

Commentary

News on intra-specific trait variation, species sorting, and optimality theory for functional biogeography and beyond

Human-driven environmental changes affect ecosystems at all levels of organization (Díaz *et al.*, 2019). In functional biogeography, community aggregated plant traits are assumed to reflect the adjustment of the vegetation to varying environmental conditions, which in turn affect ecosystem functions feeding back to the climate system (Reichstein *et al.*, 2014). A new generation of dynamic global vegetation models now aims at implementing adaptive responses of plants and their effects on ecosystem functions (Franklin *et al.*, 2020), but empirical evidence is still sparse or comes with diverse limitations. In this issue of *New Phytologist* Dong *et al.* (2020; pp. 82–94) make a major contribution here by presenting one of today's most comprehensive analyses on mechanisms of leaf trait variation and placing this in the context of optimality theory.

‘... adaptive plasticity within plant individuals, adaptation within species and selection among species combine to create predictable relationships between traits and the environment ...’

Dong *et al.* present an unprecedented dataset on traits with high functional relevance: leaf area (LA), leaf mass per area (LMA), area based leaf nitrogen content (N_{area}), and leaf internal- to ambient- CO_2 ratio (X) determined from stable isotope measurements ($\delta^{13}\text{C}$). It covers a large north–south transect with 116 sites and 705 species from tropical to temperate Australia. Dong *et al.* provide a seminal contribution on how and why intra- and inter-specific components of trait variability co-vary with environmental conditions by guiding their analysis by theoretical considerations of stomatal optimization (Cowan & Farquhar, 1977), least cost hypothesis (Wright *et al.*, 2003), and the coordination hypothesis (Chen *et al.*, 1993). Their main findings indicate that adaptive plasticity within plant individuals, adaptation within species, and selection among species combine to create predictable relationships

between traits and the environment: X and LA increase with growing season temperature, and decrease vapour pressure deficit and soil pH; N_{area} and LMA show the opposite pattern. Results of Dong *et al.* help us to understand how optimality theory can be applied for predicting vegetation functioning from environmental drivers. In the following sections we highlight some further key aspects that we hope will stimulate future research in functional biogeography and beyond.

How important is inter-specific vs intra-specific trait variation?

Environmental change impacts species distributions and abundances through the process of species sorting while migrations may be limited by dispersal capabilities or emerging non-analogue environmental conditions. Adaptive responses of the plants themselves are key mechanisms to cope with a changing environment as well (Franks *et al.*, 2014). Fitness may increase by evolution of a better adapted genotype (adaptive evolution, Merilä & Hendry, 2014) or by phenotypic plasticity of the same genotype (adaptive plasticity – also referred to as acclimation – Nicotra *et al.*, 2010).

Species sorting impacts variations in community trait values by inter-specific trait variations, and plant adaptive responses impact community trait values by intra-specific trait variations (in the following called ITV). However, studies on community trait–environment relationships are typically based on species mean trait values, thus neglecting plant adaptive responses (e.g. Tautenhahn *et al.*, 2008; Bruehlheide *et al.*, 2018). The underlying assumption that, over large spatial extents, the variation of traits between species is much larger than within species may not always be adequate (Albert, 2015; Tautenhahn *et al.*, 2019). Since environmental factors drive both species sorting and adaptive responses, testing this assumption further requires large-scale sampling campaigns accounting for intra- and inter-specific trait variation of whole communities and covering large climate gradients. This is what Dong *et al.* present here. They show that partitioning of trait variation between intra- and inter-specific variation for geographic variation in community traits is trait-specific: (1) X being dominated by ITV (> 90% explained by ITV), (2) LA being dominated by between species trait variation (< 10% explained by ITV), and (3) with N_{area} and LMA intermediate. Their results emphasize the need to account for ITV in trait-based research.

How well does intra-specific trait variation represent adaptive responses to environmental conditions?

It is tempting to interpret ITV as ‘optimal’ plant adaptive responses, as adaptive responses by definition result in ITV – but not all ITV is necessarily due to adaptation: (1) within individual

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variations as a function of ontogeny, phenology, or within canopy variations; (2) within population variations due to micro-site conditions or biotic interactions; and (3) between population variations due to stress or mal-adaptive responses. Measurement protocols have been adapted to minimize the contribution of trait variation within individuals and populations.

Trait responses between populations provide important indications of adaptive responses, especially if those show consistent co-variations with environmental factors across species (Merilä & Hendry, 2014). If such relationships are consistent with optimality theory – as highlighted in Dong *et al.* – the confidence that we see adaptation is much enlarged. But still the interpretation of ‘intra-specific responses’ as ‘adaptive responses’ should be confirmed by enhanced fitness proxies.

How do intra-specific trait responses and species sorting impact community level traits?

Disentangling species sorting and adaptive responses for community traits is important (Roos *et al.*, 2019) because their underlying mechanisms differ and may show contrasting velocities of response to changes in environmental conditions. Dong *et al.* provide a comprehensive picture of how constellations of intra-specific responses impact community traits.

A key aspect considered by Dong *et al.* is to what extent different species show universal (consistent) or species-specific (heterogeneous) responses to environmental factors. This is important, because different constellations of species-specific responses could potentially lead to similar community responses, but with different implications for ecosystem function. Fig. 1 illustrates theoretical scenarios for the contribution of intra-specific responses and species sorting to community traits.

In Dong *et al.* almost all species show universal responses of X to all analysed environmental factors (growing season temperature, aridity, and soil pH), of N_{area} to temperature and aridity, and of LMA to aridity. These responses are consistent with scenario D in Fig. 1. Such universal responses are important since intra-specific responses systematically add up to make an effect on community traits suggesting an underlying physical principle of the trait response.

Species-specific responses were found for N_{area} to soil pH (scenario F), for LMA to temperature and soil pH (scenario G), and for LA to all environmental factors (scenarios F and G). Whether such heterogeneous patterns are due to confounding effects or due to species-specific strategies might be further elucidated by analysing multivariate trait coordination.

It is remarkable that Dong *et al.* found no evidence for nonadaptive responses (scenarios A and B) which – at least for the four selected traits – makes a clear case for the importance to account for intra-specific trait responses for community traits and ecosystem functioning overall.

Intra-specific responses that are universal but contradicting to species sorting as illustrated in scenario E seem like a theoretical exercise but might be found when disentangling spatial vs temporal environmental changes. This could point to confounders that mask the direct responses or to effects of scale.

Relevance of trait predictions for future ecosystem responses to environmental change

Confronting empirical relationships with optimality theory enhances confidence in predicting values for such traits from environmental conditions – we need to move beyond simple correlation analyses. However, underlying assumptions based on optimality theory may also show limitations or need further developments. Extensive datasets may uncover limitations of current optimality models, for example in extreme environmental conditions or at the limits of species distribution ranges. Dong *et al.* here suggest incorporating stomatal responses to soil moisture in addition to VPD in the least-cost hypothesis framework to better capture trait responses in very dry environments.

Changes in community traits are expected to feed back to the climate system due to changes in ‘ecosystem functional properties’ (Reichstein *et al.*, 2014) – like radiation- or water-use efficiency – causing changes in biosphere–atmosphere exchange of matter and energy (Fig. 2). As a next step it will be important to understand how adaptive responses and species sorting propagate to ecosystem functions. Musavi *et al.* (2016) show that using species mean trait values and abundances is insufficient for identifying robust relationships between community traits and ecosystem functional properties, while spatial and temporal collocation of trait data substantially improved the fit. This highlights the importance of adaptive responses for trait-based predictions of ecosystem function.

A new generation of dynamic global vegetation models (DGVMs) now aims at implementing adaptive responses of plants and their effects on ecosystem functions (Franklin *et al.*, 2020). To identify traits that are important to treat as flexible in DGVMs, studies like Dong *et al.* are crucial. Results may help in constraining the local trait space due to the environmental dependencies. Further constraints may be obtained by a multivariate perspective on intra-specific trait coordination and trade-offs.

Clearly, one of today’s largest conceptual limitations of inferring empirically how plants respond to contemporary environmental change is the ‘space-for-time’ substitution assumption. Evolution may not keep pace with the rate of current environmental changes (Fukami & Wardle, 2005), factors like CO₂ concentrations increase rapidly in time but vary little spatially, and nonanalogue climates could occur in the future. Upcoming techniques of retrieving trait measurements from digital herbarium specimens that have been collected over centuries hold promise to close another important gap here (Lang *et al.*, 2019) to test whether relationships, theories, and models developed in space hold also in time.

A plea for integrated large-scale and long-term observations

Large-scale analyses accounting for intra- and inter-specific components of trait variation are providing invaluable insights on the functional responses of vegetation communities to changing

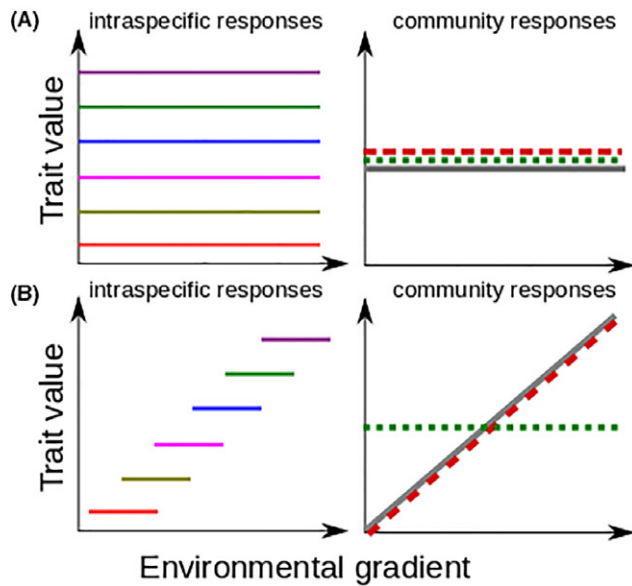
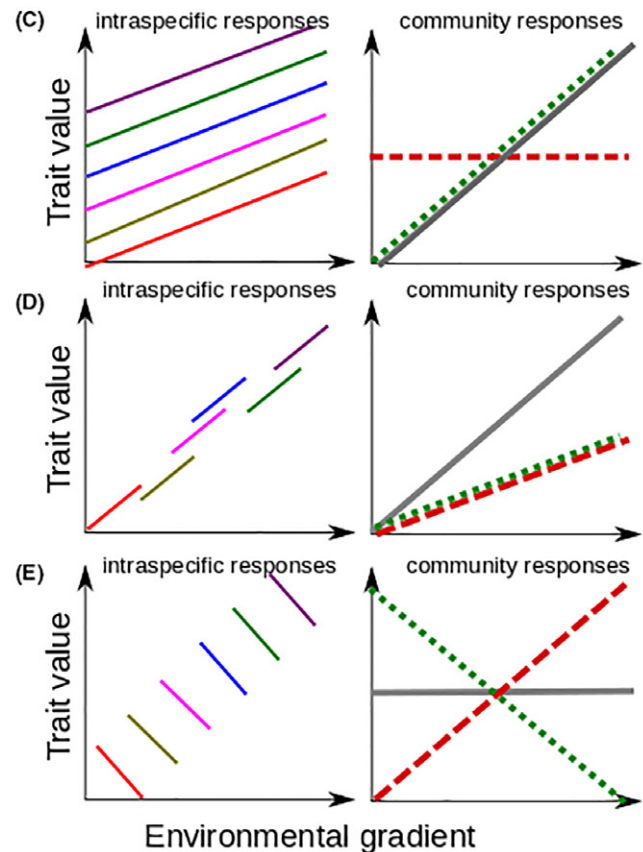
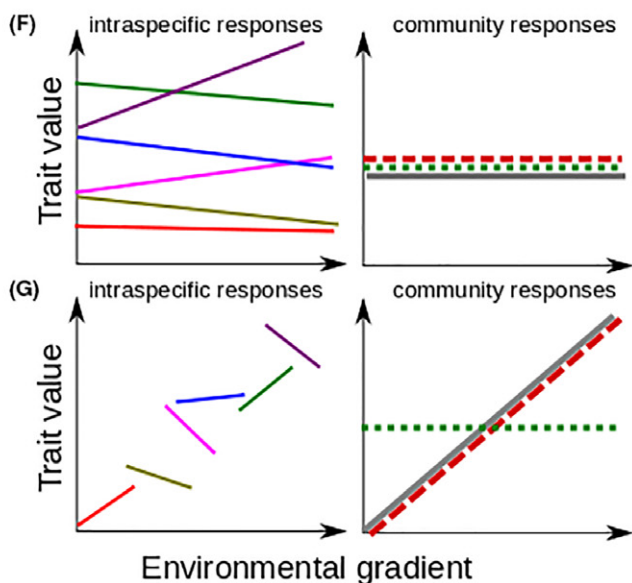
(1) invariant (no adaptive responses)**(2) parallel (universal adaptive responses)****(3) species-specific (cancelling out)****Legend**

Fig. 1 Scenarios for potential interactions of intra-specific responses (between population variation along environmental gradients) and species sorting on community mean trait values. We present three groups of scenarios: (1) with no intra-specific responses, (2) with universal intra-specific responses, and (3) with species-specific intra-specific responses. The presented scenarios show extreme cases for illustrative purpose. For each scenario the left panel shows the intra-specific responses of different species (represented by different colours) along with species sorting. The horizontal extent of the lines represents the species occurrence range along the environmental gradient. The right panel shows the consequences for community mean trait values accounting for both species sorting and intra-specific responses (grey line), accounting for only species sorting (red dashed line), or only intra-specific responses (green dotted line). Note: the left panel shows only seven species for illustration, and the right panel shows a continuous relationship which could be observed theoretically with more species following the pattern.

environmental conditions. Large data volume and a large gradient is essential to uncover robust functional relationships. Dong *et al.* emphasize the improvement of the patterns obtained compared to a preliminary analysis based on a subset of the data (Dong *et al.*, 2017). Large-scale observatory networks such as LTER (Long Term Ecological Research network, <https://lternet.edu/>), TERN

(Australia's land ecosystem observatory, <https://www.tern.org.au/>), ICOS (Integrated Carbon Observation System of Europe, <https://www.icos-cp.eu/>) or NEON (National Ecological Observatory Network of the United States, <https://data.neonscience.org/>) provide rich opportunities for studying different processes of vegetation responses to climate change and their effects on

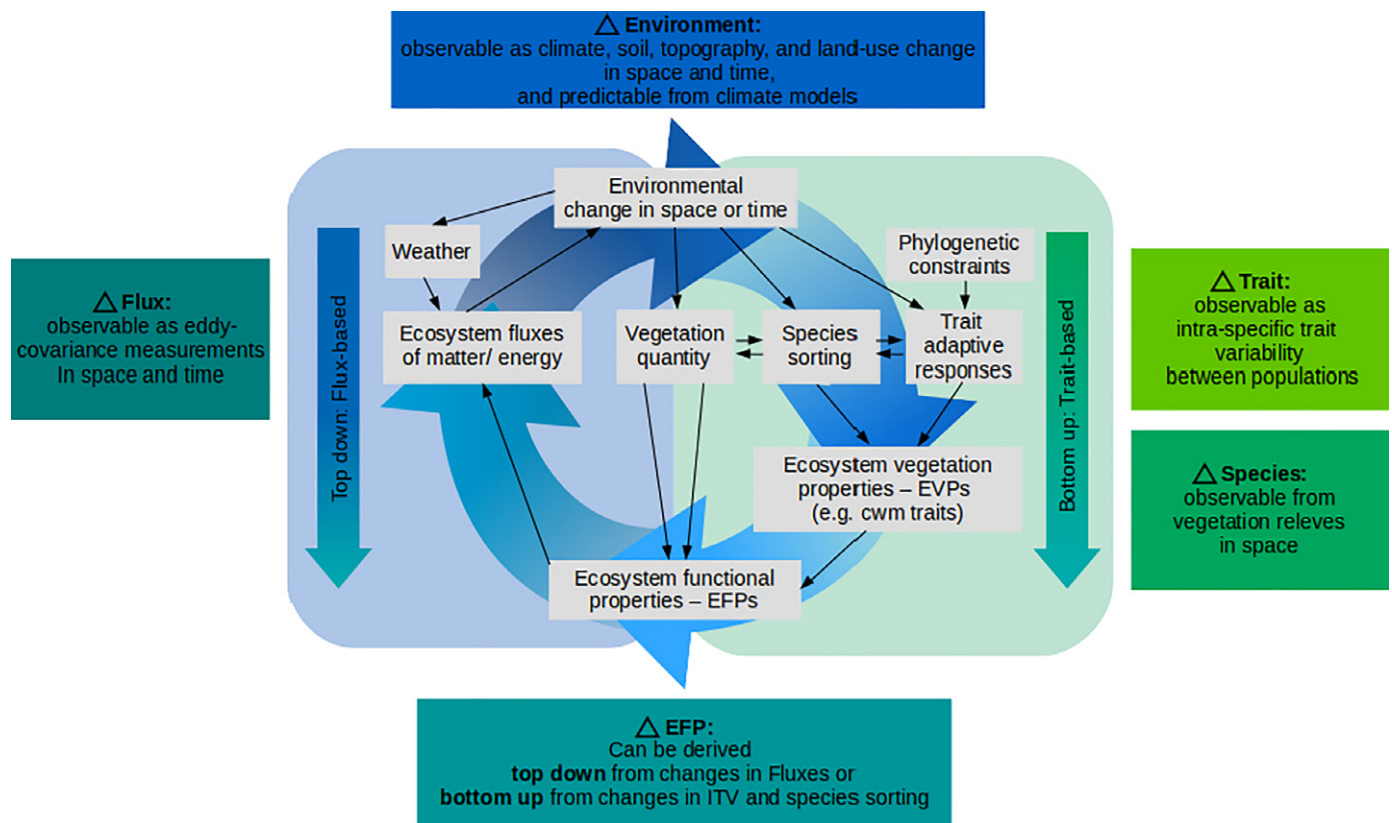


Fig. 2 Conceptual diagram on land–atmosphere interactions from a perspective of functional biogeography. The green to blue colour gradient refers to the relative importance of biological and abiotic environmental processes in controlling how changing environmental conditions propagate through changes in traits, and species composition to changes in ecosystem vegetation properties (EVPs) and ecosystem functional properties (EFPs), which in turn affect ecosystem–atmosphere fluxes and feedbacks. EFPs determine responses of biosphere–atmosphere exchanges of, e.g. carbon and energy to variations in weather (Reichstein *et al.*, 2014). They can be derived ‘top down’ from ecosystem–atmosphere flux observations (blue box). At present, we largely lack predictability of EFPs, likely because plant traits are the missing link here (green box) (Reichstein *et al.*, 2014). cwm, community weighted mean.

ecosystem functions. Also data-platforms such as TRY (Kattge *et al.*, 2020) can help by hosting data from many individual datasets of trait measurements, especially if they are supplemented with geolocation, sampling-date, developmental, and phenological state.

If observatory networks provide a temporal dimension by re-sampling trait distributions regularly we will be able to challenge the space for time substitution assumption. Year to year variations of traits help to disentangle plastic from evolutionary processes (Phillimore *et al.*, 2010). Synchronization with ecosystem flux measurements facilitates assessing the imprint of trait responses on ecosystem functioning (Musavi *et al.*, 2016; Medlyn *et al.*, 2017). All these aspects appear to be essential ingredients for improved predictability of the biosphere by providing empirical evidence and challenge for theoretical principles of vegetation dynamics in a rapidly changing world out of equilibrium.

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