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INVITED COMMENTARY

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Trees growing in Eastern North America experience higher autumn solar irradiation than their European relatives, but is nitrogen limitation another factor explaining anthocyanin-red autumn leaves?

A comment on Peña-Novas and Marchetti 2021 (https://doi.org/10.1111/jeb.13903)

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Abstract

Trees growing at a particular latitude in Eastern North America (ENA) receive more autumn solar irradiation than do trees growing at the same latitude in Europe, a difference that could partly explain the higher percentage of anthocyanin-producing deciduous species in ENA compared with European floras. A proposed link between autumn light intensity and the production of anthocyanins is their function in photoprotection, which enables plants with red leaves to resorb nutrients for a longer time than can yellow or brown leaves. The innately 4-week-shorter foliage period of ENA trees compared with European ones may also play a role, as may stronger nitrogen limitation in poorer soils in ENA. We here test for a correlation between nitrogen access and fall anthocyanin in 126 species (55 genera, 22 families) from different temperate forests, using a Hierarchical Bayesian model and accounting for phylogenetic structure in the data. None of 81 species with nitrogen-fixing symbionts produce autumn anthocyanin, whereas 42% of non-nitrogen-fixers do. Thus, when ample nitrogen is available from symbionts, the benefits of anthocyanin-derived photoprotection apparently do not outweigh the costs of anthocyanin production. If nitrogen limitation indeed plays a role in the dominance of red-autumn-colouring trees in ENA floras – while European floras predominantly produce yellow autumn leaves – there might also be continental differences in the frequency or abundance of nitrogen-fixing trees and shrubs, a new hypothesis that deserves testing.

KEYWORDS
anthocyanin, autumn solar irradiation, fall leaf colours, nitrogen, nitrogen-fixing symbionts, photoprotection-resorption hypothesis

1 | INTRODUCTION

Trees growing at a particular latitude in Eastern North America (ENA) receive significantly more autumn solar irradiation than do trees growing at the same latitude in Europe (Renner & Zohner, 2019: figure 5a). This difference has been suggested as an explanation for the fact that a higher percentage of ENA trees and shrubs produce anthocyanin in the autumn than observed in European floras (Hoch et al., 2001; Lee et al., 2003; Lev-Yadun & Holopainen, 2009; Meehan, 1881; Renner & Zohner, 2019, 2020). A proposed link between autumn light intensity and anthocyanin in leaves is the function of anthocyanins in photoprotection. Anthocyanins absorb wavelengths over a wide range of the solar spectrum, from UV-B to red, and their concentration in the vacuoles of epidermal and/or sub-epidermal cells in red leaves is optimal for their function as a sunscreen. Agati et al. (2021) and Hughes et al. (2021) have reviewed the evidence for the photoprotection hypothesis, which explains why autumn leaves of many species turn anthocyanin-red shortly before being dropped: senescing leaves are dismantling their photosynthetic apparatus, and it is during this sensitive time, that anthocyanins are limiting the generation of Reactive Oxygen Species (ROS) and scavenging ROS. This allows senescing cyanic leaves to cope for longer with the photo-oxidative stress they experience, enabling them to resorb nutrients for a longer time than do yellow or brown leaves. This idea is known as the 'photoprotection-resorption' hypothesis (Hoch et al., 2003).

Resorption of nutrients for a longer period in the autumn may be more important for ENA trees and shrubs than for European ones because of the innately 4-week-shorter vegetation time of ENA species compared with European and Asian species (occurring at the same latitude), as shown in a common garden experiment that involved 358 species of trees (Zohner & Renner, 2017). Data on the relative leaf chlorophyll degradation in autumn for ENA ($n = 73$), East Asian ($n = 222$) and European ($n = 63$) tree and shrub species, showed that ENA species flushed 9 ± 4 or 13 ± 4 days later than European or East Asian species and broke down their chlorophyll 9 ± 4 days or 11 ± 4 days earlier than European or East Asian species, respectively. The analysis accounted for species' biogeographic origin and maximum attainable growth height as well as the mean annual temperature, temperature seasonality, mean annual precipitation, and precipitation seasonality in their native range by using a hierarchical Bayesian model that included phylogenetic autocorrelation.

In combination, the higher autumn insolation and the shorter foliage period of ENA woody species compared with European ones provide an evolutionary (ultimate) explanation for the high frequency of anthocyanin-red species in Eastern North America (Renner & Zohner, 2019, 2020).

Two recent studies have suggested that nitrogen may also play a role in whether species produce anthocyanin in leaves that they are about to shed (Hughes et al., 2021; Peña-Novas & Archetti, 2021). This is based on studies in *Arabidopsis* that show that anthocyanin is part of the nitrogen limitation response (Peng et al., 2008). To test their hypothesis that low soil fertility (including low nitrogen content) might drive the evolution of anthocyanin production in autumn, Hughes et al. (2021) compared pH, organic carbon, effective cation exchange capacity, and total N and P for soils in ENA, Europe and East Asia. They found that soils of deciduous forests in ENA were significantly less fertile in all metrics examined compared with Europe, with East Asia exhibiting a mixed range of values.

Another approach was taken by Peña-Novas and Archetti (2021) who measured nitrogen resorption in autumn leaves with the expectation that resorption should be less important in species less limited by nitrogen and that these species should therefore not produce costly anthocyanin before shedding their leaves. These authors' comparison of nitrogen content of mature and senescent leaves in 55 species of trees, however, failed to reveal a correlation between the presence of anthocyanins and the efficiency of nitrogen resorption. Two methodological problems may have affected this result. Firstly, as pointed out by Hughes et al. (2021), the study failed to control for leaf mass loss during senescence. Secondly, the sampling contained species that live in symbiosis with nitrogen-fixing bacteria, such as *Albizia julibrissin*, *Gleditsia triacanthos*, *Salix sepulcralis* and species of *Alnus* and *Populus*. Such species are less nitrogen-limited than are non-nitrogen fixers and might therefore have been treated separately. Indeed, anecdotal observations suggest that trees living in symbiosis with nitrogen-fixing bacteria do not produce anthocyanin in autumn and should therefore have leaves that stay green or turn yellow (Renner & Zohner, 2019).

Here, we follow up on the idea that nitrogen limitation may play a role in whether or not anthocyanin is accumulated in autumn by testing for a correlation between species' fall colours and their symbioses with nitrogen-fixing bacteria. Our expectation was that if nitrogen limitation plays a role in red fall pigmentation, then species with nitrogen-fixing symbionts, such as Rhamnaceae, Salicaceae and many legumes should not produce costly anthocyanins in leaves that are about to be shed.

2 | METHODS

We compiled a list of 126 species (55 genera, 22 families) of deciduous trees and shrubs from different temperate forests, including the 55 species studied by Peña-Novas and Archetti (2021). In total, our compilation includes 81 nitrogen fixers from a phylogenetically diverse range of 31 genera in eight families, with the majority (49 species) belonging to the Fabaceae. To test the effect of N fixation on autumn leaf colouration, we ran a Hierarchical Bayesian (HB) model, including (i) leaf colouration as a binary response variable of whether the species turns red or not in autumn, (ii) N fixation as a binary fixed effect of whether the species is able to fix nitrogen or not, and (iii) family as random effect to control for phylogenetic structure in the data. To parameterize our models, we used the JAGS implementation (Plummer, 2003) of Markov chain Monte Carlo (MCMC) methods in the R package R2JAGS (Su & Yajima, 2014). We ran three parallel MCMC chains for 20 000 iterations with a 5000-iteration burn-in and evaluated model convergence with the Gelman and Rubin statistic (Gelman & Rubin, 1992). Noninformative priors were specified for all parameter distributions, including normal priors for alpha and beta coefficients (fixed effect mean = 0; variance = 1000), and uniform priors between 0 and 100 for the variance of the family random intercept effect, based on De Villemereuil et al. (2012).

The three independent model chains did not converge because there are zero N-fixing species with red leaves in the dataset. To achieve model convergence, we thus assumed an observer error (false negative of species with red autumn leaves falsely identified as green or yellow), by forcing a random subset of 5%, 7.5%, 10%, 15%, 20%, 25%, 30%, 40% or 50% of all study species (including the ones that were already red) to have red leaves. For each observer

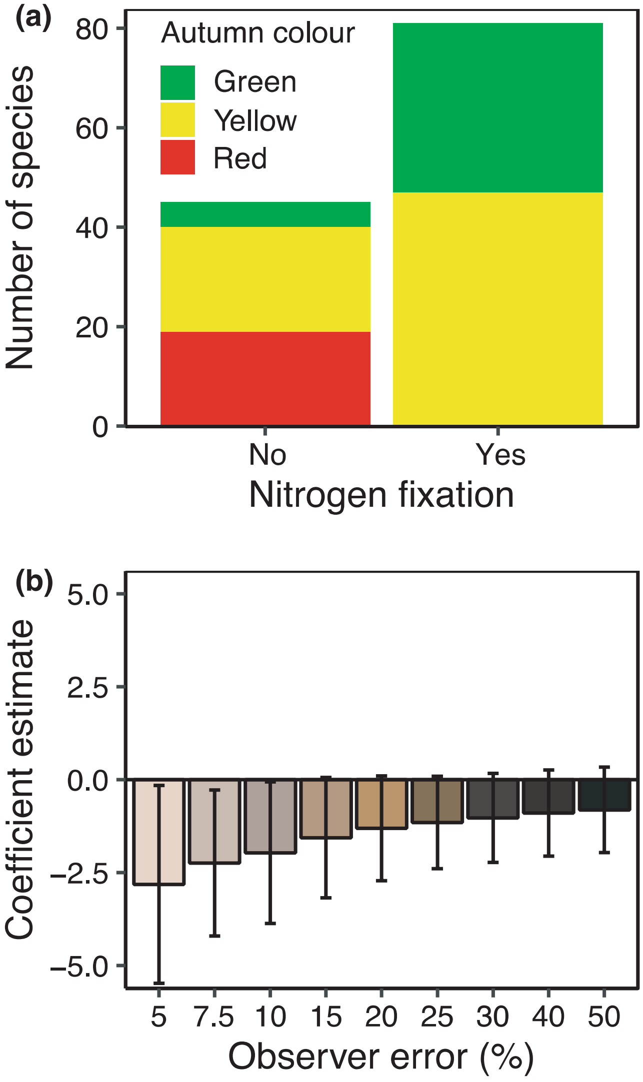

FIGURE 1 Nitrogen-fixing species do not turn red in autumn. (a) Autumn leaf colour in 126 species (55 genera, 22 families) of deciduous trees and shrubs from throughout the Northern Hemisphere, including the 55 species studied by Peña-Novas and Archetti (2021). In total, 81 (31 genera, 8 families) have nitrogen-fixing symbionts. See Table 1 for species and family names, autumn colour and nitrogen fixation ability. (b) Coefficient estimates (effective posterior means +95% credible intervals) for the effects of species-specific N-fixation ability on autumn leaf colouration (coded as binary variable of whether the leaves of a species turn red in autumn or not). Negative estimates indicate a lower probability of red colouration in species lacking the ability to fix nitrogen. Linear HB models were applied, including family random effects to account for phylogenetic structure in the data. To account for the possibility of observer error (false negative of red species falsely identified as green or yellow), we forced a random subset of 5%, 7.5%, 10%, 15%, 20%, 25%, 30%, 40% or 50% of all study species to have red leaves (see Methods)

error percentage, we created 100 random datasets, resulting in a total of 900 datasets for which we ran the model. The effective posterior means for the respective relationships are shown in Figure 1b, whereby, for each observer error percentage, we first calculated the means of the 15 000 iterations kept after burn-in for each model run and then calculated the means of the 100 models. Because there are more N-fixers than non-N-fixers in our dataset and because 42% of the non-N-fixers already had red leaves, this approach of accounting for observer error is conservative as it assumes that proportionately more N-fixers were falsely identified as non-red. The range of percentages of observer error allowed us to additionally identify up to which error the effect of N fixation on autumn leaf colouration is still visible and significant. All analyses were performed in R 4.1.0 (R Core Team, 2021) and the R code is provided in the electronic Supporting Material.

3 | RESULTS

Results show that none of the nitrogen-fixing species have anthocyanin-red autumn leaves (Figure 1a; Table 1). Instead, the leaves of 58% of the nitrogen fixers turn yellow in autumn, whereas 42% stay green. Of the non-nitrogen-fixing species, 42% have anthocyanin-red autumn leaves, 47% have yellow autumn leaves and 11% stay green. The HB model confirmed that leaves of N-fixing species are less likely to turn red in autumn than those of species that do not form symbioses with N-fixing bacteria. As expected, this effect declined with an increase in observer error (false negative), but even at an observer error rate of 50% a negative trend was still visible and the effect was significant (95% credible intervals consistently below zero) up to an observer error of 15% (Figure 1b).

4 | DISCUSSION

These results provide indirect support for the hypothesis that nitrogen limitation plays a role in anthocyanin production in autumn leaves: when ample nitrogen is available from nitrogen-fixing symbionts, the benefits of anthocyanin-derived photoprotection apparently do not outweigh the costs of anthocyanin, and hence no nitrogen-fixing species produces red leaves in autumn. In non-nitrogen fixing species, by contrast, adaptation to low-nutrient soils, such as are common in Eastern North America (Hughes et al., 2021), may rely on a strategy of early remobilization of leaf nutrients, including those used in chlorophyll, which may include the accumulation of vacuolar anthocyanins for photoprotection in senescing leaves. It would be worth testing if there are continental differences in the frequency or abundance of nitrogen-fixing species in North American versus European floras on poor soils. The continental distribution of species with different autumn senescing strategies (in terms of yellow, red, or green leaf pigments) has been tabulated in earlier studies (Renner & Zohner, 2020: Table S1), but the relative frequency and habitat-distribution of nitrogen-fixing symbioses in Asia, Europe and the Americas awaits quantification.

While nitrogen-poor soils and high autumn light intensity in Eastern North America are plausible hypotheses explaining the ‘overabundance’ of anthocyanin in the North American autumn, one other hypothesis concerning yellow or red fall colours should

TABLE 1 Anthocyanin production in autumn in 126 tree and shrub species (55 genera, 22 families) from different temperate forests, with the presence or absence of nitrogen-fixing symbioses coded from the sources cited in the footnote at the bottom of this table

Species, Family	Autumn colour	Nitrogen fixation
Acer campestre, Sapindaceae	Yellow	No
Acer freemanii, Sapindaceae	Red	No
Acer maximowiczianum, Sapindaceae	Red	No
Acer miyabei, Sapindaceae	Yellow	No
Acer rubrum, Sapindaceae	Red	No
Acer saccharinum, Sapindaceae	Red	No
Acer saccharum, Sapindaceae	Red	No
Aesculus flava, Sapindaceae	Red	No
Albizia julibrissin, Fabaceae	Green	Yes
Albizia lebbeck, Fabaceae	Green	Yes
Alnus cordata, Betulaceae	Green	Yes
Alnus firma, Betulaceae	Green	Yes
Alnus glutinosa, Betulaceae	Green	Yes
Alnus hirsuta, Betulaceae	Green	Yes
Alnus incana, Betulaceae	Green	Yes
Alnus japonica, Betulaceae	Green	Yes
Alnus maritima, Betulaceae	Green	Yes
Alnus maximowiczii, Betulaceae	Green	Yes
Alnus nitida, Betulaceae	Green	Yes
Alnus oblongifolia, Betulaceae	Green	Yes
Alnus orientalis, Betulaceae	Green	Yes
Alnus rhombifolia, Betulaceae	Green	Yes
Alnus rubra, Betulaceae	Green	Yes
Alnus serrulata, Betulaceae	Green	Yes
Alnus viridis, Betulaceae	Green	Yes
Amorpha canescens, Fabaceae	Yellow	Yes
Amorpha fruticosa, Fabaceae	Yellow	Yes
Amorpha glabra, Fabaceae	Green	Yes
Amorpha nana, Fabaceae	Yellow	Yes
Asimina triloba, Annonaceae	Green	No
Berchemia racemosa, Rhamnaceae	Green	Yes
Betula alleghaniensis, Betulaceae	Yellow	No
Betula lenta, Betulaceae	Yellow	No
Betula nigra, Betulaceae	Yellow	No
Betula papyrifera, Betulaceae	Yellow	No
Betula populifolia, Betulaceae	Yellow	No
Caragana arborescens, Fabaceae	Yellow	Yes
Caragana decorticans, Fabaceae	Yellow	Yes
Caragana erinacea, Fabaceae	Yellow	Yes
Caragana sinica, Fabaceae	Yellow	Yes
Caragana tibetica, Fabaceae	Green	Yes
Caragana ussuriensis, Fabaceae	Yellow	Yes
Carpinus betulus, Betulaceae	Yellow	No
Carpinus caroliniana, Betulaceae	Red	No
Catalpa bignonioides, Bignoniaceae	Yellow	No
Celtis occidentalis, Cannabaceae	Green	No
Cercis racemosa, Fabaceae	Yellow	Yes
Cladrastis kentukea, Fabaceae	Yellow	Yes
Cladrastis sinensis, Fabaceae	Yellow	Yes
Colletia hystrix, Rhamnaceae	Yellow	Yes
Colletia paradoxa, Rhamnaceae	Yellow	Yes
Colutea arborescens, Fabaceae	Yellow	Yes
Colutea persica, Fabaceae	Yellow	Yes
Crataegus viridis, Rosaceae	Green	No
Psorothamnus spinosus, Fabaceae	Yellow	Yes
Diospyros virginiana, Ebenaceae	Yellow	No
Elaeagnus angustifolia, Elaeagnaceae	Yellow	Yes
Elaeagnus argentea, Elaeagnaceae	Green	Yes
Elaeagnus cuspida, Elaeagnaceae	Green	Yes
Elaeagnus ebbingei, Elaeagnaceae	Yellow	Yes
Elaeagnus multiflora, Elaeagnaceae	Green	Yes
Elaeagnus umbellata, Elaeagnaceae	Yellow	Yes
Erythrina crista-galli, Fabaceae	Yellow	Yes
Erythrina variegata, Fabaceae	Yellow	Yes
Fagus grandifolia, Fagaceae	Yellow	No
Fagus sylvatica, Fagaceae	Yellow	No
Genista germanica, Fabaceae	Yellow	Yes
Genista hispanica, Fabaceae	Yellow	Yes
Genista lydia, Fabaceae	Yellow	Yes
Ginkgo biloba, Ginkgoaceae	Yellow	No
Gleditsia japonica, Fabaceae	Yellow	Yes
Gleditsia triacanthos, Fabaceae	Yellow	Yes
Halimodendron halodendron, Fabaceae	Yellow	Yes
Hippophae rhamnoides, Elaeagnaceae	Yellow	Yes
Indigofera potaninii, Fabaceae	Yellow	Yes
Laburnum alpinum, Fabaceae	Yellow	Yes
Laburnum anagyroides, Fabaceae	Green	Yes
Laburnum watereri, Fabaceae	Green	Yes
Lespedeza bicolor, Fabaceae	Yellow	Yes
Liriodendron tulipifera, Magnoliaceae	Yellow	No
Lupinus arboreus, Fabaceae	Green	Yes
Maackia amurensis, Fabaceae	Yellow	Yes
Magnolia acuminata, Magnoliaceae	Yellow	No
Magnolia virginiana, Magnoliaceae	Green	No

TABLE 1 (Continued)

Species, Family	Autumn colour	Nitrogen fixation
Metasequoia glyptostroboides, Cupressaceae	Red	No
Myrica gale, Myricaceae	Yellow	Yes
Myrica pensylvanica, Myricaceae	Green	Yes
Ostrya virginiana, Betulaceae	Yellow	No
Paulownia tomentosa, Paulowniaceae	Green	Yes
Petteria ramentacea, Fabaceae	Yellow	Yes
Platanus occidentalis, Platanaceae	Green	No
Populus deltoides, Salicaceae	Yellow	Yes
Populus nigra, Salicaceae	Yellow	Yes
Populus tremuloides, Salicaceae	Yellow	Yes
Prosopis glandulosa, Fabaceae	Green	Yes
Prosopis pubescens, Fabaceae	Green	Yes
Prosopis velutina, Fabaceae	Green	Yes
Prunus yedoensis, Rosaceae	Red	No
Quercus bicolor, Fagaceae	Red	No
Quercus imbricaria, Fagaceae	Red	No
Quercus lyrata, Fagaceae	Red	No
Quercus macrocarpa, Fagaceae	Yellow	No
Quercus michauxii, Fagaceae	Red	No
Quercus muehlenbergii, Fagaceae	Red	No
Quercus velutina, Fagaceae	Red	No
Rhamnus alpina, Rhamnaceae	Yellow	Yes
Rhus copallinum, Anacardiaceae	Red	No
Robinia ambigua, Fabaceae	Green	Yes
Robinia hispida, Fabaceae	Green	Yes
Robinia kelseyi, Fabaceae	Green	Yes
Robinia neomexicana, Fabaceae	Yellow	Yes
Robinia pseudoacacia, Fabaceae	Yellow	Yes
Robinia slavinii, Fabaceae	Green	Yes
Salix sepulcralis, Salicaceae	Yellow	Yes
Sophora davidii, Fabaceae	Yellow	Yes
Sophora japonica, Fabaceae	Yellow	Yes
Sophora tetraptera, Fabaceae	Yellow	Yes
Sorbus alnifolia, Rosaceae	Red	No
Styrax obassia, Styracaceae	Yellow	No
Tilia americana, Malvaceae	Yellow	No
Tilia cordata, Malvaceae	Yellow	No
Ulmus parvifolia, Ulmaceae	Red	No
Ulmus rubra, Ulmaceae	Yellow	No
Wisteria sinensis, Fabaceae	Yellow	Yes
Wisteria venusta, Fabaceae	Yellow	Yes
Zelkova serrata, Ulmaceae	Red	No

Note: Literature used to source N fixation: Cornelissen (1996); Craine et al., (2009); Green (2009); Kattge et al., (2009); Laughlin et al., (2011); Liebergesell et al., (2016); Preston et al., (2006); Reich et al., (2008); Tedersoo et al., (2018); Werner et al., (2014); Wright et al., (2004).

be retired. This is the (nongeographically explicit) idea that autumn tree colours are a handicap signal by which individual trees signal their defensive commitment against autumn-colonizing insect pests; insects are expected to be averse to the brightest tree individuals and to preferentially colonize the least defensive hosts (Hamilton & Brown, 2001). Hamilton and Brown analysed aphid species diversity on 262 tree species from North America and Great Britain and found that yellow (not red) colouration was significantly positively correlated with the presence of aphids. When they restricted the analysis to taxonomically-specialized aphids, the correlation between aphid presence and yellow was strengthened and a weak positive correlation between 'autumnal redness' and aphid diversity emerged. Red and yellow thus appeared to attract aphids, but as the authors state (2001, p. 1492) 'the use of comparative data to investigate the signalling hypothesis is complicated by the lack of comparative data on the damage sustained by specific tree aphid species as a result of autumnal infestation with aphids'. The authors' concern about the lack of data on the correlation between aphid overwintering stages and next year's damage was well-founded, and such data are still lacking. Experts in insect vision so far nohave discredited the notion that autumn leaf colours could be an efficient means to deter aphids(Chittka & Döring, 2007).

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CONFLICT OF INTEREST

The authors have not conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data are contained in Table 1 and the Supporting Materials.

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SUPPORTING INFORMATION

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