Commentary

The geographic mosaic of plant chemistry and its effects on community and population genetic diversity

In 1802 naturalist Alexander von Humboldt, his botanist companion Aimé Bonpland, and the Ecuadorian Carlos Montúfar attempted to ascend the 6263-m high Chimborazo volcano in Ecuador, which was then thought to be the highest mountain in the world. The small group of explorers only made it to 5875 m, higher than any European before them, but they came back with an outstanding collection of botanical specimens and unusually detailed data on plant community composition. Von Humboldt compiled these data in his famous 1805 map depicting the 'distribution of plants in equinoctial America, according to elevation above the level of the sea' (Fig. 1; von Humboldt & Bonpland, 2009). This work established that plant communities assembled according to physical properties of the habitat, such as precipitation, mean annual temperature and soil conditions, and this built the basis for many fields of modern biology, for example, biogeography, and more recently, modeling of ecosystem changes as a result of global warming. Elevational and latitudinal gradients became an important subject and tool of research in ecophysiology, community and population ecology (Lomolino & Brown, 2004). With the changes in the physical properties of a habitat, interactions among organisms change as well. Thus natural selection on a population of organisms is a function of the interactions with other species and the environmental context in which these interactions are played out, both of which are likely to vary with geographic location. A resulting mosaic of geographically differential natural selection with co-evolutionary hotspots and trait remixing was hypothesized as a major driver of population-genetic structure and speciation (Thompson, 1999).

Almost 210 years after the attempt to reach the summit of Chimborazo by von Humboldt, Bonpland and Montúfar, and only 130 km northeast, at the Yanayacu Biological Station on the Eastern slope of the Andean Antisana volcano, Glassmire *et al.* (in this issue of *New Phytologist*, pp. 208–219) studied a mid-canopy shrub, *Piper kelleyi* Tepe (Piperaceae) (Fig. 2a), which is endemic to the eastern slope of the Andes within a narrow range of between 1400 and 2400 m in altitude (Tepe *et al.*, 2014). Instead of studying communities along altitude gradients per se, they studied the interaction of variation on the population level with that on the community level and with it the increasingly appreciated interaction between ecological and evolutionary processes. Glassmire *et al.* report results of their study on the secondary metabolite variation among subpopulations of *P. kelleyi* and the effects of the phenotypic variation on herbivore and parasitoid community composition and population-genetic structure (Fig. 2). Community composition of a group of specialist lepidopteran herbivores in the *Eois* (Geometridae: Larentiinae) genus, as well as their parasitoid wasp community, varied with the concentrations of three prenylated bencoic acid derivatives that had previously been shown to negatively affect herbivores, fungi and bacteria (Jeffrey *et al.*, 2014). While the relative chemical composition of plants varied widely and with elevation, higher concentrations of chromene, prenylated benzoic acid and dimeric chromane supported lower diversity of the specialist *Eois* spp. herbivores, but higher parasitation rates by, and higher diversity of, the parasitoid community. Collectively, the data support two major predictions of the geographic mosaic hypothesis, namely that: (1) the relationships between interacting organisms (e.g. competing herbivores, parasitoids), as well as (2) the environmental circumstance in which the interactions are played out, vary at local and regional levels and so affect the strength and outcome of co-evolutionary processes (Thompson, 1999).

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The correlative nature of the dataset does not allow the relationships to be causally linked to differential natural selection and/or co-evolutionary processes. Nevertheless, the study represents one of the very rare approaches to this hypothesis framework and links plant chemistry to parasitoid community and herbivore community, and population-genetic structure in highly diverse, understudied tropical habitats. Thus, it is one of the first attempts to study the role of plant chemistry in structuring interaction networks, something recently identified as crucial to understand the evolution of plant defenses (Poelman & Dicke, 2014; Poelman & Kessler, 2016), in a tropical system. The authors provide an excellent and explicit framework of hypothesis that can readily be adapted to other study systems (Table 1 in Glassmire *et al.*). Moreover, by using path analysis and principal component analysis on extensive field and genotyping data, the study provides some

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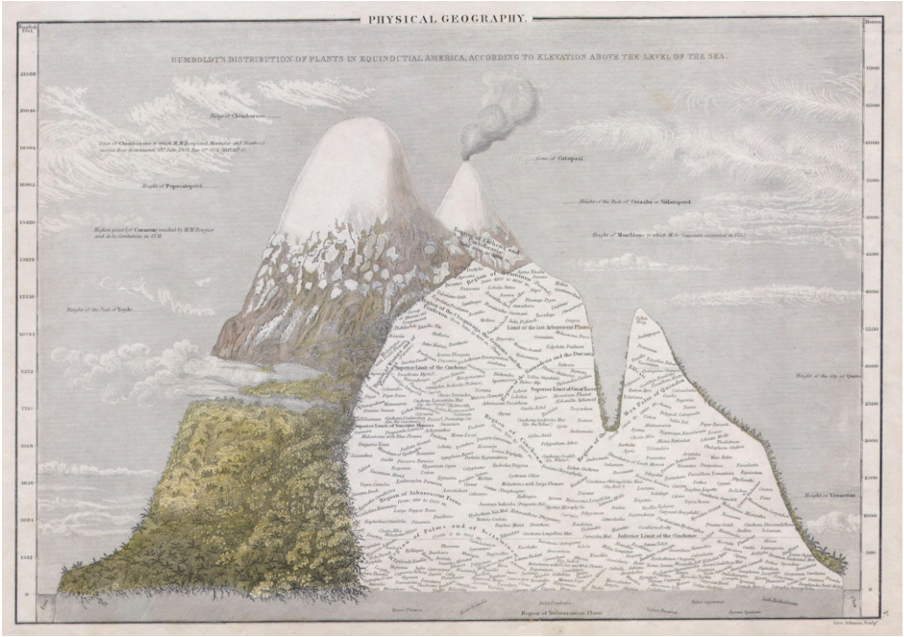

Fig. 1 Profile view of Mount Chimborazo, Ecuador, published by Adam and Charles Black in 1839, based on von Humboldt's 1805 illustration of the vegetation zones along elevational gradients in the Andes. The map was originally published as 'Humboldt's distribution of plants in equinoctial America according to elevation above the level of the sea' (see von Humboldt & Bonpland, 2009). Reproduced from https://en.wikipedia.org/wiki/File:1839_Black_%5E%5Ex2F,_Hall_Map_of_the_Mountains_%5E_Plants_of_America_-_Geographicus_-_AmericaMts2-black-1839.jpg.

Fig. 2 The *Piper kelleyi* study system. (a) *Piper kelleyi* populations in the Ecuadorian Andes vary in composition of defensive secondary metabolites along elevational gradients. The population-genetic structure of major specialist herbivores, such as (b) *Eois encina* varies with the chemical characteristics of the plant populations, as well as with altitude and plant community diversity. Photographs courtesy of Andrea E. Glassmire.

solutions to overcome the difficulties of experimentally manipulating diverse tropical systems in order to establish causal links between ecological variables.

For example, co-evolution can be evident in patterns of local co-adaptation, which ideally can be studied in reciprocal transplant common garden experiments (Garrido *et al.*, 2012). However, local co-adaptation, in turn, should also be reflected in a distinct population-genetic structure. Glassmire *et al.* used a genotype-by-sequencing approach to analyze the population genetic structure of one of the specialist geometrid species, *Eois encina* (Fig. 2b). They found distinct genetic differentiation of the herbivore populations by elevation and plant chemistry. While this is not direct evidence for co-evolution, it emphasizes one of the major suggestions derived from the data: plant chemistry is one of the main environmental factors driving selection on the herbivore population as well as shaping the overall interacting community. In how far, and in what ways, that interacting community is also affecting selection on plant chemical traits has been (Ehrlich & Raven, 1964), and still remains, one of the most important questions in interaction biology and chemical ecology. In fact, although elevational gradients in plant communities have been known at least since Humboldt and companion's visit to Ecuador, the interaction of evolutionary mechanisms that drive plant chemical-phenotype distribution along those gradients are still poorly understood. Moreover, even more general patterns of biodiversity along elevational gradients do not seem generalizable across different biomes and climate zones (Rodriguez-Castaneda *et al.*, 2016).

In this respect, one of the most interesting and forward-looking findings of the Glassmire *et al.* study is that the diversity of the *Eois* herbivore community on the focus plant species *P. kelleyi* varies with the diversity of the *Piper* spp. host plant diversity. At higher *Piper* spp. diversity, the diversity of *Eois* spp. on *P. kelleyi* was lower, which was interpreted by the authors as support for the associational resistance hypothesis (Barbosa *et al.*, 2009). By that logic, increase in diversity of potential host plants either makes finding the appropriate host more difficult for herbivores or allows herbivores to more accurately choose the most appropriate host because of the contrasts in host cues provided by the diversity of potential host plants. For the first mechanism, the lower diversity would be accompanied by a lower abundance of the herbivores for each species. For the second mechanism, overall abundances per species could stay the same, just the number of herbivore species per plant species would drop. Unfortunately, the herbivore abundances are not provided in this study, which does not allow differentiation between the two mechanisms. However, it points to a more general and utterly important question, likely crucial to understand ecological patterns along elevational gradients on a global scale: how does functional diversity of the host plant community affect herbivory and higher trophic level interactions? And, more specifically, how does plant chemistry link diversity to species interactions, community and ecosystem functions and thus affect co-evolutionary processes between specific interactors? The authors discuss the distinctly different chemotypic separation of the high-elevation populations of *P. kelleyi* as a result of natural selection by the physical environment, such as the higher UV radiation and lower temperatures. Alternatively, differential behavior of herbivores, a differential use of host cues or information space, at different levels of host plant diversity, may change natural selection on plant defensive chemical traits (Kessler, 2015) and so result in a geographic mosaic of co-evolutionary processes. A major prediction of this hypothesis for the *Piper–Eois* study system then is a higher phenotypic separation and/or integration of chemical traits on the population level with an increasing diversity of the host plant community, as well as a higher apparent specialization of the major herbivores. Higher *P. kelleyi* chemotype separation at higher elevation, and in more diverse communities, is certainly evident in the data, as is an apparent higher specialization of the *Eois* herbivores. The study introduces the proper tools to test these predictions in this and in other systems.

As with many great studies, the one by Glassmire *et al.* leaves at least as many questions as it answers but it opens new doors and suggests new tools to grow our understanding of plant biology. Specifically, the study is a good example of the current departure of chemical ecology from a primarily mechanistic analysis of chemically-mediated interactions to a functional and evolutionary analysis of chemical traits (Raguso *et al.*, 2015). Moreover, it nicely illustrates the great value of natural history as a scientific instrument that can reset research cycles (Greene, 2005), as well as being a welcome reminder that there is a biome on Earth that we are still only beginning to understand – the tropics.

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