P = 0.008$). This interaction showed that beetle capture rate declined during the season in the 1970s, but showed no such trend among weeks during the 2010s. Mean capture rates were higher in nearly all of the weeks sampled from late May–early August during 1973–1977 compared to 2015–2017 (Fig. 1).

Declines were steepest for predaceous beetles, specifically for Staphilinidae (Fig. 2). The staphylinid subfamily, Pselaphinae, which prey mostly on ants and small arthropods, was the most consistently captured taxon during in the 1970s, but was absent from all samples during the 2010s. In addition to this subfamily, 19 of the 50 taxa found in the 1970s were not recorded in the samples during the 2010s (Appendix A, Table A1). Furthermore, only one new family, Endomychidae, occurred in the 2015–2017 period that was not recorded in the 1970s. The median number of taxa detected per sample date and trap during 1973–1977 was 4, and it was 2 during 2015–2017 (Wilcoxon Test, n = 338 m = 387, Z = 10.5, df = 1, P < 0.001).

Because the magnitude of the declines observed was surprisingly large, we tested the validity of our findings in two ways. First, we determined whether we had sampled the beetle community adequately during each period by constructing accumulation curves, showing accumulation of taxa by sample date (Fig. 3). Maximum predicted values based on these curves were 53 $\pm$ 5 taxa for the 1970s and 33 $\pm$ 5 taxa for the 2010s. The total number of taxa observed, i.e., 48 for 1970s and 28 for 2010s, was within one SE of the predicted curve and within
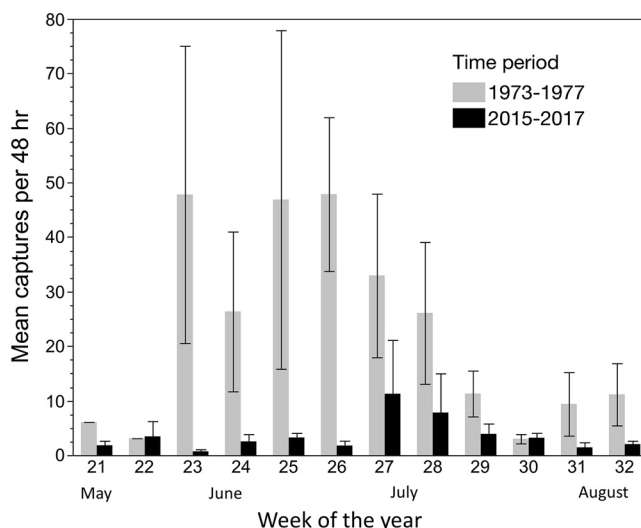

Fig. 1. Comparison of beetle capture rates between 1973–1977 and 2015–2017 at the Hubbard Brook Experimental Forest, New Hampshire, USA. Data represent means ($\pm$ SE) of weekly 48-h window-trap samples (number all Coleoptera captured per 48-h) from 3 window traps located at the mid elevation (540 m asl.) sampling site.
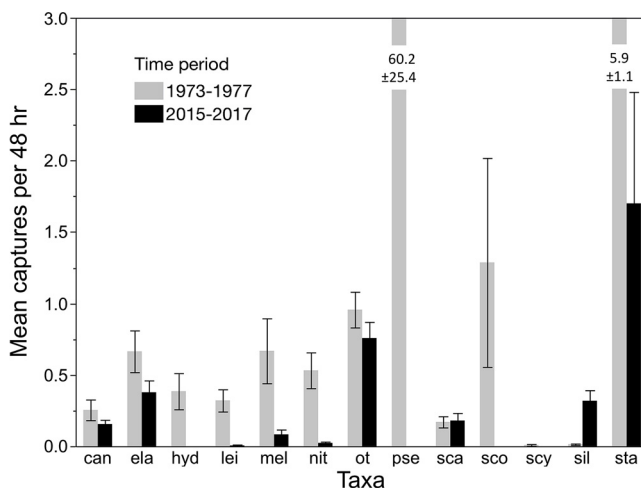

Fig. 2. Comparison of capture rates for the most abundant beetle taxa sampled in 1973–1977 and 2015–2017 at the Hubbard Brook Experimental Forest, New Hampshire, USA. Data represent the mean ($\pm$ SE) of weekly samples of beetle captures per 48-h for 3 window traps at the mid elevation (540 m asl.) sampling site. Abbreviations for the taxa are: Cantharidae (can), Elateridae (ela), Hydroscaphidae (hyd), Leiodidae (lei), Melandryidae (mel), Nitidulidae (nit), other taxa (ot; found in small numbers), Scarabidae (sca), Scolytidae (sco), Scydmaenidae (scy), Siphidae (sil), and Staphylinidae (sta). Values for Pselaphinae (pse) and Staphylinidae (sta) are shown, as they were much greater than captures of other taxa (Appendix A, Table A1 gives the full list of taxa identified).

15% of maximum predicted value, showing that both periods were sampled sufficiently to characterize the beetle community well. Second, we repeated the test of beetle capture rate between periods (1970s v. 2010s) using only taxa with total body length $\geq$ 4 mm. We did this because some differences in the sampling regime might have occurred between the widely separated sampling periods, e.g., different persons identifying the captured beetles or species with small body size being more easily misidentified or lost during collection. The finding was the same – capture rates of large beetles declined significantly, by 53% between the sampling periods (Appendix A, Table A1, Fig. A5).

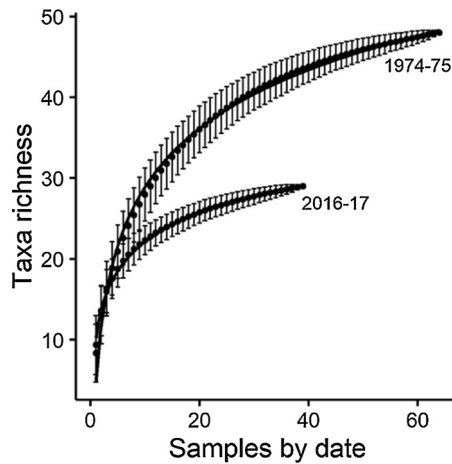We found that climate affected beetle capture rates, as evidenced by

Fig. 3. Accumulation curves for beetle (Coleoptera) taxa captured by using window traps in the Hubbard Brook Experimental Forest, New Hampshire during 1974–1975 and 2016–2017. All samples were from mid elevation (~540 m asl) in northern hardwood forest. Curves were calculated using the R package vegan and the "random" method with 1000 permutations. The R^2 value for each log fit was 0.99. Maximum predicted values were 53 ± 5 taxa for the 1970s and 33 ± 5 taxa for the 2010s as determined using Chao's method (Chao et al., 2013).
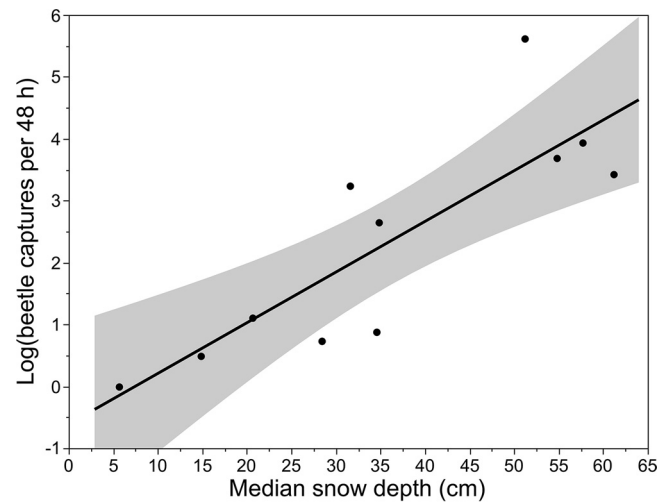

Fig. 5. Relationship between mean beetle capture rate per 48-h (all taxa combined) and median snow depth (median of daily snow-depth values) during the previous winter (Simple linear regression, $F_{1,9} = 20.96$, $P = 0.001$, $R^2 = 0.70$). Beetles were captured by window-traps within the Hubbard Brook Experimental Forest, 1973–1977 and 2015–2017. Sampling of snow depth and the beetle community occurred at mid elevation in each year 1973–1977 and 2015 and at three elevations during 2016 and 2017 with the exception that snow depth was not measured at high elevation in 2017.
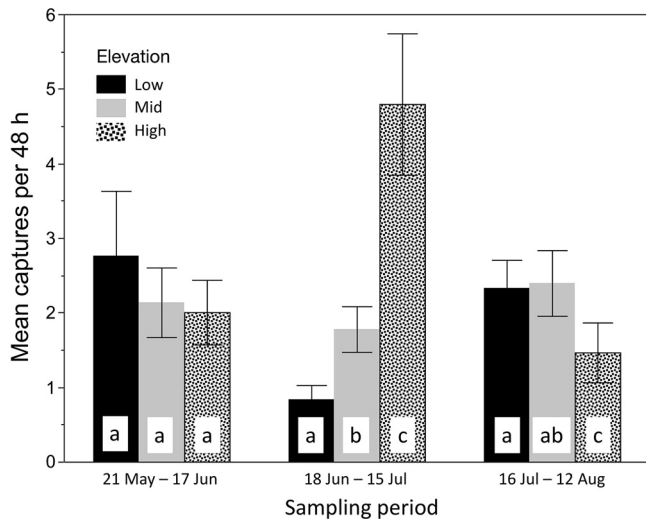
Fig. A1). Among the taxa detected, significantly more captures occurred at mid and high elevations for Silphidae and Staphylinidae (Wilcoxon tests, see Appendix A, Fig. A4) and at mid and low elevations for Scarabidae. No significant difference was found across elevation for Melandryidae, Elateridae, and Cantheridae. Data for most taxa during 2016–2017 were too sparse to test for differences in capture rate across elevations.

Because winter conditions have been shown to affect the abundance of beetles, we also tested whether snow depth or duration of snow cover during the preceding winter was associated with beetle capture rate in the subsequent summer. We found significantly lower capture rates (log10[capture rate per 48 h]) when median snow depth was less during the previous winter (Linear regression, $F_{1,9} = 20.96$, $P = 0.001$, $R^2 = 0.70$; Fig. 5). Similarly, beetle capture rate was positively associated with the duration of snow cover (number of days with snow cover) during the previous winter (Spearman's rank correlation, $n = 11$, $\rho = 0.67$, $P = 0.02$).

4. Discussion

Studies of insect declines have been criticized recently because they fail to assess critically the mechanisms that plausibly have caused the declines (e.g., Habel et al., 2019; Wagner, 2019). Here we argue that the observed declines in the abundance and richness of Coleoptera at the HBEF between 1973 and 2017 are unlikely to fall within the range of expected population variability, and that the primary cause of the declines is related to recent climate warming.

The extensive declines that we recorded, even though from widely separated periods and not a continuous record, are unlikely to have been caused by natural fluctuations in abundance for multiple reasons. First, although random variation in beetle abundance can range over orders of magnitude (e.g., den Boer, 1985; Günther and Assmann, 2004), it is unlikely to have resulted in the *simultaneous* decline of nearly all of the higher taxa sampled. Second, our data probably capture much of the variation inherent in the beetle taxa sampled because the declines that we report were based on multiple weeks of sampling conducted at the same time of year over multiple years within each of the two sampling periods. Furthermore, the taxa-accumulation curves show that additional sampling would have added few taxa to the beetle

Fig. 4. Within-season changes in beetle capture rate at three elevations within the Hubbard Brook Experimental Forest, NH, USA, during 2016 and 2017 (years combined). Data represent weekly means (± SE) of the number of Coleoptera captured per 48-h at low (320 m asl.), mid (540 m), and high (810 m) sampling sites. Three window traps were operated at each elevation from late May through early August of each year. Columns receiving a different letter differed significantly at the 0.05 level according to pairwise Wilcoxon tests.

fewer beetles being captured *when* and *where* it was warmer. Beetle capture rate was significantly lower in the 2010s when mean daily temperature was about 1.8 °C warmer (Fig. A1), and when degree-day accumulation (from 1 January to 31 July) averaged 153 more degree-days, compared to the 1970s sampling period (Appendix A, Fig. A6). For this test, we used data from just the mid elevation plot where sampling was conducted during both periods. From sampling across the elevation gradient in 2016–17, we learned that when beetles were most abundant (during mid-season), capture rate was lowest where it was warmest (at low elevation) (Wilcoxon test, df = 2, Chi-square = 16.2, $P < 0.001$; Fig. 4). Mean daily temperature at the low elevation sampling area was on average about 1.8 °C warmer during June and July of the years sampled than at the high elevation site (Appendix A,

community detected during each period (Fig. 3). Last, variation in the abundance and diversity of higher taxa, e.g., families, is expected to be much less than at the species level due to contrasting dynamics among species within higher level taxa.

4.1. Potential causes of beetle declines

The typical causes of insect decline mentioned in the literature, such as habitat loss, fragmentation and degradation, e.g., from pollutants, artificial light at night, or invasive species, do not apply to our study as it was carried out in a large, unfragmented tract of mature, second growth forest, the White Mountains National Forest. In the WMNF, forest harvesting is limited annually to a relatively few small patch cuts (~0.1% of the area of the forest annually, R. Boyer, pers. comm.). Herbicides are used only to treat patches of invasive plant species in roadside areas, but not within the forest. Insecticides are not used. Atmospheric deposition of mercury occurs, but mercury does not seem to be bioaccumulating to harmful levels within the forest (Wyman et al., 2011; Rodenhouse et al., 2019). Artificial light at night (ALN) can affect insects in multiple ways (Owens et al., 2019); however, ALN is minimal within the Hubbard Brook valley, which is categorized as Bortle Class 2 (average night sky) (Falchi et al., 2016). Last, invasive earthworms can directly and indirectly alter forest floor conditions and fauna (Ferlian et al., 2018), but they have only recently been detected within the HBEF are and are unlikely to have had any measurable impact to date (Holmes and Likens, 2016). In fact, forest floor carbon and nitrogen content have not changed on the reference watershed of the HBEF, which is adjacent to our study plots at mid and high elevation (Campbell et al., 2007). Neither has forest floor depth or mass of the organic (O) horizons changed during 1976–2013 (Johnson and Hamburg, 2015).

Ongoing non-climate related changes in the Hubbard Brook forest were likely to have been neutral or promoted beetle abundance rather than cause steep declines. These include the impact of acid deposition and subsequent slow recovery, forest aging, and beech bark disease (BBD). Acid deposition peaked at the HBEF in the early1970's (Holmes and Likens, 2016), and the forest-floor has been recovering ever since (Lawrence et al., 2015). A less acidic forest-floor, would be expected to favor arthropod abundance, not diminish it (Fisk et al., 2006; Beier et al., 2012). Forest aging could affect beetle abundance and diversity; however, evidence about the effects of forest aging on beetle abundance or diversity are mixed with some studies showing declines with age (e.g., Gandhi and Herms, 2010) and others showing no effect (e.g., Zeran et al., 2007; Vance and Nol, 2003) or an increase (Jeffries et al., 2006). Significant declines for nearly all beetle taxa, as we report, have not been associated with forest aging in any other study; thus, we argue against forest age, per se, as driving the declines observed.

Beech bark disease, caused by a combination of a scale insect and pathogenic fungi (Lovett et al., 2006), was first detected at Hubbard Brook in the late 1970s and early 1980s (Hane, 2003; Cleavitt et al., 2008) and resulted in the opening of the canopy due to the death of large, mature trees and a few years later by shading the forest-floor as root-sprouted saplings proliferated in the understory. Opening of a forest's canopy makes the forest-floor warmer and wetter, but this change is countered by closing of the subcanopy, which shades the forest making it cool and moist (Thomsen et al., 2016; Hane, 2003). The latter conditions are typically preferred by forest-floor fauna including beetles (reviewed by Pearce and Venier, 2006) and have prevailed in our study area since the early 1990s (van Doorn et al., 2011). In addition, BBD tends to increase the amount of standing dead wood and coarse woody debris, which can promote beetle abundance (Brunet et al., 2010), but is not known to cause declines (reviewed by Sandström et al., 2019). BBD has not prompted a change in tree species composition, because beech basal area and the composition of the canopy in our study area have changed little since the 1970s (van Doorn et al., 2011), suggesting that no change in leaf-litter quality has

occurred. Thus, the outcome of the changes due to BBD are likely to have been neutral or even positive for beetles.

4.2. Role of climate change

The direct and indirect effects of climate change were the most probable major contributors the observed declines in beetle abundance and taxonomic richness. Multiple lines of evidence support this proposition. First, and perhaps most importantly, observational and experimental studies at Hubbard Brook show that decreasing snow depth (Holmes and Likens, 2016) and duration (Campbell et al., 2010) have resulted in forest soils freezing to greater depths and more frequently, i.e., winter warming has resulted in harsher conditions for forest floor fauna (Groffman et al., 2001). One result of these changes is a highly significant positive relationship between beetle capture rate and the depth and duration of snow cover during the previous winter (Fig. 5). Furthermore, experimental snow removal studies done at Hubbard Brook show that soil freezing reduces the abundance of forest-floor arthropods, including adult beetles (Templer et al., 2012, but see Christenson et al., 2017). Whether the effect of snow cover on beetles is direct (i.e., due to lower survival with less snow cover and more soil freezing) or indirect (e.g., via reductions in prey for predators; Penczykowski et al., 2017), however, is not clear and merits further study.

Shorter and warmer winters could allow winter-active predators, including beetles in the families Staphlylinidae, Cantharidae and Carabidae (Jaskuła and Soszyńska-Maj, 2011) and spiders (Whitney, 2014), a longer period in which to consume diapausing prey (Pekár et al., 2015), potentially destabilizing predator-prey relationships. In addition, soil invertebrates with smaller body size might be more affected by soil freezing than larger species (Bokhorst et al., 2012), and the loss of small species would be expected to impact larger predaceous species as we found in this study. Abundance of the predaceous family Staphlinidae decreased most, particularly the subfamily Pselaphinae, which is a common predator of Collembola in the forest-floor (Newton and Chandler, 1989). Pselaphinae went from the most commonly captured taxon in the 1970s to absent during recent years, suggesting a major alteration of forest-floor predator-prey dynamics.

Second, we have shown that beetle capture rate was lowest *when* and *where* conditions were warmest, i.e., during 2015–2017 vs. the earlier sampling period, and at low elevation vs. mid and high elevation, respectively. A similar pattern across elevation was found for the beetle community in the deciduous forests of Great Smoky Mountains National Park, North Carolina (Lessard et al., 2011). Of course, climate differences across elevations are more than just differences in temperature. Climate differences also include precipitation, evapotranspiration, cloudiness and insolation, season length, the intensity and duration of freeze thaw cycles, etc., and their interactions. However, they are all related to changes in temperature. For example, precipitation was significantly less at low elevation compared to the two higher elevations (see Fig. A1), and lower precipitation is sometimes associated with reduced abundance of forest-floor arthropods (Williams et al., 2014). It is likely that precipitation was enhanced at the cooler high elevation location compared to mid and low elevation by increased canopy drip and reduced evapotranspiration (Venterea et al., 2003). These conditions also sustain higher soil moisture, available nitrogen (Venterea et al., 2003) and greater foliar nitrogen (Ollinger et al., 2002). These factors plus greater protective snow-cover probably make the high elevation forest floor more favorable than lower elevations for most beetle taxa. Climate features, soil moisture and litter quality undoubtedly interact in affecting forest-floor beetles, but additional long-term sampling over climate gradients and experiments will be needed to identify the roles of each of these factors and their interactions.

Unfortunately, comparable long-term studies of forest-floor Coleoptera are few. Recently, however, Homburg et al. (2019) reported

long-term declines in the richness of beetle taxa (species richness, phylogenetic diversity) in a small tract of primeval temperate forest in northern Germany. Interestingly, they too show largest declines for species with small body size. Contrary to reports of declining trends, however, Brooks et al. (2012) reported carabid abundance stable to increasing in small patches of woodlands and hedgerows of the UK during 1994–2008, but strong declines in non-forested montane habitats where winter conditions might have more effect on populations. The only experimental studies of the effects of climate on ground-dwelling Coleoptera were conducted in non-forest habitats, but these too are consistent with our contention that climate warming can negatively affect beetle populations. For example, Berthe et al. (2015) found that simulated climate warming of 2 °C in an agricultural habitat resulted in reduced abundance of staphylinid beetles.

4.3. Conservation implications

The conservation implications of our findings are clear. If reductions in the depth and duration of snow cover are the primary drivers of decline in the forest floor beetle community as our evidence indicates, the only solution is reduction of greenhouse gas emissions to limit climate warming. No local, management solution exists for this globally driven change. What is less clear is the long-term (decades to centuries) outcome of the trends in community structure observed. Diversity, abundances and functional capabilities of the brown food web might be expected to be resilient to the observed declines based on their responses to natural and management disturbances (Coyle et al., 2017). Plant and animal communities can move spatially and shift phenologically in response to changing resources and climate regimes (e.g., Hickling et al., 2006), as Lepidoptera species have in Massachusetts (Breed et al., 2013). However, few more southernly-distributed beetle taxa (Families) seem to have migrated into our study area. We recorded only one family in the 2010s that was not detected in the 1970s, Endomychidae, and this family has a broad distribution. The lack of migration into our study area could have occurred because of the relatively low dispersal rate of beetles (Kotze and O'hara, 2003), or because winter conditions in the forest floor have actually become more harsh for species in northern hardwood forest rather than less so with climate warming (Groffman et al., 2001), preventing the establishment of southern adapted taxa. In this unusual context, the resilience of beetle taxa remains unknown.

Also unknown are the community and ecosystem consequences of the beetle declines observed. To our knowledge, few manipulative experiments have been conducted to determine the ecological effects of particular forest beetle species or functional groups on food web dynamics or ecosystem-level processes (Coyle et al., 2017, Sitvarin et al., 2016). Functional redundancy within and among taxa is expected (Gerisch, 2014), as are naturally occurring wide fluctuations in abundance. These features of beetle populations and communities, plus the confounding effects in most locations of habitat fragmentation and degradation make it very difficult to quantify the roles of specific beetle taxa. However, some studies suggest that declines could have direct and indirect effects on ecosystem processes because of their roles as detritivores, predators, or prey for other taxa such as salamanders and birds. For example, wood boring beetles contribute significantly to the decomposition of wood (Ulyshen, 2016). Likewise, predation by beetles on pupae can mitigate outbreaks of defoliating Lepidoptera (Raymond et al., 2002), and beetles are a source of food for forest vertebrates such as salamanders (Wyman, 1998) and birds (Robinson and Holmes, 1982). However, such effects will vary among forested locations due to differences in climate, vegetation and invertebrate community structure (Bradford et al., 2014).

Some modeling and empirical evidence suggests that changes in brown food web structure could cascade upward (Chen and Wise, 1999, Lister and Garcia, 2018, but see Willig et al., 2019) even to vertebrate predators such as birds (Haché et al., 2016; Møller, 2019) or other small

terrestrial vertebrates such as salamanders and mice (Laundré et al., 2014). This could occur, in part, because of multichannel feeding linking the green (foliar) and brown food webs (Zou et al., 2016, Sitvarin et al., 2016). Both the abundance of terrestrial salamanders (predominantly the red-backed salamander, *Plethodon cinereus*) and birds have declined significantly at Hubbard Brook since the mid 1970s (Holmes and Likens, 2016); however, bird declines can be attributed largely to forest succession and the causes of salamander declines are unknown. Lowe (2012) noted that the cause of long-term decline in adult spring salamanders (*Gyrinophilus porphyriticus*) in New Hampshire is due to increased frequency and intensity of spring and fall flooding events causing larval mortality, but red-backed salamanders have no aquatic larval stage so would be unaffected by stream flooding.

It is important to note that we have no evidence that the beetle taxa not detected in recent years have been extirpated. Our data indicate that beetle community structure has changed extensively, but we cannot rule out the possibility that some taxa shifted spatially or phenologically and were not detected in our sampling. For conservation and management purposes, it is critically important to determine which and how many beetle taxa have been extirpated, and to elucidate the processes causing their demise.

5. Conclusions

Previous studies reporting significant declines in insect abundance and diversity invariably point to habitat loss, fragmentation and degradation as major drivers of the changes observed (e.g., Homburg et al., 2019; Sánchez-Bayo and Wyckhuys, 2019). However, none of these explanations applies to the beetle decline observed in our study area – a large tract of intact northern hardwood forest. Our research indicates that the direct and indirect effects of climate change were primarily responsible for the significant declines in beetle abundance, richness of taxa and loss of top predators, i.e., a major restructuring of the brown food web. The further implication is that climate warming of as little as 1 °C can have major impacts on forest diversity and potentially ecosystem processes.

Roles of the authors

Jennifer E. Harris assisted with the design of the study, field work, processing samples, data analysis, writing and editing the text.

Nicholas L. Rodenhouse obtained funding for the study and assisted with: the study design, field work, processing samples, data analysis, writing and editing the text.

Richard T. Holmes obtained funding for the study, assisted with the design of the study and edited the text.

Data availability

Data used in this study are available via the website of the Hubbard Brook Ecosystem Study (hubbardbrook.org) and by request from the authors.

Declaration of competing interest

All authors declare no actual or potential conflict of interest including financial, personal or other relationships with other people or organizations within three years of beginning the submitted work that could inappropriately influence, or be perceived to influence, the work submitted for publication.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108219.

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