

Reply to Harwood et al.: Thermophilization estimation is robust to the scale of species distribution data

We recently assessed plant community responses to macroclimate warming across European and North American temperate forests (1). To do so, we inferred the temperature preferences of understory species from distribution data by means of ecological niche, or species distribution models (SDMs). Harwood et al. (2) propose that subcanopy temperatures, instead of gridded climate data, should have been used in our analyses. Despite exciting ongoing advances in the downscaling of microclimates from macroclimatic data, Harwood et al.'s suggestion is, at present, simply not possible at the scale of our study: One would need to match the occurrence of every individual of each of 1,032 species with the microclimate in each location across two continents. More fundamentally, such downscaling is not necessary for our purpose: when applied correctly (3), SDMs can infer species' climatic tolerances without the need of those detailed field data, based on mean field approximation (4). Nonetheless, as SDMs only approximate thermal tolerances, we went beyond common practice to propagate their uncertainties into thermophilization rates (1). Even if microclimates might bias the niche models of some species (2), no bias at the level of among-region comparisons is expected given that we quantified thermophilization as the relative temporal difference in floristic temperatures per unit time. Thus, presence of bias in species' temperature preferences, as hypothesized by Harwood et al. (2), is not enough to cause bias in thermophilization rates. Our sensitivity analyses removing random subsets of species from the total pool (1) confirm that the reported thermophilization rates are robust.

We also invested substantial efforts in using the best distribution data available to fit SDMs to our species. Large unsuitable areas within the range boundary are actually excluded from our models as illustrated by

the exclusion of, for instance, highlands in central Norway from the geographic range of the most frequent European understory plant *Anemone nemorosa* (ref. 1, figure 1A). Of course, range maps are only a coarse representation of actual distributions. Alternatively, using sets of species occurrences such as those provided by the Global Biodiversity Information Facility (www.gbif.org) was clearly less desirable in this case: although invaluable in many instances, such data have been shown to be still incomplete and often geographically biased (e.g., by political boundaries) (5).

We concur with the opinion expressed by Harwood et al. (2) that "the combined effects of terrain and the biota on the microclimate experienced by species may come to be viewed as an integral part of biodiversity analysis rather than an inconvenience that may be dismissed"; this is exactly what we conveyed with our study (1). Indeed, we specifically showed that microclimatic effects should be taken into account (and not dismissed) to accurately interpret biotic responses to climate change. Hence, we believe that the issues raised by Harwood et al. (2) represent important future directions for SDMs, but they do not cast any doubt on our findings that understory plant responses to rising air temperatures were buffered by forest canopy closure across European and North American temperate forests.

Pieter De Frenne^{a,b,1}, Francisco Rodríguez-Sánchez^{b,c}, Markus Bernhardt-Römermann^d, Carissa D. Brown^e, Ove Eriksson^f, Martin Hermy^g, Fraser J. G. Mitchell^h, Petr Petříkⁱ, Hans Van Calster^j, Mark Vellend^k, and Kris Verheyen^a

^aForest and Nature Lab, Ghent University, BE-9090 Gontrode-Melle, Belgium; ^bForest Ecology and Conservation Group, Department of Plant Sciences, University of Cambridge,

Cambridge CB2 3EA, United Kingdom; ^cIntegrative Ecology Group, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, E-41092 Sevilla, Spain; ^dInstitute of Ecology, Friedrich-Schiller-University, DE-07743 Jena, Germany; ^eDepartment of Geography, Memorial University, St. John's, NL, Canada A1B 3X9; ^fDepartment of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden; ^gDepartment of Earth and Environmental Sciences, Division of Forest, Nature and Landscape, Katholieke Universiteit Leuven, BE-3001 Leuven, Belgium; ^hBotany Department and Trinity Centre for Biodiversity Research, School of Natural Sciences, Trinity College Dublin, Dublin 2, Ireland; ⁱDepartment of Geographic Information Systems and Remote Sensing, Institute of Botany, Academy of Sciences of the Czech Republic, CZ-25243 Průhonice, Czech Republic; ^jResearch Institute for Nature and Forest, BE-1070 Brussels, Belgium; and ^kDépartement de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada J1K 2R1

1 De Frenne P, et al. (2013) Microclimate moderates plant responses to macroclimate warming. *Proc Natl Acad Sci USA* 110(46): 18561–18565.

2 Harwood TD, Mokany K, Paini DR (2014) Microclimate is integral to the modeling of plant responses to macroclimate. *Proc Natl Acad Sci USA* 111:E1164–E1165.

3 Araújo MB, Peterson AT (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology* 93(7):1527–1539.

4 Bennie J, Wilson RJ, Maclean IMD, Suggitt AJ (2014) Seeing the woods for the trees: When is microclimate important in species distribution models? *Glob Change Biol*, 10.1111/gcb.12525.

5 Boakes EH, et al. (2010) Distorted views of biodiversity: Spatial and temporal bias in species occurrence data. *PLoS Biol* 8(6): e1000385.

Author contributions: P.D.F., F.R.-S., M.B.-R., C.D.B., O.E., M.H., F.J.G.M., P.P., H.V.C., M.V., and K.V. wrote the paper.

The authors declare no conflict of interest.

¹To whom correspondence should be addressed. E-mail: pieter.defrenne@ugent.be.