

Letter To The Editor

Ability of bryophytes to track areas of suitable climate depends on their habitat preferences

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The impact of climate change on biodiversity operates through a complex mixture of habitat loss and range shift through the emergence of newly suitable areas (Warren et al., 2013). The main question is therefore to determine whether species have the ability to balance the loss of suitable habitats by effectively shifting their ranges and track suitable areas under climate change (Nogués-Bravo et al., 2018). Zanatta et al. (2020) most recently simulated the dispersal of apparently extremely efficient dispersers, namely bryophytes, whose tiny spores (<20 μm on average) are wind-dispersed across large distances, under several climate change scenarios. They concluded that, despite their high dispersal capacities, bryophytes will lose suitable areas at a faster rate than they will colonize newly suitable areas. Paradoxically, mounting evidence points to striking range expansions in epiphytic floras in the context of the sharp decrease of SO₂ concentrations since the 1980s and climate warming (Tuba et al., 2011). Here, we addressed this apparent controversy by reassessing the results of Zanatta et al. (2020) in the light of the repartitioning of the data per habitat type.

We compared the median ratios between the predicted rates of range loss and gain reported by Zanatta et al. (2020) for 40 selected bryophyte species in 2050, reanalyzing the results when the species are assigned to three main habitat types, namely epiphytes, saxicolous, and ground-dwelling habitats, based on Hill et al. (2007). This analysis reveals that habitat preferences of bryophyte species have a clear impact on the ratios of range loss versus expansion, whose median ranged, for the RCP (representative concentration pathway) 4.5 scenario under the MPI-ESM-LR (the low resolution version of Max-Planck-Institute Earth system model) Global Circulation Model, from 52.53 for ground-dwelling bryophytes to 30.28 for saxicolous bryophytes and 28.27 for epiphytic bryophytes (Fig. 1). Similar trends were observed for the RCP8.5 scenario and for both scenarios under the HadGem2-ES Global Circulation Model.

The observed difference in the ability of bryophytes from different habitats to track areas of suitable climate, which we highlight here, suggests that habitat preferences of

bryophytes play a leading role in determining current and future species' ranges. Because epiphytes constantly need to switch from one host tree to another in a dynamic landscape for persistence (Snäll et al., 2005), they are expected to display high dispersal capacities, and it would thus be tempting to interpret their observed higher colonization rates in terms of the selection for effective dispersal traits rather than a consequence of epiphytism itself. In mosses, epiphytism is in fact typically associated with a suite of morphological features (Hedenäs, 2012). These traits associated with epiphytism, such as short setae and large spores, typically tend, however, to hamper spore dispersal. For instance, epiphytic mosses are characterized by the reduction of the peristome, a structure comprised of a series of teeth located at the mouth of the capsule and whose hygroscopic movements enhance spore dispersal (Hedenäs, 2012). Peristome reduction is further associated with hydrochasy, that is, the release of spores under wet conditions, which typically does not favor long-distance dispersal (Zanatta et al., 2018).

The fact that higher colonization rates were predicted for epiphytes, despite their traits that typically do not promote dispersal, indicates that height of release is the most important parameter driving colonization potential. This is an implicit consequence of the application of the Wald model (Katul et al., 2005), wherein the release height is one of the key parameters of the dispersal kernel. This result is further supported by recurrent reports of a positive relationship between plant height and dispersal distance (Muller-Landau et al., 2008), so that plant height has a substantially stronger explanatory power than seed mass (Thomson et al., 2011).

Nevertheless, the higher colonization rates predicted for epiphytes based upon simulations with the Wald model are at odds with the counterselection of dispersal-efficient traits in epiphytic bryophytes and, in fact, epiphyte communities typically display aggregated patterns (Snäll et al., 2003; Löbel et al., 2006) and strong spatial genetic structures (Snäll et al., 2004; Ledent et al., 2020). We suggest that the apparent conflict between high colonization rates and

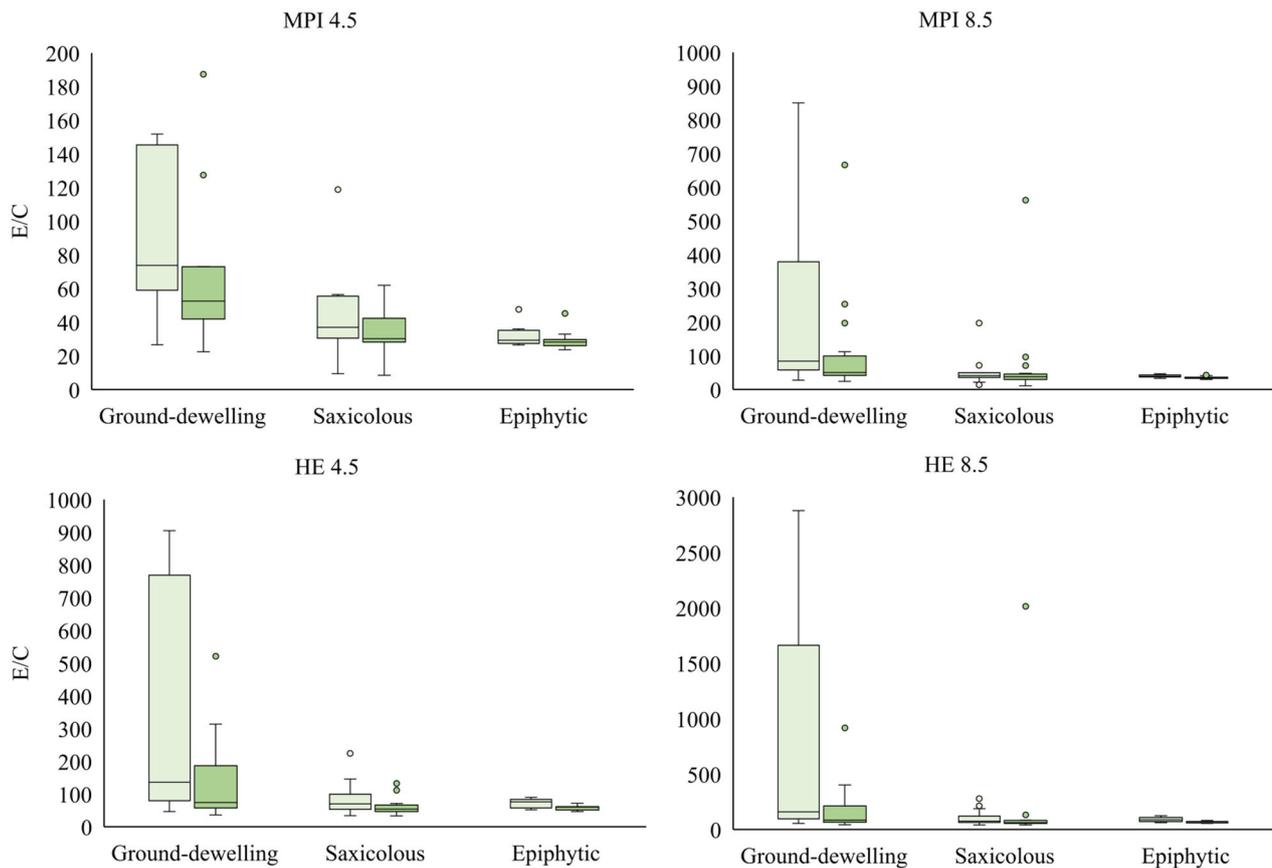


Fig. 1. Predicted rates of future extinction and colonization of areas becoming newly suitable due to climate change in 40 European bryophytes (Zanatta et al., 2020). The box plots represent the extinction to colonization ratios (E/C), averaged over 30 MigClim replicates, between the rate of range loss and the percentage of newly suitable pixels effectively colonized at the end of the simulation in 2050, wind speed set to maximum, and the probability of long-distance dispersal set to 0.0 (light green) and 0.1 (dark green), respectively. Results are shown for three habitat preferences, two global circulation models, MPI-ESM-LR (MPI) and HadGem2-ES (HE), and two climatic scenarios, RCP4.5 and 8.5.

counterselection of dispersal capacities in epiphytes, which results in aggregated patterns, can be interpreted in terms of a fat-tailed dispersal kernel that reflects a “dual” dispersal strategy (see Vanderpoorten et al., 2019 for review). On the one hand, spore density is higher within the near vicinity of the mother plant, resulting in the locally aggregated pattern. On the other hand, a higher proportion of spores travels across long distances.

It therefore appears that release height in epiphytes effectively counterbalances the impact of a series of life-history traits that typically do not promote dispersal. Nevertheless, factors other than height may still control the dispersal capacities of epiphytes. For instance, Mota de Oliveira & ter Steege (2015) counterintuitively reported that individuals of communities from the tree base, but also from the outer canopy, had lower chances of dispersal outside of the community than individuals from the other height zones, suggesting that species inhabiting the canopy had lower chances to engage in long-distance dispersal events than species from lower height zones.

Congruent with the fact that epiphytes exhibit the highest colonization rates, range expansions have recurrently been reported in the European bryophyte flora as a response to climate warming and decreasing pollution loads (see Tuba et al., 2011; Sérgio et al., 2016 for review). Except for a recent report of range expansion in subtropical epiphyllous liverworts (Tang et al., 2018), there is a complete lack of information on bryophyte range expansions in other continents and, in particular, in high-elevation tropical mountain ranges, which are cradles of biodiversity particularly vulnerable to climate change. The use of epiphytic bryophyte range shifts during the last decades, which are unparalleled in other land plants, as indicators of climate change, would require accurate and spatially explicit information of their current distribution ranges. In the same line as the long-term monitoring program of heavy-metal deposition loads in Europe in the context of the International Cooperation Program on the Impact of Air Pollution on Natural Ecosystems and Crops (Godzik, 2020), we call here for a large international monitoring network of epiphytic bryophyte range shifts.

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References

- Godzik B. 2020. Use of bioindication methods in national, regional and local monitoring in Poland – changes in the air pollution level over several decades. *Atmosphere* 11: 143.
- Hedenäs L. 2012. Morphological and anatomical features associated with epiphytism among the pleurocarpous mosses – one basis for further research on adaptations and their evolution. *Journal of Bryology* 34: 79–100.
- Hill MO, Preston CD, Bosanquet SDS, Roy DB. 2007. *BRYOATT: Attributes of British and Irish mosses, liverworts and hornworts*. Huntingdon: Centre for Ecology and Hydrology.
- Katul GG, Porporato A, Nathan R, Siqueira M, Soons MB, Poggi D, Horn HS, Levin SA. 2005. Mechanistic analytical models for long-distance seed dispersal by wind. *The American Naturalist* 166: 368–381.
- Ledent A, Gauthier J, Pereira M, Overson R, Laenen B, Mardulyn P, Gradstein SR, de Haan M, Ballings P, der Beeten IV, Zartman CE, Vanderpoorten A. 2020. What do tropical cryptogams reveal? Strong genetic structure in Amazonian bryophytes. *New Phytologist* 228: 640–650.
- Löbel S, Snäll T, Rydin H. 2006. Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. *Journal of Ecology* 94: 856–868.
- Mota de Oliveira S, ter Steege H. 2015. Bryophyte communities in the Amazon forest are regulated by height on the host tree and site elevation. *Journal of Ecology* 103: 441–450.
- Muller-Landau HC, Wright SJ, Calderón O, Condit R, Hubbell SP. 2008. Interspecific variation in primary seed dispersal in a tropical forest. *Journal of Ecology* 96: 653–667.
- Nogués-Bravo D, Rodríguez-Sánchez F, Orsini L, de Boer E, Jansson R, Morlon H, Fordham DA, Jackson ST. 2018. Cracking the code of biodiversity responses to past climate change. *Trends in Ecology & Evolution* 33: 765–776.
- Sérgio C, Carvalho P, Garcia CA, Almeida E, Novais V, Sim-Sim M, Jordão H, Sousa AJ. 2016. Floristic changes of epiphytic flora in the Metropolitan Lisbon area between 1980–1981 and 2010–2011 related to urban air quality. *Ecological Indicators* 67: 839–852.
- Snäll T, Ehrlén J, Rydin H. 2005. Colonization–extinction dynamics of an epiphyte metapopulation in a dynamic landscape. *Ecology* 86: 106–115.
- Snäll T, Fogelqvist J, Ribeiro PJ Jr., Lascoux M. 2004. Spatial genetic structure in two congeneric epiphytes with different dispersal strategies analysed by three different methods. *Molecular Ecology* 13: 2109–2119.
- Snäll T, Ribeiro PJ Jr., Rydin H. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: Local conditions versus dispersal. *Oikos* 103: 566–578.
- Tang X, Gradstein SR, Sun L-W, Zhu M-J, Shi R-P, Wei Q-Q, Chen Y-Q, Zhou X-X, Wang J. 2018. A contribution to the knowledge of epiphyllous bryophytes in Tianmushan National Nature Reserve (Zhejiang, China), with remarks on climate warming and nature conservation. *Lindbergia* 41: 1–7.
- Thomson FJ, Moles AT, Auld TD, Kingsford RT. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. *Journal of Ecology* 99: 1299–1307.
- Tuba Z, Slack NG, Stark LR. 2011. *Bryophyte ecology and climate change*. Cambridge: Cambridge University Press.
- Vanderpoorten A, Patiño J, Désamoré A, Laenen B, Górski P, Papp B, Holá E, Korpelainen H, Hardy O. 2019. To what extent are bryophytes efficient dispersers? *Journal of Ecology* 107: 2149–2154.
- Warren R, VanDerWal J, Price J, Welbergen JA, Atkinson I, Ramirez-Villegas J, Osborn TJ, Jarvis A, Shoo LP, Williams SE, Lowe J. 2013. Quantifying the benefit of early climate change mitigation in avoiding biodiversity loss. *Nature Climate Change* 3: 678–682.
- Zanatta F, Engler R, Collart F, Broennimann O, Mateo RG, Papp B, Muñoz J, Baurain D, Guisan A, Vanderpoorten A. 2020. Bryophytes are predicted to lag behind future climate change despite their high dispersal capacities. *Nature Communications* 11: 5601.
- Zanatta F, Vanderpoorten A, Hedenäs L, Johansson V, Patiño J, Lönnell N, Hylander K. 2018. Under which humidity conditions are moss spores released? A comparison between species with perfect and specialized peristomes. *Ecology and Evolution* 8: 11484–11491.