

RESEARCH ARTICLE

Chlorophyll and topographic patterns demonstrate stress conditions drive the brightness of autumn leaf colour

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Keywords

Fagus crenata Blume; multispectral drone; normalized difference red edge index; topographic position index; visible atmospherically resistant index (VARI).

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[Correction added on 11 March 2025, after first online publication: The copyright line was changed.]

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ABSTRACT

- Autumn leaf colour brightness is an important cultural ecosystem service. As its spatial patterns and ecophysiological mechanisms remain unclear, we analysed relationships among autumn leaf colour brightness, late summer chlorophyll content, and topographic position in both canopy-based micro-scale analysis and site-based macro-scale analysis.
- Multispectral drone observations were made in three *Fagus crenata* forests at elevations of 300, 600, and 900 m in Niigata Prefecture, Japan. In a drone-acquired digital surface model of canopy area distribution, we analysed the canopy-averaged autumn leaf colour brightness, four vegetation indices, topographic position index, and elevation.
- The macro-scale pattern showed brighter yellow leaves at lower elevations, suggesting the effect of temperature through productivity or evaporative stress. The micro-scale pattern showed brighter yellow leaves in canopies that had a low late summer chlorophyll content, or that grew on ridges. The negative correlation between autumn leaf colour and chlorophyll content suggests that low-chlorophyll trees experience stresses (e.g. irradiance, desiccation, senescence) that induce higher carotenoid content to defend against such stresses. Increased autumn leaf coloration on ridges is consistent with a stress gradient.
- Although further research is needed to reveal the underlying physiological and ecological mechanisms, autumn leaf colour brightness has different meanings at different scales and thus has potential not only as a cultural ecosystem service but also in forest management through early detection of stress.

INTRODUCTION

In northern cool temperate regions, autumn is clothed with colourful red, yellow, and orange foliage in deciduous forests. This autumn leaf colouring is an important cultural ecosystem service (Hernandez-Morcillo *et al.*, 2013; Fox *et al.*, 2021), providing scenic views and recreation opportunities (Zhang *et al.*, 2017). It also has commercial importance for tourism (Ge *et al.*, 2013), estimated to create USD 400 million a year in the autumn foliage tourism industry in parts of the northeastern USA and southeastern Canada (Hall *et al.*, 2011). Many web pages of autumn leaf colouring report or project the stage of leaf colouring (e.g. <https://smokymountains.com/fall-foliage-map/>, accessed on 2023/8/14). The timing of leaf colouring has economic importance when it corresponds with holidays or festivals (Wang *et al.*, 2017). Correspondence with such events is expected to change with climate change, potentially increasing or decreasing income (Liu *et al.*, 2019).

Previous works focused on the timing (phenology) of autumn leaf colouring. The main driver of the timing of leaf colouring or senescence was reported to be temperature (Heide & Prestrud, 2005; Fu *et al.*, 2018; Liu *et al.*, 2018), followed by day length, especially at high latitudes (Fracheboud *et al.*, 2009; Soolanayakanahally *et al.*, 2013), and drought (Lim

et al., 2007). On the other hand, the ecological meaning (evolutionary explanation) of red autumn leaf colouring is still under discussion. Photoinhibition is considered the main function, increasing nutrient resorption into the stem or roots (Hoch *et al.*, 2003; Kitao *et al.*, 2022), but a counterargument suggests that anthocyanin synthesis can dispose of carbohydrates thus relieving photosynthetic control (Mattila & Tyystjarvi, 2023). In addition, red leaves might prevent or reduce insect herbivory attacks (Rolshausen & Schaefer, 2007; Doring *et al.*, 2009). However, the ecological meaning of yellow autumn leaf colouring is still not clear. To approach such an ultimate factor as yellow autumn leaf colouring, analyses of proximate factors are needed as a first step.

Previous studies have scarcely considered the brightness of autumn leaf colours (Koide *et al.*, 2019) despite their importance for human interest (Zhang *et al.*, 2017). Although Xie *et al.* (2018) assessed red colour brightness, further investigation of the physiological mechanisms is needed because a year with no autumn colour was reported in Japanese alpine shrubs (Koide *et al.*, 2019). Autumn reds or yellows are a result of the accumulation and concentration of anthocyanins and carotenoids, with a simultaneous reduction in chlorophylls (Junker & Ensminger, 2016). Temperature and solar radiation determine the physiological responses of these pigments and the

brightness of autumn leaf colour (Schaberg *et al.*, 2003; Archetti *et al.*, 2013; Xie *et al.*, 2018). Stress factors, such as irradiance, drought, nutrient deficiency, salinity, and biotic agents, are also related to pigment dynamics (Herbinger *et al.*, 2007; Nestola *et al.*, 2018; Gomez-Sagasti *et al.*, 2023). These reports were based mainly on sampling by individuals or pot experiments, and broad-scale observations and comparisons are still lacking, hindering landscape-level studies of the ecophysiological mechanisms.

For broad-scale observations, remote sensing techniques are essential. Satellite observation is a powerful tool (Parazoo *et al.*, 2014; Yebra *et al.*, 2015; Nagai *et al.*, 2016), but its coarse spatiotemporal resolution makes it difficult to distinguish daily changes in canopy colour. Drone observation offers a suitable spatial resolution for study at the individual canopy level, and recent technical improvements in multispectral drone observations (Hardenbol *et al.*, 2021; Meivel & Maheswari, 2022) can provide meaningful data to approach the ecophysiological mechanisms behind autumn leaf colouring. Multispectral drones observe not only the RGB colour bands but also the near-infrared (NIR) and red edge colour bands simultaneously. Their use enables us to calculate several vegetation indices that reflect amounts of leaf colour pigments. Many vegetation indices are used to monitor leaf nitrogen or chlorophyll content, a basic parameter of photosynthetic productivity (Nestola *et al.*, 2018). Multispectral drone observation enables us to clarify relationships between autumn leaf colour brightness and chlorophyll content at an individual level, considering abiotic and biotic environmental effects. However, our literature review found no such approach has been used.

We aimed to clarify the spatial pattern of autumn leaf colour brightness at the individual level and effects of possible environmental factors on it. We used Siebold's beech (*Fagus crenata* Blume) as a target species because of its carotenoid-based yellow autumn leaf colouring (Naramoto *et al.*, 2006; Yamazaki *et al.*, 2007). This species is dominant in Japanese cool-temperate deciduous forests, especially on the heavily snowy Sea of Japan side, providing an ideal situation in which to compare individual canopies within a species. Based on previous knowledge, we hypothesize a positive correlation between autumn leaf colour and summer chlorophyll content. A high chlorophyll content potentially increases productivity, so that large amounts of yellow carotenoids (brighter autumn leaf colour) can occur in such individuals. This hypothesis is consistent with previous reports of high amounts of both carotenoids and chlorophylls under high light (Hansen *et al.*, 2002; Wieser *et al.*, 2003; Herbinger *et al.*, 2007). Alternatively, a negative correlation between autumn leaf colour and summer chlorophyll content might also be expected. Although other physiological systems or anatomical structures play important roles

(Arena *et al.*, 2013), carotenoids also defend against several stress conditions, including high irradiance, drought, extreme temperatures, and biotic attacks (Gomez-Sagasti *et al.*, 2023), and tend to increase in such conditions (Herbinger *et al.*, 2007; Nestola *et al.*, 2018). Under these less productive conditions, the chlorophyll or leaf nitrogen content is predicted to decrease (Galle & Feller, 2007; Wang *et al.*, 2021), leading to a negative relationship between autumn leaf colour brightness and summer chlorophyll content. To reveal which pattern occurs in Japanese beech forests, we chose three different elevational sites, calculated vegetation indices in late summer and leaf colour brightness in autumn, and tested the two hypotheses while accounting for other possible factors, such as topographic conditions.

MATERIAL AND METHODS

Study sites

We chose study sites in the heavily snowy Sea of Japan side of Japan (Table 1, Fig. 1), which is characterized by the dominance of *F. crenata*, as deep snow protects beech fruits against attack by rodents (Homma *et al.*, 1999). Heavy pressure by deep snow (>1 m) suppresses other species, thus increasing the dominance of the snow-pressure-tolerant beech (Homma, 1997). This dominance (>80% of the stand basal area is covered by beech in this area (Shimano, 2006)) is ideal because it minimizes the effect of other species. We selected three study sites along an elevational gradient (Fig. 1) in secondary forests that have low anthropogenic disturbance. The highest elevation site (Amamizu-Tōge) is located at 900 m a.s.l. It includes a small catchment surrounded by ridges, with a shallow valley at the center, descending from west to east. It is relatively far from lowland settlements, suggesting low anthropogenic disturbance. Its broader crown area than at the other two sites also suggests less disturbance and an older population. The middle-elevation site (Rusuhara) is located at 600 m a.s.l. It is on a small ridge in a satoyama landscape, where active and abandoned terraced paddy fields are distributed. The lowest elevation site (Bijinbayashi) is located at 300 m a.s.l. It is on a gentle southeast slope in a satoyama landscape, surrounded by paddy fields and coniferous plantations. Although anthropogenic influences seem to be stronger here, the crown area at this site is almost the same as at the middle elevation site.

Drone observation of vegetation index and autumn leaf colouring

At the end of September 2022 (late summer), we acquired the vegetation index with a P4 Multispectral drone (DJI, Shenzhen,

Table 1. Environmental factors at each site.

Site	altitude [m]	temperature [°C]	precipitation [mm]	maximum snow depth [cm]	global solar radiation [MJ m ⁻²]
Amamizu-Tōge	900	8.1	2350.7	263	1280
Rusuhara	600	9.5	2447.3	240	1240
Bijinbayashi	300	10.7	2633.6	222	1220

Climate data are annual means (temperature, radiation) or sums (precipitation) and were obtained from the 2010 mesh climatic data (<https://niftp.mlit.go.jp/kj/gml/datalist/KsjTmplt-G02.html>, accessed 2023/8/14).

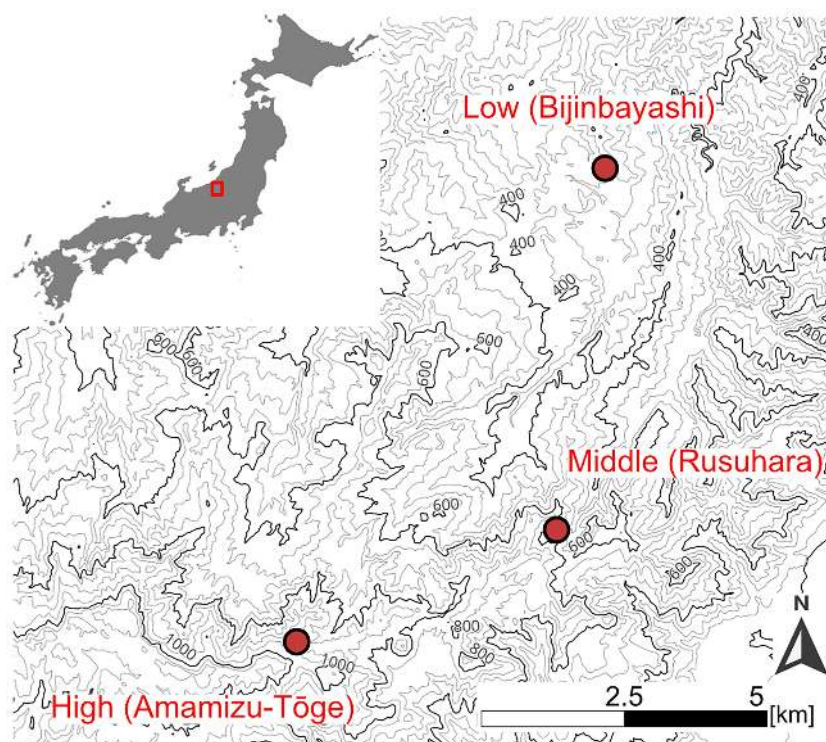


Fig. 1. Map of the three study sites in Niigata Prefecture, Japan.

China). This drone, equipped with a multispectral camera, observes in five colour bands: blue (450 ± 16 nm), green (560 ± 16 nm), red (650 ± 16 nm), red edge (730 ± 16 nm), and infrared (840 ± 26 nm). We chose late summer to capture the chlorophyll content just before autumn. Although chlorophyll content changes seasonally in the target species, late summer chlorophyll content was reported to be a maximum for the year (Awaya *et al.*, 2009), so we assume it is representative. The observation height was set at 130 m, and the overlap ratio was set at 90%.

In October and November, we acquired autumn leaf colour brightness with a Mavic Mini RGB drone (DJI). This drone does not contain red edge and infrared band observation, but it observes blue, green, and red bands, enabling analyses for autumn colour brightness in the VARI index in the latter part. We surveyed each site twice, 3–5 days apart. The survey timing was chosen as when the colour brightness was higher based on visual observation.

Analysis

We constructed a digital surface model (DSM) from the late summer data. Ortho-mosaic analysis upscaled the spatial resolution to 25 cm. Then we constructed a digital height model (DHM) as $DHM = DSM - DEM$, where DEM is a digital elevation model from the Geospatial Information Authority of Japan (<https://fgd.gsi.go.jp/download/menu.php>, accessed 2023/8/14) upscaled from 10 m to 25 cm for each site using the inverse-distance-weighted interpolation method.

To delineate drone image data for each canopy individual, we first detected the crown area of each individual in the DHM. The canopy-top grid point at each site was detected

using the variable window filter method (<https://search.r-project.org/CRAN/refmans/ForestTools/html/vwf.html>; accessed 2023/8/14). Crown areas were then detected using the marker-controlled watershed segmentation method (<https://search.r-project.org/CRAN/refmans/ForestTools/html/mcws.html>, accessed 2023/8/14). Since small crowns tend to have high variability, trees whose crown area was >50 m² were picked as target individuals for analyses.

Within each target individual's canopy area, we clipped out the autumn leaf colour and vegetation index images to calculate the average value of each index. Autumn leaf colour brightness was indexed as the VARI value ($VARI = (Red - Green) / (Red + Green - Blue)$), which has relatively stable performance under in-situ environmental fluctuations (Koide *et al.*, 2019). Note that here, and also in Koide *et al.* (2019), the numerator was converted from the original (i.e. $Green - Red$) to focus on red. We prepared four vegetation indices: the normalized difference vegetation index ($NDVI = (NIR - Red) / (NIR + Red)$), the green NDVI ($GNDVI = (NIR - Green) / (NIR + Green)$), the normalized difference red edge index ($NDRE = (NIR - RedEdge) / (NIR + RedEdge)$), and the leaf chlorophyll index ($LCI = (NIR - RedEdge) / (NIR + Red)$). We also calculated the canopy average elevation from the DEM data, but the elevation data were separately statistically standardized in each site to reveal micro-scale within-site individual elevation differences. Macro-scale elevation differences were treated by site factor, avoiding duplicating the meaning of each explanatory variable. We prepared a topographic position index (TPI) from the DEM data to analyse the effects of topography on autumn leaf colouring. This index shows whether the target cell is on a ridge or convex topography (positive value) or in a valley or concave topography (negative value). We then

excluded individuals whose canopy-average VARI was ≤ 0.05 , suggesting no autumn-coloured crown, from the later analyses. Drone-based images were created in DJI Terra v. 3.5.5 software. QGIS v. 3.28 software was used to analyse GIS data, and R statistical software v. 4.2.2 was used with the 'ForestTools', 'raster', and 'sf' packages.

Linear mixed models were constructed and compared using all combinations of the explanatory variables. We set the canopy-average VARI as the objective variable, the four vegetation indices, canopy-average elevation, and canopy-average TPI as explanatory variables, and the site factor as a random intercept. The best model was selected using Akaike's Information Criterion. To remove multi-collinearity, we removed explanatory variable combinations which had significant correlations among them. To detect significant differences in VARI, NDRE, and TPI among the three sites, the Kruskal-Wallis test was conducted, and its effect sizes also calculated considering a relatively big sample size ($n = 1825$). R statistical software v. 4.2.2 was used for statistical analysis with the 'lme4', 'lmerTest', 'car', and 'MuMIn' packages.

RESULTS AND DISCUSSION

Model selection

The model containing NDRE and TPI as explanatory variables best explained the canopy-average VARI (Table 2). Among the four vegetation indices, NDRE was selected, possibly because of its high representativeness of chlorophyll or nitrogen content, especially in the late growing season (Li *et al.*, 2014; Lo *et al.*, 2019). NDRE (summer leaf chlorophyll content) had a negative correlation with VARI (autumn leaf colour brightness; Fig. 2A), supporting our second hypothesis. This negative correlation was consistent at each site, suggesting that this relationship is common, at least in the range of our research sites. Pearson's R of the correlation between VARI and NDRE was -0.09 ($P < 0.05$, $n = 724$) at the highest site, -0.19 ($P < 0.001$, $n = 526$) at the middle site, and -0.07 ($P < 0.1$, $n = 575$) at the lowest site. A positive correlation between the topographic index (TPI) and VARI means a brighter yellow leaf colour on ridges (Fig. 2B). A significant correlation was observed at the lower two sites, 0.36 ($P < 0.001$, $n = 526$) at the middle site, and 0.19 ($P < 0.001$, $n = 575$) at the lowest site although it was not significant at the highest site ($R = 0.02$, $P > 0.1$, $n = 724$). While the TPI range was widest at the middle site, it was narrower at the lowest site than at the highest site (Fig. 3), suggesting that this inconsistency was not due to the difference in topographic range among the sites.

Site (macro-scale) differences in VARI, NDRE, and TPI

Macro-scale patterns in VARI, NDRE, and TPI differed among sites. VARI values decreased with increasing elevation (Fig. 3). Since autumn observation was intended to catch the maximum peak of brightness, this means that higher elevations never reach the brightness of lower sites, at least in this year. Lower sites are warmer, so autumn colour and temperature are correlated there, although the possibility of other factors should be considered. NDRE was almost the same among sites, which means that the amount or ratio of chlorophyll did not differ among sites, so chlorophyll content is not the driver of the

Table 2. Top 10 linear mixed models that explain individual autumn leaf colour brightness (VARI).

Model parameters	AIC	marginal R^2	conditional R^2
NDRE + TPI	-6247.9	0.032	0.601
LCI + TPI	-6246.8	0.032	0.599
TPI	-6235.0	0.024	0.6
NDRE + Elev + TPI	-6234.4	0.032	0.6
LCI + Elev + TPI	-6233.4	0.032	0.599
GNDVI + TPI	-6225.1	0.026	0.599
NDVI + TPI	-6223.9	0.025	0.596
Elev + TPI	-6221.1	0.024	0.599
GNDVI + Elev + TPI	-6211.5	0.026	0.599
NDVI + Elev + TPI	-6210.2	0.025	0.595

All models include site as a random factor. Marginal and conditional R^2 represent variance explained by fixed factors only and both fixed and random factors, respectively.

Elev, elevation; GNDVI, green NDVI; LCI, leaf chlorophyll index; NDRE, normalized difference red edge; NDVI, normalized difference vegetation index; TPI, topological position index.

macro-scale pattern. TPI had the broadest range in the middle site, followed by the highest and lowest sites. Although all three variables in Fig. 3 showed significant differences among sites under the Kruskal-Wallis test ($P < 0.001$ for all three variables), this might be affected by the large sample size ($n = 1825$). The effect size showed a large magnitude only in VARI ($\eta^2[H] = 0.466$) but moderate to small magnitude in NDRE (0.0644) and TPI (0.0464). These results suggest that the macro-scale VARI pattern is independent of NDRE and TPI.

Lower sites had higher VARI values (Figs. 2–4), creating a positive VARI–elevation correlation. This pattern of high carotenoid content at lower elevations is consistent with a report for European beech (*Fagus sylvatica*) in Poland (Kraj & Zarek, 2021). Among several environmental differences between our three sites, temperature seems to play an important role in this macro-scale pattern (Archetti *et al.*, 2013). Lower sites have warmer temperatures and thus likely higher productivity, creating a higher carotenoid content and brighter autumn leaf colour. Since the lowest site's temperature condition in the warmth index (WI: the sum of monthly mean temperature -5°C when the monthly mean temperature is above 5°C) is 87.4°C month and it is close to the warmer edge of the species distribution range (WI: $45\text{--}85^\circ\text{C}$ month; (Koide *et al.*, 2016)), this temperature condition is possibly too warm to show high productivity performance so caution is needed for this interpretation. On the other hand, warmer temperatures would also increase evaporation and thus the risk of desiccation or radiative stress (Crimmins *et al.*, 2011; Williams *et al.*, 2013), possibly prompting more allocation to carotenoids (Herbinger *et al.*, 2007; Nestola *et al.*, 2018; Gomez-Sagasti *et al.*, 2023). However, photoinhibitory damage to *F. crenata* was not evident, even under midday depression of net CO_2 assimilation rate (Iio *et al.*, 2004), so an explanation of the macro-scale VARI–temperature pattern needs further local research.

Among the other possible drivers, nitrogen can affect the macro-scale VARI pattern because lower sites may be closer to human activities where the nitrogen load can be higher,

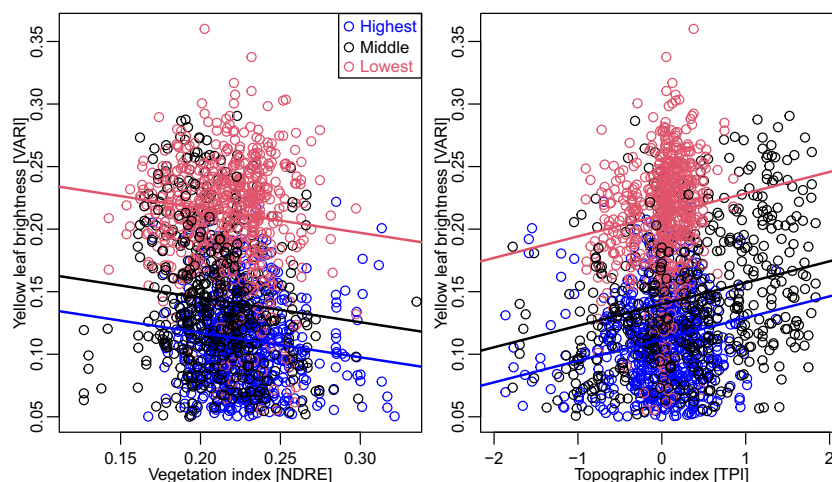


Fig. 2. Effects of NDRE (chlorophyll) and TPI (topography) on VARI (visible atmospherically resistant index: leaf colour brightness). Linear regressions were drawn according to the best model in Table 2, containing NDRE and TPI as explanatory variables and random intercepts for each site to predict VARI.

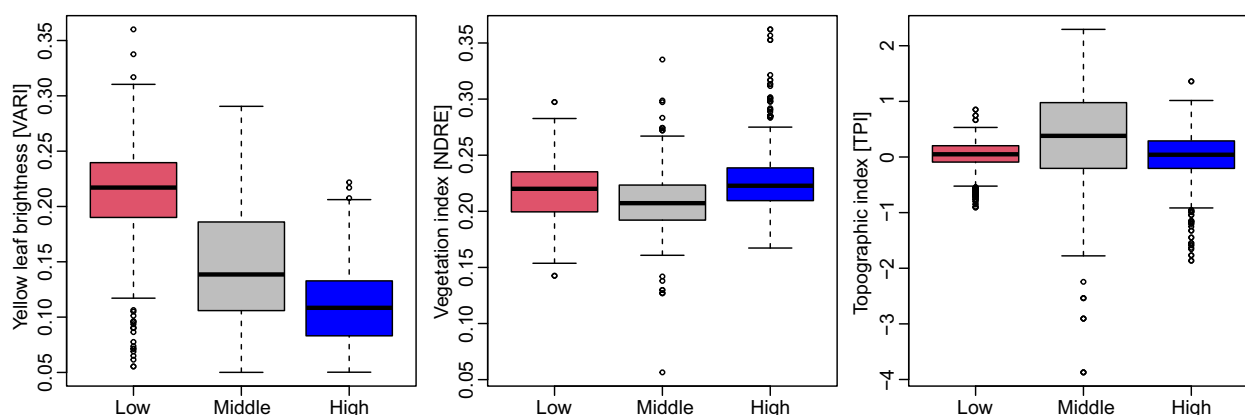


Fig. 3. Differences in VARI (leaf colour brightness), NDRE (chlorophyll), and TPI (topography) among sites.

possibly creating more productive conditions and increasing the amount of carotenoids. However, high nitrogen conditions would have little effect on our results, as fertilization experiments on *F. sylvatica* showed almost the same amounts of leaf pigments as in control samples (Teglia *et al.*, 2022). Ozone stress is another candidate, as anthropogenic ozone concentrations can be high at lower elevations. However, Herbinger *et al.* (2007) showed limited effects of ozone on leaf carotenoid content in *F. sylvatica* seedlings, so this factor is minor.

Individual (micro-scale) patterns at each site

Micro-scale individual patterns were consistent with the best model (Fig. 2), although each site had different ranges of VARI and TPI values (Figs. 3, 4). The highest site had the lowest VARI values (Fig. 4). VARI had no spatial pattern and no correlation with TPI. NDRE was higher in lower canopies and had a significant negative correlation with VARI ($R = -0.09$, $P < 0.05$, $n = 724$). The middle site had higher VARI on the ridges, and the ridges had slightly lower NDRE values, creating a negative VARI–NDRE relationship ($R = -0.19$, $P < 0.001$, $n = 526$). The lowest site had the highest VARI values. VARI

showed a significant spatial pattern with topography (VARI–TPI at the lowest site, $R = 0.19$, $P < 0.001$, $n = 575$), with higher values on the ridges. NDRE was lower in lower canopies.

The micro-scale individual-level pattern had a negative correlation of summer chlorophyll content (NDRE) with autumn colour brightness (VARI) (Table 2, Fig. 2). This means that low-NDRE (low-chlorophyll) individuals had higher VARI (brighter autumn colour), supporting our second hypothesis. This result seems to be inconsistent with previous work showing a higher foliar carotenoid content in chlorophyll-rich sun leaves than in chlorophyll-poor shade leaves (Hansen *et al.*, 2002; Herbinger *et al.*, 2007). However, our research compares the same sunny crown parts of different individuals, not sun and shade leaves in the same individual, and therefore different reasoning is required for our results. We assume that individual stress gradients would affect this micro-scale negative VARI–NDRE correlation. Xanthophylls (a part of carotenoids) restrict radiative energy (Lichtenthaler, 2007). Carotenoids are also associated with several stress conditions, such as drought, heat stress, biotic attacks, and senescence (Galle & Feller, 2007; Nestola *et al.*, 2018; Gomez-Sagasti

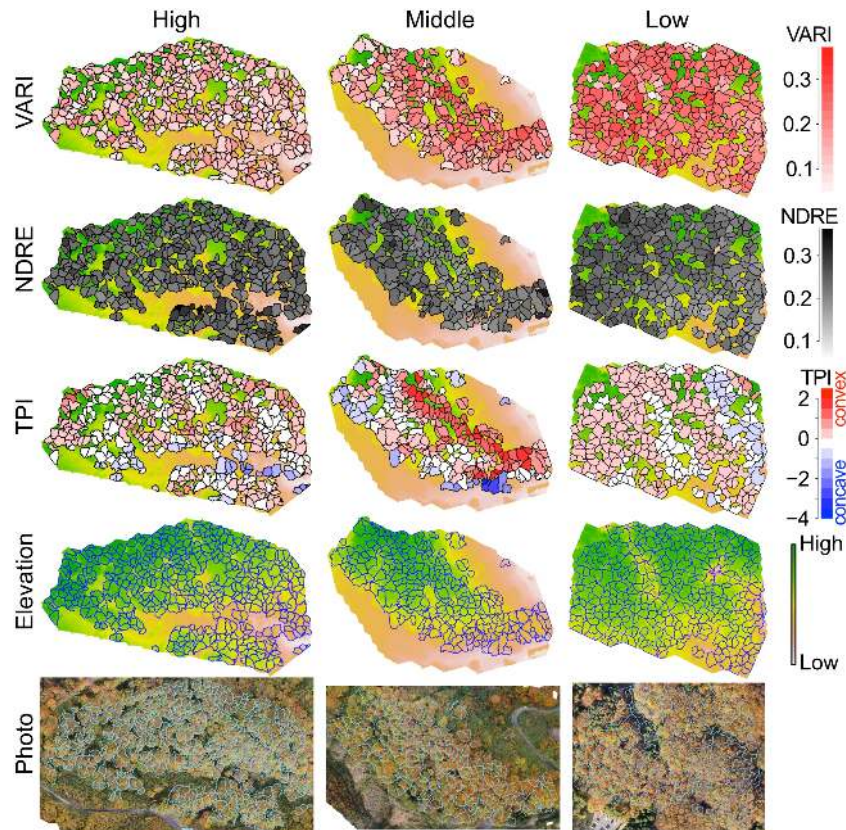


Fig. 4. Map of individual average VARI (leaf colour brightness), NDRE (chlorophyll), and TPI (topography) with elevation and ortho-mosaic drone imagery at the three sites.

et al., 2023). Thus radiative- or drought-stressed individuals should need more carotenoids (higher VARI) to persist under such conditions. Stress reduces productivity and thus possibly chlorophyll (Galle & Feller, 2007; Wang *et al.*, 2021), or promotes early reduction of chlorophyll (Morley *et al.*, 2020; Kraj & Zarek, 2021), reducing NDRE in summer (the timing of our research). Although the detailed mechanism is unclear, this stress gradient seems to drive the observed negative NDRE–VARI correlation.

This stress gradient explanation is consistent with topographical effects, especially at the middle site, with the higher VARI and lower NDRE on the drier and brighter ridge (Figs. 2, 4). Unexpectedly, we did not find reports of the topographic locations of bright autumn colours in our literature review. We consider that the necessity for high-resolution images (e.g. around several meters) at a specific timing (the autumn colour season spans only 2–3 weeks) would omit satellite data, which in turn omits cloud cover. Drone observation techniques would match this spatiotemporal resolution, but it is a relatively new methodology that is not yet frequently used in autumn leaf colour studies. However, our work shows the importance of topographic effects on autumn colour brightness (Figs. 2, 4). Furthermore, TPI was selected in all top 10 models (Table 2), suggesting the higher importance of TPI than of NDRE in explaining VARI. This result strengthens the stress gradient explanation, but further research on ecophysiological mechanisms in the topographic context is still needed.

Limitations

Although we tried to include the seasonal shift of optical indices and related physiological conditions, our observation period was limited. NDRE was acquired during late summer, but chlorophylls and carotenoids are synthesized in spring (Lichtenthaler, 2007; Junker & Ensminger, 2016). The spring-to-summer vegetation index of the current year or the previous year possibly plays a more important role in VARI. This point should be investigated, although we think that the stress-altering explanation remains valid, considering the VARI–TPI relationship (Figs. 2, 4). Also, although we focused on the peak timings of chlorophyll content and autumn colour brightness, temporally dense and simultaneous drone observations for both NDRE (with other vegetation indices) and VARI are ideal. This care for seasonal changes should be a future task. The pattern of VARI can differ with the timing of observations and of peak VARI among individual trees. However, we plotted VARI twice and found almost the same pattern (Table S1), so this effect seems to be minor.

There are several indices to explain carotenoid or carotenoid/chlorophyll ratio (e.g. PRI: Photochemical reflectance index, CCI: Chlorophyll carotenoid index, SIPI: Structure intensive pigment index, PSRI: Plant senescence reflectance index, CCRI: Carotenoid chlorophyll ratio index (Wong *et al.*, 2019; Song & Wang, 2022)), but we could not use these indices because the observed colour band did not match with

them. VARI is not a direct index of carotenoids, so further analyses with these indices would be ideal.

Our drone-based remote sensing lacked ground truth observations of physiological parameters. Periodic measurements of leaf pigment amounts and several parameters of photosynthesis under different stress factors would be desirable in understanding the detailed mechanisms of the macro- and micro-scale VARI patterns. Since our results are all based on correlations, such detailed temporal observations are ideal for checking proximate causation. However, considering the large effort required, we omitted such ground observations from our current research, but this should be investigated in the future.

CONCLUSION

The macro-scale pattern of brighter autumn leaf colour at lower sites should point to possible relationships with macro-scale factors, such as climate change. If temperature is very important in this macro-scale pattern, future warming will cause an overall shift of bright colour zones. The bright colour's vulnerability or future shifts of the zones should be assessed on a broad spatial scale for sustainable use of the cultural ecosystem service. The bright leaf colour is important not only for cultural and economic features but also for forest management and conservation, considering its possible function as an alert for stress conditions. By avoiding or converting stressed sites, this signal has potential for wise use in forest management for some specific targets (e.g. carbon storage), and also for forest conservation for endangered local populations or genotypes.

Apart from the macro-scale pattern, micro-scale topographic or micro-environmental conditions also altered the leaf colour brightness. This could help find local hotspots for ecotourism and stressed individuals to prevent forest losses. However, since the bright colour has double meanings, as positive for ecotourism and negative for stress condition, local-scale forest management should select which phase to consider in each site and create a regionally well-balanced policy. The drone-based individual-level assessment can contribute to arguing and

creating such selection. Spatial conservation prioritization tools (e.g. Takenaka *et al.*, 2021) would also be useful for smooth and quantitative assessment.

Research on autumn leaf colour brightness is still scarce (Koide *et al.*, 2019), but can provide multiple new viewpoints, as suggested here. Although further research is needed to reveal the physiological and ecological mechanisms, autumn leaf colour brightness has potential for analysing wide research topics and combining these topics to create harmonized forest management.

AUTHOR CONTRIBUTIONS

DK: Conceptualization, Data Curation, Funding Acquisition, Investigation, Methodology, Project Administration, Resources, Software, Visualization, Writing – Original Draft Preparation, Writing – Review & Editing. MK: Investigation, Resources, Writing – Review & Editing.

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SUPPORTING INFORMATION

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

Data S1: Supporting Information.

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