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

Wilfried Thuiller

(wilfried.thuiller@ujf-grenoble.fr): Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Université J. Fourier, Grenoble I, BP 53, 38041 Grenoble Cedex 9, France

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. It paves the way for more comprehensive assessments of the values 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 investigate the environmental correlates of plant species distribution and predict their potential distributions in space and time using SDMs (Thuiller et al. 2008). In theory, the overall SDM approach is rather simple: it starts with gathering informative species distribution and environmental data, which feed 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 et al. 2005).

A major issue here is the assumption that the input variables have inherent effects on the species of interest (Guisan et al. 2005, Soberón 2007). Most plant distribution modelling relies on climatic variables only, 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), and 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 (Dubuis et al. 2013, Elmendorf et al. 2008). For instance, plants are influenced by soil pH as very basic conditions may hamper the release of important ions (e.g. NO_3^- or 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 the ones also including edaphic variables. Predictive accuracy was estimated by 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 nitrogen 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 nitrogen 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 of all, it is interesting to note that although Dubuis et al. (2013) incorporated several edaphic variables, only pH, and sometimes N, came out 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 into the field whilst the topo-climatic variables came from spatial interpolation and likely to bear 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 assimilable form of these elements (e.g. NO_3^-, NH_4^+ or $H_2PO_4^-$) 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 the detectability 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 second importance in shaping species boundaries or species absence, but be of prime importance in determining population growth rate and abundance (e.g. Elmendorf et al. 2008). These three hypotheses will need to be tested explicitly.

In addition to this, 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 statistically representative. It is hard to believe that consistent patterns of soil importance will emerge at coarse grain resolution knowing that soil properties are usually heterogeneous in space (pH) and time (e.g. nitrogen). The few studies that have included soil variables in plant species distribution models have been carried out using vegetation plots with high-resolution soil information (e.g. Dullinger et al. 2012).

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

References

Crawford, RMM. Plants at the margin - Ecological limits and climate change. Cambridge University Press; Cambridge, UK: 2008.

Dubuis A, Giovanettina S, Pellissier L, Pottier J, Vittoz P, Guisan A. Improving the prediction of plant species distribution and community composition by adding edaphic to topo-climatic variables. Journal of Vegetation Science. 2013; 24:593–606.

Dullinger S, Gattringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, Willner W, Plutzar C, Leitner M, Mang T, Caccianiga M, Dirnböck T, Ertl S, Fischer A, Lenoir J, Svenning J-C, Psomas A, Schmatz DR, Silc U, Vittoz P, Hülber K. Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change. 2012; 2:619–622.

Elmendorf SC, Moore KA. Use of community-composition data to predict the fecundity and abundance of species. Conservation Biology. 2008; 22:1523–1532. [PubMed: 18847440]

Gobat, J-M.; Aragno, M.; Matthey, W. The living soil. Fundamentals of soil science and soil biology. Science Publishers; Enfield, NH, US: 2004.

Guisan A, Thuiller W. Predicting species distribution: offering more than simple habitat models. Ecology Letters. 2005; 8:993–1009.

Kleyer M, Dray S, de Bello F, Leps I, Meier T, Pakeman RJ, Strauss B, Thuiller W, Lavorel S. Assessing species and community functional responses to environmental gradients: which multivariate methods? Journal of Vegetation Science. 2012; 25:805–821.

Soberón J. Grinnellian and Eltonian niches and geographic distribution of species. Ecology Letters. 2007; 10:1115–1123. [PubMed: 17850335]

Thuiller W, Albert C, Araújo MB, Berry PM, Cabeza M, Guisan A, Hickler T, Midgley GF, Paterson J, Schurr FM, Sykes MT, Zimmermann NE. Predicting global change impacts on plant species' distributions: Future challenges. Perspectives in Plant Ecology, Evolution and Systematics. 2008; 9:137–152.