

Letters

Further analysis of 1532 deciduous woody species from North America, Europe, and Asia supports continental-scale differences in red autumn colouration

A response to Peña-Novas & Archetti (2020) 'Biogeography and evidence for adaptive explanations of autumn colors'

Peña-Novas & Archetti (2020) criticize our recent review of evolutionary explanations for the well-established empirical observation that red autumn foliage is more common in eastern North American (ENA) trees and shrubs than in European and East Asian ones (Lee *et al.*, 2003; Lev-Yadun & Holopainen, 2009; Renner & Zohner, 2019). Our review had concluded that anthocyanins and xanthophylls in autumn leaves of ENA trees and shrubs mainly serve photoprotection. By contrast, Peña-Novas & Archetti (p. 809 in this issue of *New Phytologist*) maintain that autumn colours 'evolved, instead, as warning signals to insects'. They suggest that our conclusion is based on faulty evidence, faulty logic, failure to understand the difference between proximate (mechanistic) and ultimate (adaptive) explanations, and a misunderstanding of the logic of the coevolution hypothesis.

Our review newly showed that ENA species in the autumn experience higher irradiation than do European species, with Asian species intermediate (our Fig. 5 quantified the average daily short-wave irradiation for September from 1901 to 2010 for relevant longitudes). We also referred to the higher temperature fluctuations in North America compared to Asia and Europe (e.g. Zohner & Renner, 2017; Zohner *et al.*, 2017). The higher irradiation and less predictable temperature suggested to us that the higher proportion of red-colouring species in North America may be due to a greater need for photoprotection in this region. We agree with Peña-Novas & Archetti that our new explanation needs further testing, and we are currently undertaking such a test. In the following, we outline fundamental flaws in the criticisms raised by Peña-Novas & Archetti and show that their analysis is biased.

The fundamental predictions of Hamilton & Brown's (2001) signalling hypothesis are that (1) trees use leaf colouration as an honest signal to communicate their defensive capacities to insects and (2) differences in leaf colours change the behaviour of insects. Over the past 18 years, neither of these predictions has been

supported by experimental or comparative data (Wilkinson *et al.*, 2002; Chittka & Döring, 2007; Ougham *et al.*, 2008; Renner & Zohner, 2019). Papers cited by Peña-Novas & Archetti as confirming that pest insects prefer green to red leaves, that red foliage has higher chemical defences than green, or that insects grow better, in spring, on trees that had more green leaves in autumn, fail to explain why this would be of greater selective benefit in ENA compared to Europe and Eastern Asia.

Most importantly, however, Peña-Novas & Archetti are wrong in claiming that there are no significant differences in the proportion of red-colouring species among the floras of North America, Europe, and Asia. Any test of whether species from North America are more likely to turn red than non-American species during leaf senescence, must include only species that exhibit autumn leaf senescence, i.e. deciduous species. Instead, Peña-Novas and Archetti include evergreen conifers and angiosperms in their analysis, which obviously do not become senescent in the autumn. The photoprotection hypothesis, different from their coevolution hypothesis, applies only to deciduous species, as only senescing leaves have to be protected from unfavourable autumn environments, such as high solar radiation and low temperatures.

To demonstrate the validity of our analysis, we combined our own and Peña-Novas and Archetti's observations, resulting in leaf colouration data for 1532 deciduous woody species from North America, Europe, and Asia (Supporting Information Table S1). We then analysed these new data in a hierarchical Bayesian framework, which additionally allowed us to control for phylogenetic structure by including genus- and family-level random effects in our models (see methods and electronic supporting information Note S1 in Hofmann *et al.* (2019) for details on model structure and code). The results confirm our previous results: the European deciduous flora has a significantly lower proportion of red-colouring species than do the Asian and North American floras (9%, 25% and 27% red-leaved species, respectively; Fig. 1).

Our hierarchical Bayesian model allowed us to quantify continental-scale differences in red colouration of deciduous species in a comparative, phylogenetically-informed framework. The results uphold the continental-scale differences in red colouration, and we therefore fail to see how our explanation (Renner & Zohner, 2019) for the higher incidence of red colouration in ENA compared to Europe and Asia is based on faulty evidence or logic. We agree with Peña-Novas & Archetti, however, that the concept of proximate and ultimate explanations is relevant to the controversy. Proximate explanations cite the more immediate cause of a trait, for example, the genes or developmental pathways that cause the occurrence of a trait in an organism. Ultimate explanations cite the evolutionary cause of a trait in a species (Ereshefsky, 2017). This goes back to Aristotle's theory of causal pluralism, commonly known as the doctrine of the four causes (Falcon, 2019). For Aristotle, a firm grasp of what a cause is,

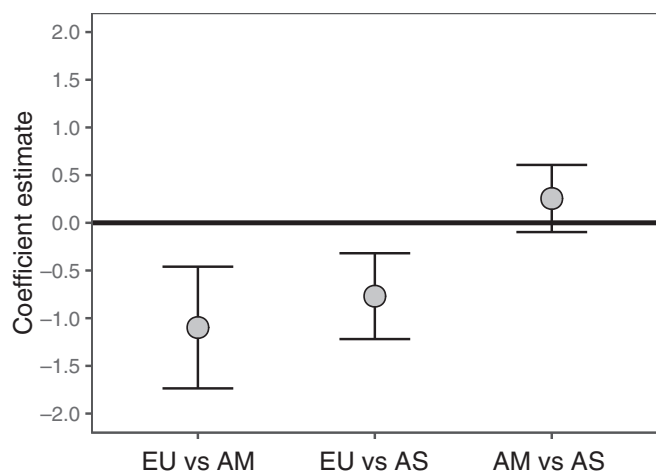




Fig. 1 Hierarchical Bayesian model showing pairwise comparisons between species-level red colouration in Europe (EU), North America (AM), and Asia (AS). Coefficient estimates (effective posterior means \pm 95% credible intervals) for the differences in red colouration for the EU vs AM, EU vs AS, and AM vs AS comparison. All variables were standardized to allow for direct effect size comparisons. Sample sizes: EU 201, AM 431, Asia 900. The dependent variable (binary character of whether a species exhibits red autumn leaves or not) was modelled in response to species' native continent (fixed effect) and species' genus and family identity (random effects).

and how many kinds of causes there are, is essential for a successful investigation of the world around us. In our view, the phenomenon at hand that needs an ultimate explanation is the lower frequency of red-colouring species in Europe compared to Asia and North America. This is precisely where Hamilton & Brown's (2001) insect/plant coevolution (or plant-to-insect signalling) hypothesis falls short. In fact, Peña-Novas & Archetti's observation that the continental-scale differences in leaf colouration are not significant when including evergreen species contradicts the coevolution hypothesis as an explanation for the biogeographic differences in leaf colouration because both evergreen and deciduous species are affected by this hypothesis.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Leaf colouration data for 1532 deciduous woody species from North America, Europe and Asia.

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