Light accelerates plant responses to warming

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Competition for light has profound effects on plant performance in virtually all terrestrial ecosystems. Nowhere is this more evident than in forests, where trees create environmental heterogeneity that shapes the dynamics of forest-floor communities[1-3]. Observational evidence suggests that biotic responses to both anthropogenic global warming and nitrogen pollution may be attenuated by the shading effects of trees and shrubs[4-9]. Here we show experimentally that tree shade is slowing down changes in below-canopy communities due to warming. We manipulated levels of photosynthetically active radiation, temperature and nitrogen, alone and in combination, in a temperate forest understorey over a 3-year period, and monitored the composition of the understorey community. Light addition, but not nitrogen enrichment, accelerated directional plant community responses to warming, increasing the dominance of warmth-preferring taxa over cold-tolerant plants (a process described as thermophilization[6,10-12]). Tall, competitive plants took greatest advantage of the combination of elevated temperature and light. Warming of the forest floor did not result in strong community thermophilization unless light was also increased. Our findings suggest that the maintenance of locally closed canopy conditions could reduce, at least temporarily, warming-induced changes in forest floor plant communities.

Competition for light is asymmetrical, meaning that, in multi-layered canopies, large individuals capture a disproportionate amount of the resource[1]. This effect is clearly evident in structurally diverse habitats such as forests[1-3]. A anthropogenic changes to nutrient cycles and the climate system have often enhanced tree growth over the last century which, together with important changes in forest land management, has contributed to higher standing stocks of trees in temperate forests across Europe and most of North America[13-15]. Denser forests and more shading by trees and shrubs have the potential to modulate the effects of both climate warming and eutrophication from nitrogen (N) on below-canopy organisms: shading by vegetation can buffer the temperature experienced by organisms sheltered below[4-8] and thus explain the apparent lags between observed biotic responses and climate change[6,10,12], while light has been shown to control plant community responses to eutrophication[3,9,16-19]. However, due to the absence of full-factorial field experiments that manipulate light, temperature and N availability together, our understanding of the interplay of these factors on forest community dynamics remains incomplete. This limits our ability to predict how global environmental change and land management affect forest ecosystems.

Here we experimentally manipulated levels of light, temperature and N in the field to test the hypothesis that light addition to the forest floor accelerates community responses to warming and eutrophication. In addition to the naturally-occurring species, we transplanted rhizome fragments of three relatively tall, competitive native species in all plots to overcome dispersal limitation (see Methods). We demonstrate that low light levels limit plant responses to warming, and thus single out light limitation as a likely explanation for the slow biotic responses observed in temperate forests[6,10]. Using an experimental set-up with fluorescent tubes installed in an ancient, temperate forest in Western Europe (Belgium), we document strong shifts of understorey plant communities with joint experimental warming and light addition in just 3 years. Communities also responded to combined warming and nitrogen addition, but were mostly unresponsive to separate manipulations of temperature. Our experiment also failed to detect substantial effects due to inorganic N fertilization alone (Fig. 1; Supplementary Figs 1–6 and Table 1).

To assess responses to climate warming at the community level, we quantified the thermophilization of understorey assemblages using novel methods that scale up from species' thermal tolerances (inferred by ecological niche modelling based on distribution data) to plot-level thermal profiles[6,10-12,20]. We calculated the floristic temperature[10] of each plot by randomly sampling 500 values from the thermal response curves of all recorded species, weighted by their relative abundances in the plot[6,20]. The thermophilization was then calculated as the mean difference between the post-treatment and pretreatment floristic temperatures and expressed in °C per year. These analyses reveal that these communities shifted by the relative replacement of cold-tolerant species by warmth-preferring species. Warmth-preferring species rapidly increased in dominance in vegetation plots that were both warmed and illuminated. These plots showed the highest thermophilization rate of $0.63 \, °C.yr^{-1} \pm 0.14$ (mean ± 1 s.e.m.), and strongest community reordering over time (Fig. 1). In contrast, lower levels of thermophilization occurred in control plots and in plots that were N fertilized (but not warmed or illuminated), warmed (but not illuminated or fertilized), and illuminated and fertilized (but not warmed) (Fig. 1).

The combination of experimental warming and illumination also led to functionally altered communities, as shown by changes in key life-history traits (specific leaf area [SLA], plant height, seed mass) that are central to the leaf-height-seed framework of plant ecological strategies[21,22]. These analyses revealed particularly increased abundance of tall, competitive plants in plots with joint manipulations of elevated light and temperature (Fig. 2): the community-mean weighted plant height increased from 14.1 ± 1.7 cm in the control plots to 41.2 ± 10.5 cm in plots with combined warming and light. This community trait shift was attributable to both direct responses of species' traits (that is, phenotypic plasticity of established individuals) as well as changes in species abundances (see Supplementary Methods and Results). There were no significant changes in community-mean weighted SLA or seed mass (see Supplementary Fig. 7 for complementary analyses of Grime's

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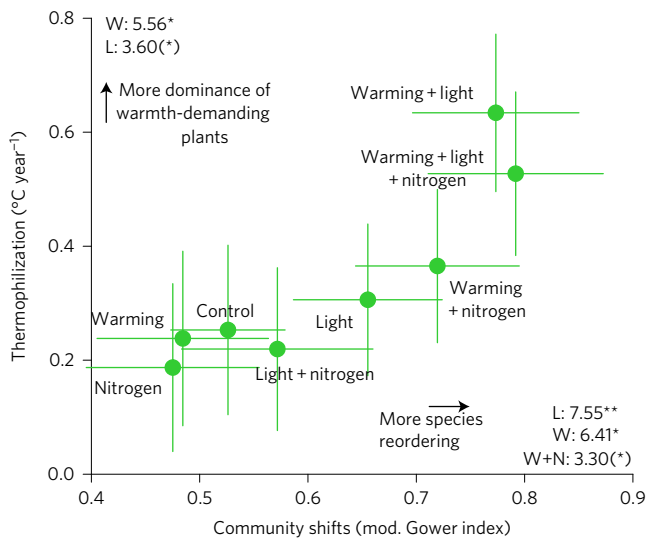
Figure 1 | Community-level effects of light, warming and nitrogen addition in forest understoreys. Each circle refers to the mean value of five plots. Plots receiving increased light and warming together experienced the largest community shifts and thermophilization rates. Overall, communities with more species reordering also experienced increasing dominance of warmth-preferring over cold-tolerant taxa (thermophilization) (Spearman's rank correlation rho = 0.389, n = 40, P = 0.0138). Values along each axis are F values from ANOVAs testing for light (L), warming (W) and nitrogen (N) and all two-way interactions (three-way interactions were never significant). ns: non-significant (P > 0.1); (*)P < 0.1; *P < 0.05; **P < 0.01. Error bars denote 1 s.e.m.

competitor, stress-tolerator, ruderal triangular strategy scheme[22], species richness and evenness).

Artificial light addition to the forest floor thus boosted taxonomic replacement as well as functional plant responses to warming. Our results demonstrate that relatively tall, competitive and warmth-preferring plant species are limited in their growth and survival by both light availability and temperature under closed-canopy conditions. Hence, maintaining locally closed-canopy conditions could reduce, at least temporarily, forest plant community changes in response to macroclimate warming. These results contrast with previous recommendations of keeping growing stocks low as one strategy to adapt to climate change in forests[23]. In addition, while many temperate forests across Europe

and most of North America have become consistently denser and darker during the last decades[6,9,13–15], this might change in the future due to increased demand for woody biomass or expected changes in management cycles[24,25]. More frequent and intense forest disturbances caused by wind, pests, pathogens and wildfires as a result of climate change[26] might also lower forest canopy closure. Because forest floors harbour the vast majority of temperate forest plant diversity[2], more open canopies and increasing light availability could thus accelerate the impact of global climate change on this important component of biodiversity.

Our experiment also sheds light on the long-running debate about the role of light in eutrophication-driven biodiversity loss[16–19,22,27]. Additional inputs of N had strikingly small effects in our forest-floor plant assemblages (Figs 1 and 2; Supplementary Figs 5–7). Nevertheless, N availability is most likely not limiting plant growth at our study site: levels of atmospheric N deposition are high (25.3 kg N ha^{-1} yr^{-1} in 2009[28]) and indications of soil N saturation are present (the nitrate seepage flux was 12.9 kg N ha^{-1} yr^{-1} in 2009, much higher than the threshold of 5 kg nitrate-N ha^{-1} yr^{-1} indicative of N saturation in forest ecosystems[28,29]). The existence of N saturation is characteristic for many forest ecosystems in Europe and North America[29] and may have resulted in the absence of strong community responses to extra N addition[18,19], even with supplementary light from above. However, N fertilization combined with warming did cause strong community shifts, comparable in magnitude to those in the jointly warmed and illuminated plots. Eutrophication research from herbaceous-dominated plant communities has shown that addition of light to short-statured plants below taller individuals, for example by herbivory, can reduce species loss due to eutrophication[16,17]. Our data, on the other hand, do not support the assertion that illumination from above enhances species' responses to N availability, possibly due to thermal limitation.

To conclude, our experimental data unambiguously show that tree shade can hamper potential encroachment of tall, competitive thermophilous species and thus be delaying the thermophilization of understorey communities in forests. Experimentally warmed communities changed little unless light availability was also increased. These results may contribute to explaining the observed lags in biotic community responses to global warming[6,10,12]. Our results also have key land management and policy implications for the conservation of forests in the face of climate change by directly demonstrating that closed-canopy conditions can slow down taxonomic, thermal and functional shifts of understorey plant communities in response to climate warming. Further
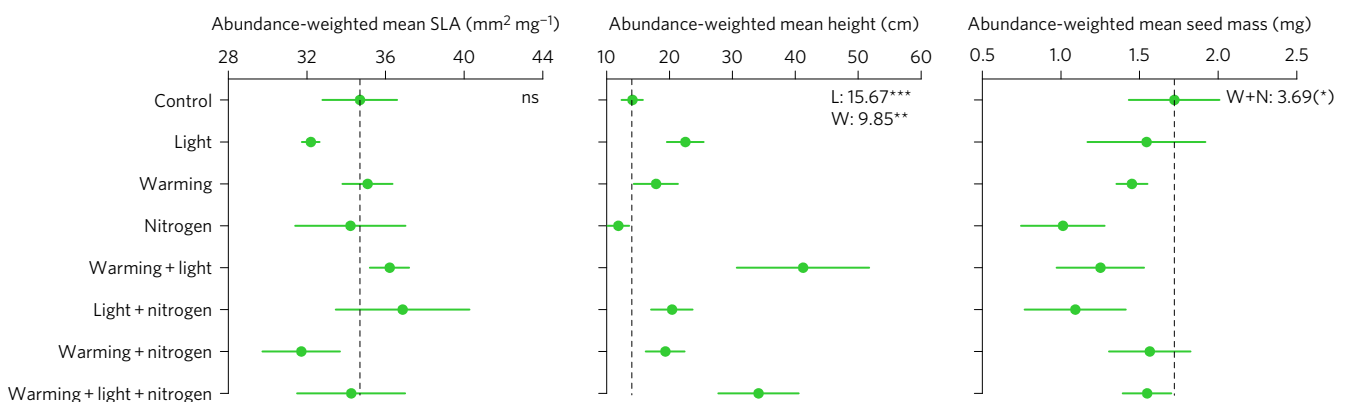
Figure 2 | Effects of light, warming and nitrogen addition on abundance-weighted mean traits of understorey plant communities. Values in each upper right corner are F values from ANOVAs testing for light (L), warming (W) and nitrogen (N) and all two-way interactions (three-way interactions were never significant). ns: non-significant (P > 0.1); (*)P < 0.1; *P < 0.05; **P < 0.01; ***P < 0.001. Error bars denote 1 s.e.m. across each of five replicate plots per treatment. The dashed line indicates the mean level of the control plots.

research is needed to assess the relative benefits of forest management regimes that aim to promote stand structural complexity and landscape heterogeneity (for example, by creating gaps) versus those that maintain relatively closed-canopy conditions in order to conserve temperate forest plant diversity in the face of climate change.

Methods

We established this experiment in 2011 in an ancient, temperate deciduous forest in Belgium (50.97°N, 3.81°E). Experimental manipulations consisted of light (plots with two 14 W fluorescent tubes suspended at 65 cm above the soil surface providing more than ten times as much additional daytime-only radiation, vs plots without additional light but with dummy lamps; Supplementary Fig. 2), warming (passively warmed by 0.59 °C in the air, 0.87 °C at the soil surface and 2.96 °C in the soil with hexagonal open-top chambers, vs plots experiencing ambient temperatures; Supplementary Fig. 3), and N enrichment (fertilized plots with 10 g N m^{-2} year^{-1} as ammonium nitrate, resulting in a mean topsoil concentration increase of 4.39 g inorganic-N kg^{-1} dry soil, vs control plots with no supplementary nutrients added). Experiments that increase understorey light levels by manipulating the tree canopy directly would indirectly also affect soil temperatures (due to higher solar radiation) and nutrient cycling (due to temperature effects on mineralization). In contrast, our full-factorial design allows us to mechanistically unravel the separate and combined effects of each of these environmental factors. We applied each unique treatment and all possible combinations to five replicate plots in compliance with a full factorial design for a total of 40 plots, plus established five additional 'structural control' plots without dummy lamps. In addition to the naturally-occurring species, we introduced three relatively tall, competitive native species (*Urtica dioica*, *Rubus fruticosus* agg. and *Aegopodium podagraria*) at the start of the experiment in all plots by transplanting rhizome fragments from the same forest. This was key for the experiment because these species are expected to strongly respond to resource alterations and affect understorey dynamics, but hardly occurred in any of the plots due to closed-canopy conditions before the experiment. Transplantation was thus needed to overcome dispersal limitation because experimentally illuminated plots are surrounded by dense forest and these species would most likely not naturally colonize the plots within the time frame of this study. Hence, we can disentangle the effects of resource manipulations on plant performance, species interactions and community change unequivocally (more information on the transplants is available in Supplementary Methods and Results). We here report on 4 years of measurements (pretreatment year 2011 and three post-treatment years 2012–2014) and, unless specifically mentioned otherwise, data are expressed as the plot-level change in community characteristics between the post-treatment means of the years 2012–2014 minus the pretreatment year 2011. We recorded the per cent ground cover of all plant species in each plot twice per year, in spring and summer (only summer survey in 2011; an analysis including only summer species is available in Supplementary Fig. 4). From this, community shifts and thermophilization were estimated by means of beta diversity indices[30] and ecological niche modelling[6,12,20], respectively. First, community shifts were quantified as the modified Gower beta diversity index[30] (results for the Euclidean and Jaccard indices are available in Supplementary Table 1). Second, thermophilization was calculated by sampling from the estimated thermal tolerances of species. The long-term mean temperature in the growing season (April to September) was used to estimate thermal response curves by means of ecological niche modelling using a variety of modelling approaches (see Supplementary Methods and Results). To account for variability and uncertainty in thermal preferences[20], the distribution of plot-level floristic temperatures at each survey was constructed by resampling 500 times from species' thermal response curves[6,20], weighted by their relative abundance and averaged per plot and year. Three key functional life-history traits that are part of the leaf-height-seed strategy scheme[21], that is, plant height, specific leaf area and seed mass, were measured on five individuals per species and plot. We then calculated abundance-weighted mean community trait values as the plot-averaged species' trait values weighted by species abundances. Soil samples from each plot were analysed for plant-available ammonium, nitrate, phosphate and pH (see Supplementary Methods and Results for a detailed account of the methods and supporting analyses).

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Author contributions

P.D.F., A.D.S., D.A.C., M.H. and K.V. designed the research; P.D.F. and A.D.S. performed the research; P.D.F. and F.R.S. analysed the data; all authors wrote the paper.

Additional information

Supplementary information is available online. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to P.D.F.

Competing interests

The authors declare no competing financial interests.