



## COMMENTARY

# On the importance of edaphic variables to predict plant species distributions – limits and prospects

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### Abstract

Although the importance of edaphic parameters on plant growth and survival is known, they are rarely incorporated as predictors in plant species distribution models (SDM). Dubuis et al., in this issue, show they may improve the performance of plant SDMs in Alpine ecosystems. This paves the way for more comprehensive assessments of the value of including edaphic variables into SDMs.

The field of plant ecology recently made an important shift toward a more predictive science, based on recent statistical developments and the availability of large databases on species and environmental distribution and functional traits (Kleyer et al. 2012). More and more studies are using species distribution models (SDMs) to investigate the environmental correlates of plant species distribution so as to predict potential distributions in space and time (Thuiller et al. 2008). In theory, the overall SDM approach is rather simple: it starts with gathering informative species distribution and environmental data, which are fed into adequate statistical models (e.g. logistic models). These models are then used to extract the importance of variables and to predict the potential distribution of the species of interest (Guisan & Thuiller 2005).

A major issue here is the assumption that the input variables have inherent effects on the species of interest (Guisan & Thuiller 2005; Soberón 2007). Most plant distribution modelling relies on climatic variables alone, in view of their widespread availability. More importantly, the climatic variables are known to have direct physiological roles in limiting the ability of plants to survive and grow, such as the number of growing degree-days, minimum temperature or actual evapotranspiration. Winter temperature is, for instance, likely to discriminate between species based on their ability to assimilate soil water and nutrients, and continue cell division, differentiation and tissue growth at low temperatures (lower limit), while some species have a chilling requirement for processes such as bud break and seed germination (upper limit).

However, looking only at the abiotic environment, plants are influenced not only by climate but also by light availability and soil resources. Proxies for light availability encompass topographic variables such as aspect or solar radiation (direct and diffuse) and are commonly included into distribution models. In contrast, soil resources are

poorly integrated into plant SDMs, although they are known to strongly influence species demography (Elmendorf & Moore 2008; Dubuis et al. 2013). For instance, plants are influenced by soil pH, as very basic conditions may hamper the release of important ions (e.g.  $\text{NO}_4^{3-}$  or  $\text{PO}_4^{3-}$ ), while very acid conditions lead to unsuitable forms of these elements, and for instance, aluminium becoming toxic for calciphile species at high concentration (Gobat et al. 2004).

A puzzling question is, therefore, why edaphic variables are not commonly used in plant SDMs. Dubuis et al. (2013) built on this question to assess whether the inclusion of edaphic variables significantly improved the predictive ability of SDMs that were originally based on topo-climatic variables. Their methodology relied on a stratified vegetation plot survey in an Alpine valley. For each of the 252 vegetation plots, they recorded species presence (and from that inferred absence for the other species), measured critical plant functional traits and measured the soil properties for each plot. Topo-climatic variables were then extracted from high-resolution gridded data for each plot. They then compared the predictive ability of SDMs calibrated with topo-climatic variables only to those also including edaphic variables. Predictive accuracy was estimated with a cross-validation procedure using a standard protocol (i.e. area under the operating characteristic curve). From this comparison, they concluded that pH, and sometimes soil N content, were important predictor variables to complement topo-climatic variables. They supported their conclusion by showing that species for which the inclusion of pH or N increased the predictive ability of the SDM were species with low specific leaf area and acidophilic preferences, thus tolerating low soil pH and high humus content.

From this short summary, I could, in theory, conclude that soil variables must be included when modelling plant

species distribution. In theory only, because the answer is slightly more complicated. First, it is interesting to note that although Dubuis et al. (2013) incorporated several edaphic variables, only pH, and sometimes N, were shown to be important for the 115 plant species modelled. This sounds incredibly odd given the appropriateness of the sampling design and that the soil variables were measured in the field, while the topo-climatic variables were obtained from spatial interpolation and likely have more uncertainty. Although it might seem surprising that N and P did not seem to be important predictors, the fact that the availability of the form of these elements that could be assimilated (e.g.  $\text{NO}_3^-$ ,  $\text{NH}_3^+$  or  $\text{H}_2\text{PO}_4^-$ ) was not directly quantified might be relevant (Dubuis et al. 2013). The fact that these elements vary through the growing season and are strongly linked with the presence of specific mycorrhizas might also influence detection of their importance. Another plausible and non-exclusive explanation relates to the strong climatic gradient of the study area, where temperatures, together with land use, are likely drivers of soil properties, especially since soil properties are strongly influenced by climatic conditions in extreme environments (Crawford 2008). To me, another key explanation might also relate to the modelled entities. The authors here focused on presence-absence but not on demographic parameters (e.g. abundance or density). Given that soil properties are likely to influence nutrient uptake, they might be of secondary importance in shaping species boundaries or species absence, but of primary importance in determining population growth rate and abundance (e.g. Elmendorf & Moore 2008). These three hypotheses will need to be tested explicitly.

In addition, a closer look at the importance of spatial grain seems fundamental to me. Indeed, formal tests of the importance of edaphic variables require vegetation plots for which explicit soil measurements are available and are statistically representative. It is hard to believe that consistent patterns of soil importance will emerge at coarse grain resolution, given that soil properties are usually heterogeneous in space (pH) and time (e.g. N). The few studies that have included soil variables in plant SDMs have been carried out using vegetation plots with high-resolution soil information (e.g. Dullinger et al. 2012).

To summarize, the relevance of edaphic variables for predicting plant species distribution and abundance deserves more attention, and further tests are necessary to corroborate or generalize the results of Dubuis et al. (2013).

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