Light accelerates plant responses to warming

Pieter De Frenne[1]*, Francisco Rodríguez-Sánchez[2], An De Schrijver[1], David A. Coomes[3], Martin Hermy[4], Pieter Vangansbeke[1] & Kris Verheyen[1]

[1]Forest & Nature Lab, Ghent University, Geraardsbergsesteenweg 267, BE-9090 Gontrode-Melle, Belgium;

[2]Integrative Ecology Group, Estación Biológica de Doñana (EBD-CSIC), Avda. Américo Vespucio, E-41092 Sevilla, Spain;

[3]Forest Ecology and Conservation Group, Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge, CB2 3EA, United Kingdom;

[4]Department of Earth & Environmental Sciences, Division of Forest, Nature and Landscape, K.U.Leuven, Celestijnenlaan 200E, BE-3001 Leuven, Belgium.

*email: Pieter.DeFrenne@UGent.be

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, for the first time, that tree shade is slowing down changes in below-canopy communities due to warming. By independently manipulating levels of photosynthetically active radiation (light), temperature and nitrogen in a temperate forest understorey, we demonstrate that light addition, but not nitrogen enrichment, accelerates 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]). Analyses of life-history traits reveal that 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 increased too. Our findings not only provide key land management and policy implications, but also advance our understanding of the rate, lags and drivers of forest dynamics in response to climate change.

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]. Yet, anthropogenic changes to nutrient cycles and the climate system have often enhanced tree growth during the last century which, together with important changes in forest land management, 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 (*cf.* Methods). We demonstrate that low light levels limit plant responses to warming, and thus point 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 three 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, and Supplementary Figs. 1−6 and Supplementary 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 posttreatment 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} ± 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 nor illuminated), warmed (but not illuminated nor 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 (i.e., 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 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 temperate 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. Since 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 and Supplementary Fig. 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, e.g., 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 explain 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 research is needed to assess the relative benefits of forest management regimes that aim to promote stand structural complexity and landscape heterogeneity (e.g., by creating gaps) vs. 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 did almost not occur in any of the plots due to closed-canopy conditions before the experiment. Transplantation was thus needed to overcome dispersal limitation since 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 four years of measurements (pretreatment year 2011 and three posttreatment years 2012-2014) and, unless specifically mentioned otherwise, data are expressed as the plot-level change in community characteristics between the posttreatment means of the years 2012 to 2014 minus the pretreatment year 2011. We recorded the percent 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 S1). 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 (*cf*. 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], i.e., 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).

References

1. Freckleton, R. P. & Watkinson, A. R. Asymmetric competition between plant species. *Funct. Ecol.* **15**, 615-623 (2001).
2. Gilliam, F. S. *The herbaceous layer in forests of eastern North America*. 2 edn (Oxford Univ. Press, 2014).
3. Coomes, D. A. & Grubb, P. J. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecol. Monogr.* **70**, 171-207 (2000).
4. Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E. & Evans, T. A. Microhabitats reduce animal's exposure to climate extremes. *Glob. Change Biol.* **20**, 495–503 (2013).
5. Melin, M. *et al.* Moose (*Alces alces*) reacts to high summer temperatures by utilizing thermal shelters in boreal forests - an analysis based on airborne laser scanning of the canopy structure at moose locations. *Glob. Change Biol.* **20**, 1115-1125 (2014).
6. De Frenne, P. *et al.* Microclimate moderates plant responses to macroclimate warming. *Proc. Natl Acad. Sci. USA* **110**, 18561-18565 (2013).
7. Kearney, M. R. Activity restriction and the mechanistic basis for extinctions under climate warming. *Ecol. Lett.* **16**, 1470-1479 (2013).

8. von Arx, G., Pannatier, E. G., Thimonier, A. & Rebetez, M. Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. *J. Ecol.* **101**, 1201-1213 (2013).
9. Verheyen, K. *et al.* Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *J. Ecol.* **100**, 352-365 (2012).
10. Bertrand, R. *et al.* Changes in plant community composition lag behind climate warming in lowland forests. *Nature* **479**, 517-520 (2011).
11. Gottfried, M. *et al.* Continent-wide response of mountain vegetation to climate change. *Nature Clim. Change* **2**, 111-115 (2012).
12. Devictor, V. *et al.* Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Clim. Change* **2**, 121-124 (2012).
13. Gold, S., Korotkov, A. V. & Sasse, V. The development of European forest resources, 1950 to 2000. *Forest Policy Econ.* **8**, 183-192 (2006).
14. Rautiainen, A., Wernick, I., Waggoner, P.E., Ausubel, J.H. & Kauppi, P.E. A national and international analysis of changing forest density. *PlosOne* **6**, e19577 (2011).
15. Pretzsch, H., Biber, P., Schuetze, G., Uhl, E. & Roetzer, T. Forest stand growth dynamics in Central Europe have accelerated since 1870. *Nature Commun.* **5**, 4967 (2014).
16. Hautier, Y., Niklaus, P. A. & Hector, A. Competition for light causes plant biodiversity loss after eutrophication. *Science* **324**, 636-638 (2009).
17. Borer, E. T. *et al.* Herbivores and nutrients control grassland plant diversity via light limitation. *Nature* **508**, 517-520 (2014).
18. Gilliam, F. S. Response of the herbaceous layer of forest ecosystems to excess nitrogen deposition. *J. Ecol.* **94**, 1176-1191 (2006).
19. De Schrijver, A. *et al.* Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecol. Biogeogr.* **20**, 803-816 (2011).
20. Rodríguez-Sánchez, F., De Frenne, P. & Hampe, A. Uncertainty in thermal tolerances and

climatic debt. *Nature Clim. Change* **2**, 636-637 (2012).

21. Westoby, M. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil* **199**, 213-227 (1998).
22. Grime, J. P. *Plant strategies, vegetation processes, and ecosystem properties*. 2 edn (Wiley, 2001).
23. McDowell, N. G. & Allen, C. D. Darcy's law predicts widespread forest mortality under climate warming. *Nature Clim. Change* **5**, 669-672 (2015).
24. Schulze, E.-D., Körner, C., Law, B. E., Haberl, H. & Luyssaert, S. Large-scale bioenergy from additional harvest of forest biomass is neither sustainable nor greenhouse gas neutral. *GCB Bioenergy* **4**, 611-616 (2012).
25. Verkerk, P. J., Anttila, P., Eggers, J., Lindner, M. & Asikainen, A. The realisable potential supply of woody biomass from forests in the European Union. *Forest Ecol. Manag.* **261**, 2007-2015 (2011).
26. Seidl, R., Schelhaas, M.-J., Rammer, W. & Verkerk, P. J. Increasing forest disturbances in Europe and their impact on carbon storage. *Nature Clim. Change* **4**, 806-810 (2014).
27. Dickson, T. L. & Foster, B. L. Fertilization decreases plant biodiversity even when light is not limiting. *Ecol. Lett.* **14**, 380-388 (2011).
28. Verstraeten, A. *et al.* Impact of declining atmospheric deposition on forest soil solution chemistry in Flanders, Belgium. *Atmos. Environ.* **62**, 50-63 (2012).
29. De Schrijver, A. *et al.* Nitrogen saturation and net ecosystem production. *Nature* **451**, E1 (2008).
30. Anderson, M. J. *et al.* Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* **14**, 19-28 (2011).

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.

Acknowledgements We are grateful to Luc Willems, Robert Gruwez, Kris Ceunen, Greet De bruyn, Predrag Miljkovic, Lennart Nelen, Katja Van Nieuland and Niels Verdoodt for field and laboratory assistance. Support for this work was provided by FWO post-doctoral fellowships to P.D.F. and A.D.S., and an ERC Consolidator Grant 614839 - PASTFORWARD to K.V.

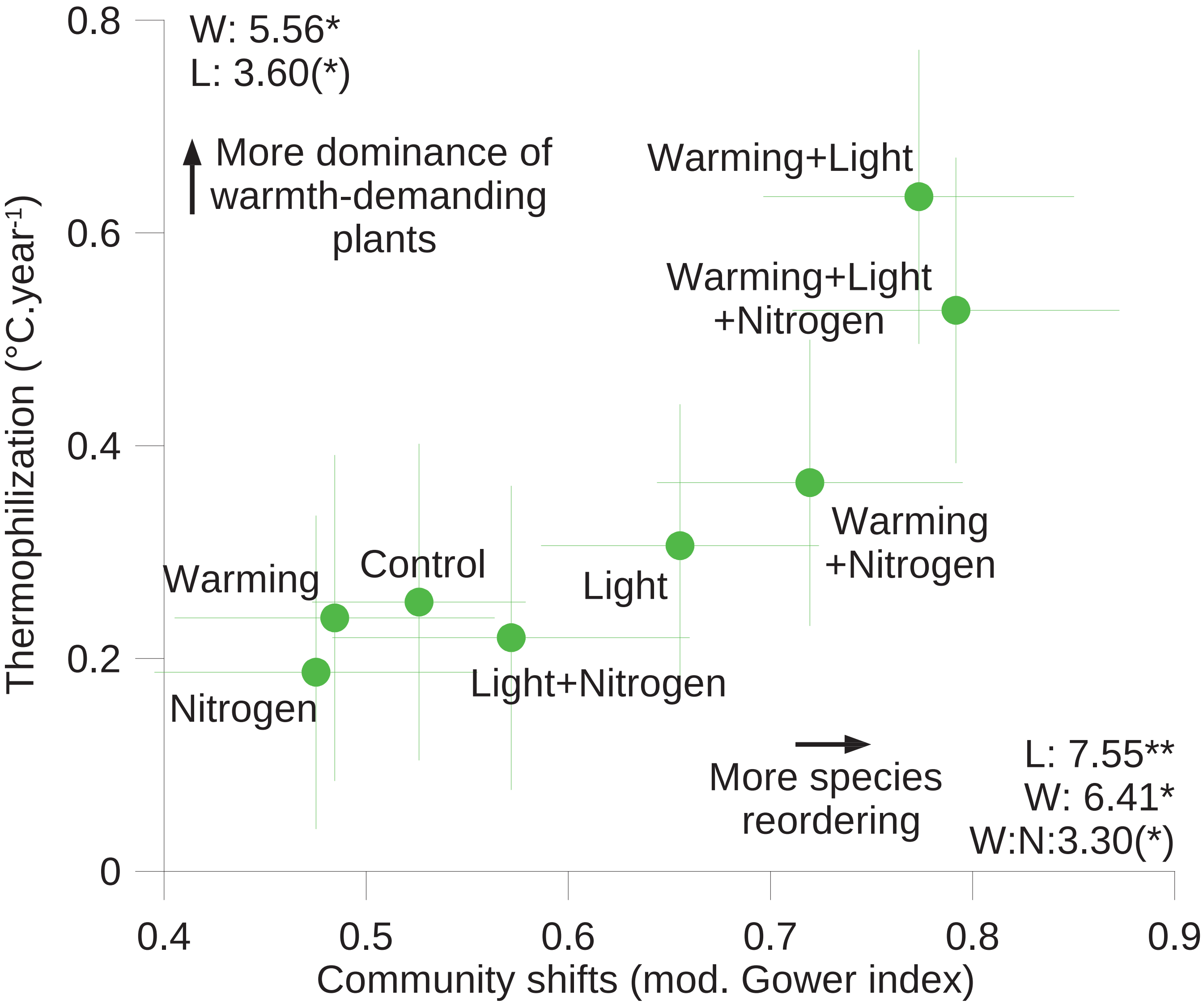
Author contributions P.D.F., A.D.S., D.A.C., M.H., K.V. designed research; P.D.F. and A.D.S. performed research; P.D.F. and F.R.S. analysed data; all authors wrote the paper.

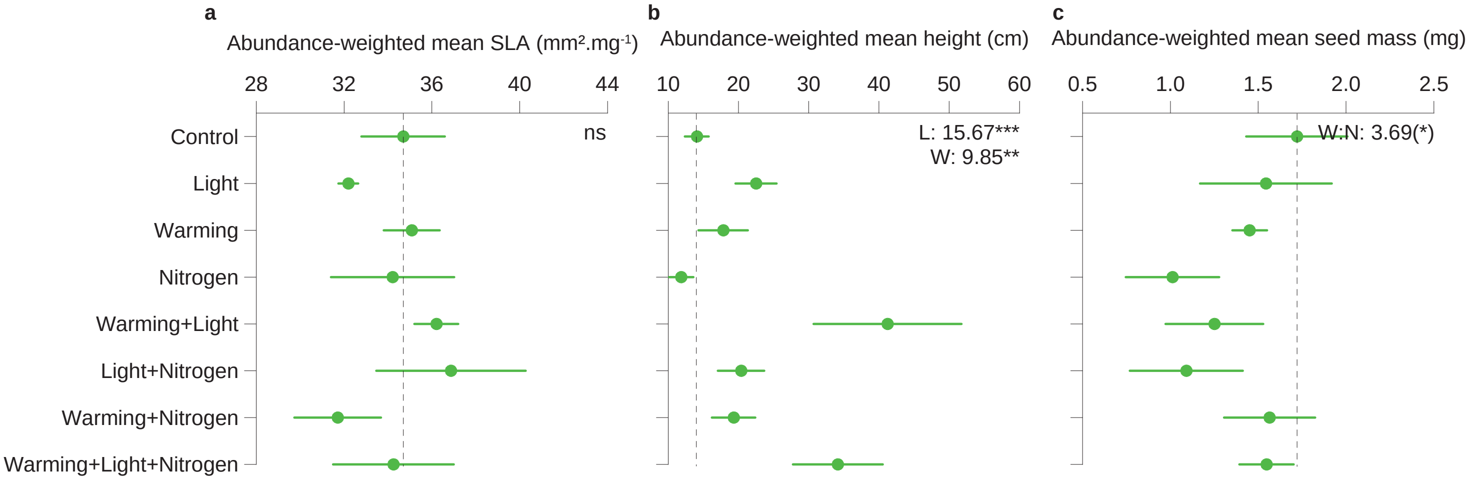
Competing financial interests The authors declare no competing financial interests.

Figure legends

Figure 1 | Community-level effects of light, warming and nitrogen addition in forest understories. 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). Symbols indicate: (*): $P < 0.1$, *: $P < 0.05$, **: $P < 0.01$. Error bars denote 1 s.e.m.

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). Symbols and letters indicate: 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 5 replicate plots per treatment. The dashed line indicates the mean level of the control plots.


W: 5.56*
L: 3.60(*)
More dominance of warmth-demanding plants
Warming+Light
Warming+Light +Nitrogen
Warming +Nitrogen
Light
Control
Warming
Nitrogen
Light+Nitrogen
More species reordering
L: 7.55**
W: 6.41*
W:N:3.30(*)
Thermophilization (°C.year-1)
0.8
0.6
0.4
0.2
0
0.4
0.5
0.6
0.7
0.8
0.9
Community shifts (mod. Gower index)


a
Abundance-weighted mean SLA (mm².mg⁻¹)
28
32
36
40
44
ns
b
Abundance-weighted mean height (cm)
10
20
30
40
50
60
L: 15.67***
W: 9.85**
c
Abundance-weighted mean seed mass (mg)
0.5
1.0
1.5
2.0
2.5
W:N: 3.69(*)
Control
Light
Warming
Nitrogen
Warming+Light
Light+Nitrogen
Warming+Nitrogen
Warming+Light+Nitrogen