

## Commentary

# In search of the links between decomposition ecology and evolution: the *Arabidopsis* connection

Starting in the 1970s, plant community ecology was significantly transformed from a descriptive to a predictive science, particularly due to the development of assembly rules for plant species (Keddy, 1992; i.e. rules that specified which subset of species from the regional pool would tolerate specific conditions and form a community). An unexpected outfall of this transition was that researchers working in plant community ecology somehow lost interest in intraspecific variation to focus almost exclusively on interspecific differences between co-occurring species (Violle *et al.*, 2012). With the rise of plant functional ecology, which links the conceptual frameworks of community and ecosystem ecology, the emphasis on interspecific differences deepened. Almost 20 years later, however, studies have shown how variation within species may also feedback on communities and ecosystems as part of evolutionary processes operating at ecological scales (<https://natureecoevocommunity.nature.com/users/71845-simone-des-roches/posts/26332-how-variation-within-species-links-ecology-and-evolution>). This recent evidence has revived interest in intraspecific variability as part of the links between environment, evolution, communities and ecosystems (Violle *et al.*, 2012). However, in spite of the relevance of those links for some of the core assumptions on which plant functional ecology is built (Calow, 1987), we still understand relatively little about the evolutionary mechanisms behind them.

*‘... the authors take a first step in reconciling the ecological and evolutionary drivers of decomposability ...’*

The work presented by Kazakou *et al.* in this issue of *New Phytologist* (2019; pp. 1532–1543) represents a creative and timely contribution to our mechanistic understanding of the effects of intraspecific variation on ecosystem processes. The study brings together analytical approaches from quantitative genetics with those from functional ecology, to describe how the genetic variability in the extremely well-studied plant species, *Arabidopsis thaliana* affects the rate of degradation of senescent plant material

(decomposability). The authors also evaluate whether decomposability at the intraspecific level is driven by some of the classic drivers of decomposition, and which is the effect of the controls of these drivers. Specifically, the authors test: (1) how much of the intraspecific heritable variation in an effect trait such as decomposability is associated with variation in secondary metabolites, (2) how much is related to variation across the leaf economic spectrum (LES; that is a universal spectrum of relationships among leaf chemical, structural and physiological properties describing leaf economic variation at the global scale, Wright *et al.*, 2004), and (3) and how much of that variation is related to climate variability in the sites of origin of genotypes. By doing this, the authors take a first step in reconciling the ecological and evolutionary drivers of decomposability, while the results of the study challenge some of the core assumptions in functional ecology.

Leaf litter decomposition regulates carbon and nutrients within plant–soil systems and, through this, decomposition determines the balance between the carbon that is released to the atmosphere and the aboveground carbon that is sequestered in soils (Prescott, 2010). We know that variation in leaf litter decomposability relates well to variation in plant attributes and that this association is consistent across floras and climates (Cornwell *et al.*, 2008). It is widely assumed that evolutionary processes would reproduce the same patterns at the intraspecific level (Pan *et al.*, 2014). Nevertheless, although the idea that leaf litter decomposability should be considered a component of plant fitness was proposed 25 years ago (Berendse, 1994), almost no work has attempted to place leaf litter in an evolutionary context (but see Pan *et al.*, 2014, and references cited there in). Understanding how evolution operates at the intraspecific level in effect traits such as decomposability and in its drivers (both response and effect traits), and how those variables are related to environmental variability, is indispensable to test the hypothesis of the relationships found at the interspecific level (Keddy, 1992; Lavorel & Garnier, 2002).

Kazakou *et al.* found a 2.7-times range in *Arabidopsis* decomposability due to genetic variability from a polygenic origin, which was comparable in magnitude to the variability found at interspecific level along regional climatic gradients. Moreover, *Arabidopsis* decomposability showed a medium value of narrow-sense heritability ( $h^2 = 0.25$ ; Hansen *et al.*, 2011), that is the genetic additive fraction of the total phenotypic variance, or the one with short-term evolutionary potential (Visscher *et al.*, 2008). The authors also show that genetic variability in *Arabidopsis* decomposability appears to be mainly related to the concentration of secondary metabolites, to the size of leaves, and to rainfall-related variables across the sites of origin of the genotypes, while it does not seem to be associated with LES traits (Figs 3c,d and 5 in Kazakou *et al.*). The importance of secondary metabolites on decomposition is not new, particularly their role in determining interspecific differences in decomposition (Chomel *et al.*, 2016); however, the

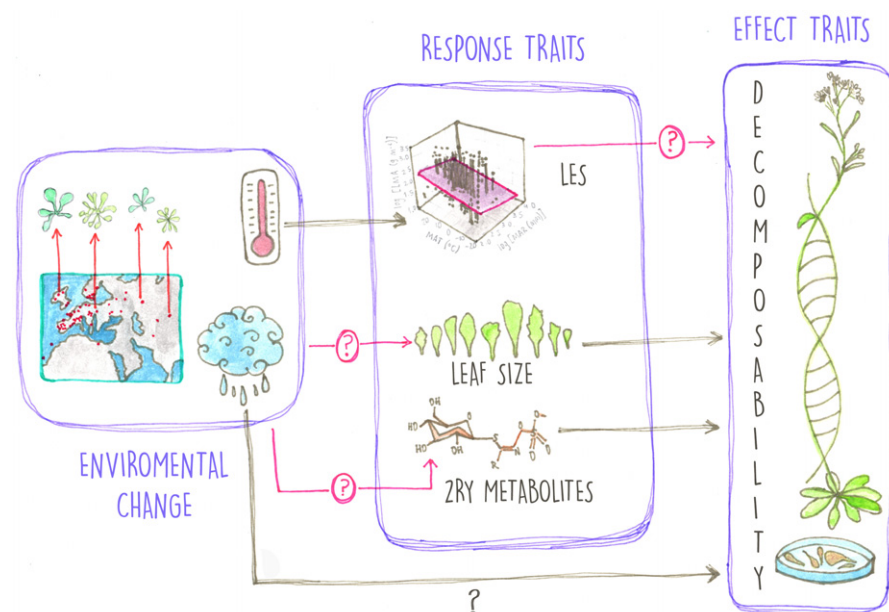
This article is a Commentary on Kazakou *et al.*, 224: 1532–1543.

finding that both genetically-driven decomposability and secondary metabolite concentration appears to be linked to genes operating on cell and organelle membranes opens up many new questions. For instance, the identification of those common components of membranes appears as a relevant avenue to explore, while evaluating how those components vary along environmental gradients could be a complementary alternative. In particular, as the authors suggest, the use of 'reciprocal transplants of different genotypes along specific environmental gradients to measure changes in metabolomic profiles and decomposition rate' would allow for the determination of the environmental drivers of metabolomic differences. At the same time, the lack of a relationship between secondary metabolites and precipitation variables, which are the environmental drivers of *Arabidopsis* decomposability in this study, suggests that other environmental drivers could be relevant in determining metabolite concentrations. Among those drivers, herbivory pressure could be the first obvious candidate (De Vos *et al.*, 2007) and, in consequence, experiments manipulating herbivory on different genotypes, in combination with climate manipulation, may also shed light on those relationships. Additionally, due to the fact that glucosinolates, well-characterized anti-herbivore defense compounds, are among the secondary metabolites that definitively impact decomposability (Fig. 4 in Kazakou *et al.*), their evaluation in the context of the previously described manipulations could help to unravel some of the mechanisms of interaction among the multiple drivers of decomposability at the species level.

In addition to the patterns Kazakou *et al.* show us, and the questions those patterns pose, if we place the findings of Kazakou *et al.* in the context of functional ecology (Fig. 1), we can recognize that environmental variability from the geographic origin of the genotypes affects leaf attributes related to the LES and genotype decomposability as expected. We can also recognize that, at the intraspecific level, *Arabidopsis* mimicked the relationships among LES leaf traits previously demonstrated at the interspecific level. This

is consistent with variability in both trait values and decomposability found at the intraspecific level in *Arabidopsis* being comparable to that found at interspecific level, and only moderately lower than the one found at global scale (Cornwell *et al.*, 2008). In spite of the former patterns, the effect of climate variability on genotypes decomposability was not driven by changes along the LES, and, while changes along the LES among the genotypes were related to temperature, changes in decomposability were related to rainfall (Fig. 1). This not only indicates some disconnection between the controls of decomposability and the LES at intraspecific level but, what is more important is that these results serve as a caution for the assumption that the relationship between LES and ecosystem processes is monotonic and scale independent. These results imply that a better understanding of the relationship between traits and fitness is still needed to build a solid theoretical framework that allows the transition between organization levels (Violle *et al.*, 2012) and to understand eco-evolutionary feedbacks (Hendry, 2016).

In conclusion, Kazakou *et al.* show that, in *Arabidopsis*, less decomposable genotypes have higher concentrations of secondary metabolites, smaller leaves and originated from wetter climates. But we still do not really know the identity of the most important secondary metabolites driving decomposition (although there are some hints to explore cell and organelle walls, and glucosinolates) or on the basis of precisely which traits wettest climates determine lower decomposability on their leaves, or how leaf size is modulated by climate (Fig. 1). The work presented by Kazakou *et al.* also shows us that there is indeed room for natural selection to operate on decomposition (i.e. variability in genetically driven decomposability and in leaf traits), but we do not know if natural selection is truly operating on that variability or in which direction or under which selection pressures it operates. In other words, the work presented by Kazakou *et al.*, as any novel research on a challenging problem, leaves us with many more questions than answers. As such, we hope this work will inspire future studies to bring together not only different analytical approaches but, most importantly, different



**Fig. 1** Summary of the results presented in this issue of *New Phytologist* by Kazakou *et al.* (pp. 1532–1543) depicted within a modified version of the conceptual model framework of Lavorel & Garnier (2002). LES, leaf economic spectrum.



conceptual frameworks to foster our understanding of the ecological and evolutionary rules that determine both community assembly and ecosystem functioning.

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## References

- Berendse F. 1994. Litter decomposability – a neglected component of plant fitness. *Journal of Ecology* 82: 187–190.
- Calow P. 1987. Towards a definition of functional ecology. *Functional Ecology* 1: 57–61.
- Chomel M, Guittonny-Larcheveque M, Fernandez C, Gallet C, DesRochers A, Pare D, Jackson BG, Baldy V. 2016. Plant secondary metabolites: a key driver of litter decomposition and soil nutrient cycling. *Journal of Ecology* 104: 1527–1541.
- Cornwell W, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurakawa H, Perez-Harguindeguy N *et al.* 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters* 11: 1065–1071.
- De Vos M, Jae HK, Jander G. 2007. Biochemistry and molecular biology of Arabidopsis–aphid interactions. *BioEssays* 29: 871–883.
- Hansen TF, Pélabon C, Houle D. 2011. Heritability is not evolvability. *Evolutionary Biology* 38: 258–273.
- Hendry AP. 2016. *Eco-evolutionary dynamics*. Princeton, NJ, USA: Princeton University Press.
- Kazakou E, Vasseur F, Sartori K, Baron E, Rowe N, Vile D. 2019. Secondary metabolites have more influence than morphophysiological traits on litter decomposability across genotypes of *Arabidopsis thaliana*. *New Phytologist* 224: 1532–1543.
- Keddy PA. 1992. Assembly and response rules: two goals for predictive community ecology. *Journal of Vegetation Science* 3: 157–164.
- Lavelle S, Garnier E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.
- Pan X, Cornelissen JHC, Zhao WW, Liu G-F, Hu H-F, Prinzing A, Dong M, Cornwell WK. 2014. Experimental evidence that the Ornstein–Uhlenbeck model best describes the evolution of leaf litter decomposability. *Ecology and Evolution* 4: 3339–3349.
- Prescott CE. 2010. Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry* 101: 133–149.
- Violle C, Enquist BJ, McGill BJ, Jiang L, Albert CH, Hulshof C, Jung V, Messier J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology and Evolution* 27: 244–252.
- Visscher PM, Hill WG, Wray NR. 2008. Heritability in the genomics era – concepts and misconceptions. *Nature reviews Genetics* 9: 255–266.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.

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