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Global patterns and a latitudinal gradient of flower disparity: perspectives from the angiosperm order Ericales.

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Summary

- Morphological diversity (disparity) is an essential but often neglected aspect of biodiversity. Hence, it seems timely and promising to re-emphasize morphology in modern evolutionary studies. Disparity is a good proxy for the diversity of functions and interactions with the environment of a group of taxa. In addition, geographical and ecological patterns of disparity are crucial to understand organismal evolution and to guide biodiversity conservation efforts.
- Here, we analyse floral disparity across latitudinal intervals, growth forms, climate types, types of habitats, and regions, for a large and representative sample of the angiosperm order Ericales.
- We find a latitudinal gradient of floral disparity and a decoupling of disparity from species richness. Other investigated factors are inter-correlated and we find the highest disparity for tropical trees growing in African and South American forests.
- Explanations for the latitudinal gradient of floral disparity may involve the release of abiotic constraints and the increase of biotic interactions towards tropical latitudes, allowing tropical lineages to explore a broader area of the floral morphospace. Our study confirms the relevance of biodiversity parameters other than species richness and is consistent with the importance of species interactions in the tropics in particular with respect to angiosperm flowers and their pollinators.

Key words

Angiosperms, biodiversity, Ericales, flower morphology, latitudinal gradient, morphospace, disparity, diversity.

Introduction

Life on Earth is distributed unevenly due to varied geological and climatic conditions over time and space. In addition to these abiotic conditions, dynamics of speciation, extinction, migration and biotic interactions likely play important roles in shaping species richness and species composition in different regions and communities (Gaston, 2000; Jablonski *et al.*, 2017; Schluter & Pennell, 2017). Generally, species richness decreases with altitude, ocean depth, and latitude (Vamosi & Vamosi, 2010; Hillebrand, 2004; Kerkhoff *et al.*, 2014; Brown, 2014; Tomašových *et al.*, 2016; Jablonski *et al.*, 2017). In particular, the origin and unevenness of the latitudinal gradient of species richness has generated extensive debates, and many potential explanatory factors have been proposed including temperature, climate stability, biotic interactions, and available energy (e.g. mean summer temperature). As a general trend, all of these factors increase towards tropical latitudes (Jablonski *et al.*, 2017; Brown, 2014; Pianka, 1966; Rohde, 1992; Mittelbach *et al.*, 2007; Mannion *et al.*, 2014; Belmaker & Jetz, 2015; Fine, 2015; Pontarp *et al.*, 2018).

In addition to species number, biodiversity includes aspects such as phylogenetic diversity, morphological diversity, dominance and rarity of species as well as the diversity of their ecosystem functions (Hillebrand *et al.*, 2018; Stevens & Tello, 2018). On a global scale, our knowledge about these additional aspects is fragmentary at best (Gaston, 2000). In particular, we still have only a very limited understanding of the geographic and ecological distribution of functional and of morphological diversities (for plants see e.g. Hillebrand *et al.*, 2018; Lupia, 1999; Swenson, 2012; Cornwell *et al.*, 2014; Chartier *et al.*, 2014; Zanne *et al.*, 2014; Chartier *et al.*, 2017; Mander, 2018; Weiser *et al.*, 2018). *Functional diversity* summarises traits predicting growth and survival rates (for plants: Cornwell *et al.*, 2014; Swenson & Enquist, 2007; Swenson *et al.*, 2012), while morphological diversity, also called *disparity*, is used to quantify and compare the variability of organisms belonging to a clade, or a group of taxa (Foote, 1999; Erwin, 2007; Minelli, 2015). Disparity is calculated from a multidimensional set of morphological traits and can be estimated by different indices such as, for example, the *range* (the largest difference between two taxa in a group), the *total variance* (the sum of variances of all characters), or the *mean character difference* (the average difference among taxa in a group; Erwin, 2007; Foote, 1999; Wills *et al.*, 1994; Ciampaglio *et al.*, 2001). The choice of disparity index depends on sample size, number and type of traits, and on the proportions of missing data in the morphological matrix (Ciampaglio *et al.*, 2001). Furthermore, the interpretation of disparity patterns strongly depends on the phylogenetic and geographic scale investigated, and, importantly, on the biological functions of the traits disparity estimates are based on.

For angiosperms, a central aspect of structural and functional diversity lies in the richness of biotic interactions and reproductive strategies, both of which are largely tied to their reproductive units, i.e. their flowers. Flowers produce and protect the gametes, they are the place for pollination and

fertilization, and, finally, they produce fruits and seeds that disperse and propagate. Most angiosperms are pollinated by animals and their sexual reproduction is thus tightly linked to plant-pollinator interactions. Changes in floral morphology, therefore, directly affect fitness and can also lead to speciation through reproductive isolation (Grant, 1994; Harder & Barrett, 2006; Reyes *et al.*, 2015; Baack *et al.*, 2015).

Floral disparity and its distribution have rarely been quantified (reviewed in Chartier *et al.*, 2014). For the large, diverse, and globally distributed angiosperm order Ericales (Rose *et al.*, 2018), we have earlier shown that, with some exceptions, clade disparity generally increases with clade species richness. We also found that floral disparity was not correlated with clade crown age (Chartier *et al.*, 2017). The two families accounting for most of the disparity in the order were Lecythidaceae (16% partial disparity; Brazil nut family) and Sapotaceae (14% partial disparity; shea tree family), corresponding to 3% and 9%, respectively, of the order's species richness (Chartier *et al.*, 2017). Plants in both tropical families typically grow as trees, the flowers of which are most probably pollinated by diverse types of animals (Kubitzki, 2004). It is thus likely that, in addition to species richness, patterns of floral disparity in the order are partly shaped by ecological and geographical factors. Here, we investigate whether there is a latitudinal gradient of floral disparity in Ericales. As outlined above, we might expect such a gradient because biotic interactions are more diverse, and species richness is higher in the tropics. In addition, we investigate and compare the variation of floral disparity among climate types, geographic regions, ecosystems (type of habitat), and life modes (plant growth form) to find other potential factors explaining global patterns of floral disparity in Ericales.

Material and methods

All analyses were performed using the software R v.3.0.0 (R Core Team, 2016). Functions are referred to in the following format: *function name*{*package name*}. A more detailed version of these methods is available as Supplementary Information (SI).

Taxon sampling

We used the taxon sampling from Chartier *et al.* (2017). This dataset describes 380 species belonging to 274 genera (79.5 % of the 346 genera of Ericales), sampled across the 22 families of Ericales (Rose *et al.*, 2018; Schönenberger *et al.*, 2005). Our aim was to give the best representation possible of each taxonomic group, and of the morphological variation found in the whole order.

Morphological matrix

To estimate morphological diversity (disparity), we used the morphological dataset from Chartier *et al.* (2017). This dataset consists of 36 morphological characters describing the anthetic flower for all sampled species. The data were scored using the database PROTEUS (Sauquet, 2019). The morphological matrix contains a total of 12,512 data entries (13.4 % missing data) and is available in the online supplementary material of Chartier *et al.* (2017).

Factor matrix

All sampled species were additionally coded for the four following factors: *growth form*, *habitat*, *climate type*, and *region*. In this manuscript, we use abridged expressions such as « floral disparity of trees », which should be understood as « floral disparity in species displaying an arborescent growth form ».

For each factor, the assignment of each species to one or more categories was made retrieving information from the literature cited in Chartier *et al.* (2017), and by crossing this information with the maps and descriptions from Cox (2001), Peel *et al.* (2007), and Loarie *et al.* (2009). This new dataset is available as *SI* (“Dataset.xlsx”) and stored in the online database PROTEUS (Sauquet, 2019), with at least one bibliographic reference linked to each entry. It contains 1,800 new data entries (3.6 % missing data).

We divided the factor *growth form* into the five categories occurring in Ericales (Kubitzki, 2004): [1] *trees*, [2] *shrubs*, [3] *lianas and climbers*, [4] *herbs (including aquatic herbs)*, and [5] *root parasites*.

We defined *habitat* factor categories by taking the biome descriptions from Loarie *et al.* (2009), and simplifying them into the three habitat states: [1] *forests*, [2] *open habitats*, and [3] *wet habitats* (including mangroves and flooded forests/grassland/savannahs).

For the factor *climate type* (Fig. 1a), we used the Köppen-Geiger climate classification based on temperature and precipitation, applying the five main categories described in Peel *et al.* (2007): [1] *tropical*, [2] *arid*, [3] *temperate*, [4] *cold*, and [5] *polar* (see *SI* section 1.2). Tropical high elevation species were coded as *temperate*.

Finally, we divided the factor *region* into [1] *North America*, [2] *Eurasia*, [3] *South America*, [4] *Africa*, [5] *Indo-Pacific*, and [6] *Australia*. We followed the revised biogeographical delimitations of Floral Kingdoms as suggested by Cox (2001) for continent delimitations. Each species was assigned to its native region(s) only.

Disparity

We computed floral *disparity* (\bar{D}) for the different factor categories of taxa (e.g. *trees* from factor *growth form*) using the morphological matrix. From this matrix, we first created a distance matrix by calculating a dissimilarity index for each pair of taxa: the *mean character difference* (D), following Sneath & Sokal (1973), and Foote (1999). D is a version of the Gower index, suited for datasets like ours that contain at the same time continuous, categorical ordered, categorical unordered, and binary data. The detailed calculation of D is given in Chartier *et al.* (2017). *Disparity* (\bar{D}) was then estimated for a category as the *mean pairwise dissimilarity* (\bar{D} = the average D) among all taxa from that category (Foote, 1999), by averaging distances in the distance matrix for all taxa belonging to that category. The mean pairwise dissimilarity is less sensitive to large differences in group sizes than other disparity estimations such as for example the range (Ciampaglio *et al.*, 2001); this makes it well suited to our data.

There are two types of polymorphism in our data: [1] polymorphism in the morphological matrix (2.2 %), [2] polymorphism in the factor matrix (16.5 %). [1] As our calculation method of \bar{D} cannot take polymorphism into account in the morphological dataset, and since the percentage of polymorphism in this matrix is very low, a morphological matrix without polymorphism was randomly sampled and the distance matrix was re-computed prior to each computation of \bar{D} and each test (see below). This did not impact our results (data not shown). [2] Some species belong to several factor categories (for example, some species grow in *temperate* as well as in *cold* areas). When computing disparity for these categories, such species were included in each of these categories (but not when performing tests, see below).

For each factor, we compared \bar{D} among factor categories (for example among all *growth form* categories) with one-way permutation ANOVAs (analyses of variance) on the morphological distance matrix. This analysis consists of comparing the F-ratio of the dataset to the distribution of the F-ratio calculated for 9,999 permutations of the dataset. For each permutation, a random morphology - row in the matrix - is assigned to each species without replacement. For the F-ratio formula, see Hawkins (2014 p. 167). In our case, a permutation test is preferable to an ANOVA or a Kruskal-Wallis test, because we compare pairwise distances whereby each species contributes to multiple distance values, creating a lack of independence among values and inflating the degrees of freedom. As post hoc tests, we made pairwise comparisons of \bar{D} among factor categories with permutation tests on central tendencies following Bonnini *et al.* (2014). This test consists, for a pair of categories, of calculating the difference (here noted T) between the average D of each category, and compare it to the distribution of T calculated for 9,999 permutations of the dataset without replacement (like described above). We applied a Bonferroni correction for multiple comparisons to these post hoc tests. To deal with polymorphism in the factor matrix (the grouping variables of these tests), a factor matrix without polymorphism was randomly sampled and each permutation

ANOVA and corresponding post hoc tests performed 100 times; p-values and statistics for each test are thus presented as an average \pm standard deviation (SD) over these 100 calculations. To save execution time, calculations were ran in parallel on multiple computer cores using packages *foreach* (Microsoft Corp. & Weston, 2020), *parallel* (R Core Team 2016) and *doParallel* (Microsoft Corp. & Weston, 2019). Finally, for these tests, we excluded the category *root parasitic* (n = 2) from factor *growth form*.

Associations among factor categories

We performed a series of chi-squared tests to investigate associations among categories belonging to different factors and detect ecological/biogeographic trends in Ericales (e.g. do arborecent species more often grow in tropical areas?, i.e. is there an association between categories *tree* from factor *growth form*, and *tropical* from factor *climate*?).

To meet the chi-squared test criteria, and for these analyses only, we merged the categories *polar* (n = 7 species) and *cold* (n = 56) from factor *climate*, and excluded the category *root parasitic* (n = 2) from factor *growth form*. Associations were not tested among categories belonging to the same factors.

We performed the chi-squared tests using *chisq.test{stats}*. For significant tests ($p < 0.05$), the strength of the association was estimated from the Pearson residuals (*PR*; Hawkins, 2014). Multiple correlations are usually visualized using a correlation table (*SI* section 1.3). To visualize multiple correlations more easily and detect clusters of associated factor categories, we plotted these categories with a non-metric multidimensional scaling (nMDS) applied to a distance matrix computed from the *PR* values among categories, using *metaMDS{vegan}* with the Bray-Curtis distance (Anderson, 2001; Oksanen *et al.*, 2017; *SI* sections 1.3). This allowed us to draw an *association network* in which significantly positively associated categories fall close to each other and are linked by red lines, whereas significantly negatively associated categories fall far from each other and are linked by blue lines (Fig. 3). Inter-correlated categories appear linked together on that graph (clusters).

Variation of disparity accounting for associations among factor categories

Some factor categories are significantly associated with one another (see *Results*). Comparing disparity among categories for each factor independently might thus lead to ambiguous interpretations about the link between these factors and variation in disparity.

We solved this issue by first (i) keeping one factor constant while looking at the variation of disparity for the others (e.g. is there a difference among the *climate* categories if we look at *trees* only?). This was, however, only possible in a few cases that we report in the text, since category sizes become small once split and once polymorphism is sampled; all trends are shown in *SI* section

2.3. We furthermore (ii) calculated disparity for the two clusters of associated factor categories identified from the association network representation (Fig. 3). \bar{D} was in that case calculated for a given cluster by including all species belonging to the intersection of each factor and, within factors, the union of each category. For example, if a cluster is composed of the categories *tropical* and *temperate* (from factor *climate*), and *shrub* (from factor *growth form*), all *tropical shrubs* and *temperate shrubs* were included in the calculation of \bar{D} for that cluster. This is a strict representation of these clusters as more species might present some of but not all the characteristics of each cluster. We compared disparity between the two clusters with a permutation test on central tendencies as described above, with 99,999 permutations without replacement.

Latitudinal distribution of species and disparity

We estimated the latitudinal distribution of the species from the dataset by extracting location records (latitude and longitude) from the Global Biodiversity Information Facility online database (GBIF, <https://www.gbif.org/>) using `occ_search{rgbif}` (Chamberlain, 2017; *SI* section 1.4). Distribution maps (*SI* section 3) were then plotted using the package `maptools` (Bivand & Lewin-Koh, 2017) and manually checked for atypical and non-native records by using data from the literature and online trustworthy websites (such as the IUCN website, <http://www.iucnredlist.org/>). This allowed us to estimate the presence/absence of 347 (91 %) of the study species in each ten-degree latitude interval across the globe (see also *SI* section 2.5).

Disparity (\bar{D}) was then calculated for the species occurring in each given latitude interval. Finally, we tested for the correlations between latitude and species richness, latitude and disparity, and species richness and disparity (for each latitudinal interval) with Pearson correlation tests using `cor.test{stats}` and `lm{stats}`. For these tests, latitude values were treated as absolute values, to represent distances (north or south) from the Equator.

An additional permutation test was performed to show that the observed latitudinal variation in disparity was not due to the latitudinal variation in species number (*SI* section 2.4).

Results

Variation of floral disparity

Floral disparity (\bar{D}) significantly differed among categories of growth forms (excluding the two root parasitic species from the analysis; permutation ANOVA: $F = 485.43 \pm \text{SD}92.59$, $p = 7.00 \cdot 10^{-5} \pm \text{SD}1.43 \cdot 10^{-4}$), habitat types ($F = 366.00 \pm 75.26$, $p = 9.55 \cdot 10^{-4} \pm 1.50 \cdot 10^{-3}$), climate types ($F = 382.51 \pm 67.98$, $p = 7.00 \cdot 10^{-5} \pm 1.26 \cdot 10^{-4}$), and regions ($F = 101.43 \pm 67.98$, $p = 0.017 \pm 0.008$). Post hoc tests are summarized by red letters in Fig. 2 and the main trends of variation are described below.

Growth form. Overall (i.e. when including the entire dataset in the analysis), disparity decreased slightly from *trees* ($\bar{D} = 0.225 \pm \text{SD } 0.090$) to *herbs and aquatic herbs* ($\bar{D} = 0.201 \pm 0.101$), *lianas and climbers* ($\bar{D} = 0.189 \pm 0.101$) and *shrubs* ($\bar{D} = 0.182 \pm 0.082$; Fig. 2a). The two root parasitic species sampled (*Mitrastemon matudae* and *M. yamamotoi*) were not included in the analyses and only differed from each other in their number of carpels. To get around potential correlations among factors (e.g. *growth form* and *climate*), we compared the disparity of growth forms within each category of the other factors. For example, we investigated whether, when looking at *tropical* species only, trees were still showing more disparity than the other growth form categories. We did so for each category of the factors *climate*, *habitat* and *region* (SI section 2.3). The general pattern of disparity variation among growth forms was recovered within categories *forest* (from factor *habitat*) and *South America* (from factor *region*). Although not significantly, the tendency for *trees* to display the highest disparity was retrieved within all factor categories (SI section 2.3).

Habitat. Overall, floral disparity was highest in *forests* ($\bar{D} = 0.231 \pm \text{SD } 0.093$), intermediate in *wet habitats* ($\bar{D} = 0.211 \pm 0.091$), and lowest in *open habitats* ($\bar{D} = 0.192 \pm 0.085$; Fig. 2b). This result was only recovered within category *South America* (from factor *region*; SI section 2.3).

Climate: Overall, *tropical* species ($\bar{D} = 0.238 \pm \text{SD } 0.097$) displayed the highest level of floral disparity, followed by species distributed in *arid* ($\bar{D} = 0.196 \pm 0.101$) and *temperate* ($\bar{D} = 0.196 \pm 0.085$) areas (Fig. 2c). Disparity in *cold* ($\bar{D} = 0.186 \pm 0.086$) and *polar* areas ($\bar{D} = 0.090 \pm 0.050$) did not significantly differ from the other categories. The decrease of floral disparity from tropical to temperate climate categories held within categories *tree* (from factor *growth form*) and *Africa* (from factor *region*), and was only a tendency for category *forest* (factor *habitat*, SI section 2.3). Within category *South America* (factor *region*), floral disparity was higher for tropical species than for arid species. Although not significantly, the tendency for disparity to decrease from tropical, to temperate, to cold and polar climate categories was retrieved within all factor categories but one (SI section 2.3).

Region. Overall, disparity was highest for *African* species ($\bar{D} = 0.245 \pm \text{SD } 0.107$). *South American* ($\bar{D} = 0.222 \pm 0.101$), *Indo-Pacific* ($\bar{D} = 0.217 \pm 0.081$), and *Eurasian* ($\bar{D} = 0.215 \pm 0.083$) species displayed similar lower levels of disparity. *North American* ($\bar{D} = 0.176 \pm 0.086$) and *Australian* ($\bar{D} = 0.134 \pm 0.087$) species displayed the lowest levels of disparity (Fig. 2d). This trend was only recovered for the category *forest* of factor *habitat* (SI section 2.3).

Variation of floral disparity when combining factor categories

We found significant associations among categories for each pair of factors (Table 1). Post hoc test details are illustrated in Fig. 3a.

Our data show two clusters of associated categories that describe two large groups of species sharing particular ecological/biogeographic trends in Ericales (Fig. 3a). Cluster 1 corresponds to species belonging to the categories *forest* (factor *habitat*), *tropical* (factor *climate*), *tree* (factor *growth form*), and *Africa* or *South America* (factor *region*). Cluster 2 corresponds to species belonging to the categories *open habitat*, or *wet habitat* (factor *habitat*), *temperate*, *arid*, or *cold and polar* (factor *climate*), *herbs and aquatic herbs*, or *shrubs* (factor *growth form*), and *North America* or *Eurasia* (factor *region*). Species strictly representing Cluster 1 ($n = 76$) showed significantly higher (26 %) floral disparity ($\bar{D} = 0.247 \pm \text{SD } 0.108$) than those ($n = 65$) representing Cluster 2 ($\bar{D} = 0.169 \pm 0.082$; permutation test on central tendency: $T = 0.0782$, $p = 0$; Fig. 3b). Note that there was no significant association in our dataset for categories *liana* and *Indo-Pacific* to any other category.

Latitudinal distribution of species richness and disparity.

The estimated species richness and floral disparity both significantly decreased towards the poles (Figs. 1b, 4a, and 4b). Species richness peaked in the subtropical area of the northern hemisphere and near the equator, between latitudes 40° and 20° (113 species), and between latitudes 0° and 10° (124 species; Fig. 1b), and steeply decreased with latitude ($r = -0.78$, $p < 10^{-5}$; linear regression: intercept = 103.7, slope coefficient = -1.336, Fig. 4a). On the other hand, disparity peaked in the southern hemisphere, between latitudes -10° and -20° ($\bar{D} = 0.266 \pm \text{SD } 0.105$; Fig. 1b). It decreased with latitude ($r = -0.77$, $p = 0.001$; linear regression: intercept = 0.26, slope coefficient = -0.002), with a weak decrease towards the North Pole, and a steeper decrease towards the South Pole (Figs. 1b and 4b). This correlation held when removing the three latitudinal intervals containing five species or less ($r = -0.90$, $p < 10^{-3}$).

There was no clear correlation between disparity and species richness. A weak positive correlation is due to three latitudinal intervals each containing only 5 species or less ($r = 0.63$, $p = 0.015$) and this correlation disappears when these intervals are not included ($r = 0.33$, $p = 0.329$; Fig. 4c). The permutation test we performed also showed that the increase of disparity near the equator was not due to the higher number of species present at these latitudes (*SI* section 2.4).

Discussion

Our results indicate that, in the order Ericales, floral disparity is significantly higher in the tropics than in other climate zones. Both floral disparity (morphological diversity) and species richness increase with lower latitudes. However, floral disparity is highest in southern tropical seasonal forests, while species richness is higher in northern tropical and subtropical latitudes (Fig. 1). In a previous study, we used the same morphological dataset to investigate changes in disparity across floral modules and among ericalean lineages (Chartier et al. 2017). We showed that flower

morphology differed among Ericalean clades, that these clades filled the morphospace in a mosaic pattern, and that clade floral disparity increased with clade size, albeit with notable exceptions, e.g. Balsaminaceae (touch-me-not family) and Sapotaceae (shea tree family). Disparity was not correlated to clade crown age and there was no phylogenetic pattern of distribution of disparity among families, suggesting that there are other factors that drive variations in floral disparity in the Ericales (Chartier *et al.* 2017). The present analyses show that different categories of growth form, region, climate type and habitat show slightly different levels of disparity (Fig. 2). These factor categories are inter-correlated, which renders their respective effects on disparity variations difficult to separate at this taxonomic scale and given the structure of the order Ericales (see discussion below). Nevertheless, there is a strong signal that, in Ericales, tropical trees growing in forests of Africa and South America (among them the speciose and very diverse family Lecythidaceae) show higher floral disparity than other Ericalean representatives (Fig. 3).

Contrary to species richness, disparity is a complex and subjective measure of biodiversity, as it can be estimated from many different combinations of traits. As a consequence, trends in disparity variation will not always reflect the same evolutionary or biogeographic processes and will strongly depend on the ecological or physiological function of the measured traits. For example, no latitudinal gradient was found for the disparity of moth wing ornamentation in the New World, because this trait is under strong selective pressure to match resting backgrounds and avoid predators at all latitudes (Ricklefs, 2009). For plants, there is also no latitudinal gradient in pollen ornamentation disparity (Mander, 2018): currently, it is still unclear which of the measured morphological pollen traits are adaptive and thus whether variation in these traits is driven by chance, taxonomy, or reflects evolutionary processes (Lupia, 1999; Mander, 2016, 2018). In contrast, it has been found that tree functional diversity is higher at low latitude and in tropical seasonal forests across North and South America (Swenson & Enquist, 2007; Swenson *et al.*, 2012, but see Lamanna *et al.*, 2014). The measured traits predict plant growth and survival rates and thus reflect the demographic dynamics of plant communities. These results indicate that an increase in functional diversity may be promoted in regions where abiotic selective constraints are weaker, and where biotic interaction rates and niche partitioning are more important, triggering morphological differentiation (Swenson & Enquist, 2007; Swenson *et al.*, 2012).

Our analysis of floral trait points towards a role of climate as well as latitude in floral disparity patterns, probably linked to biotic interactions. For example, the most variable traits in Ericales flowers are petal union and stamen types, both linked to functional aspects of pollination biology (Chartier *et al.*, 2017). Biotic interactions directly impacting floral evolution are mainly due to pollinators. About 88 % of angiosperms are pollinated by animals, and this proportion has been estimated to be as high as 99 % at tropical latitudes (Regal, 1982; Bawa, 1990; Ollerton *et al.*, 2011). Several studies investigating plant clades and pollination networks have also brought

forward evidence for an increase in plant-pollinator interaction dynamics in the tropics. For example, it has been shown that the number of different pollination systems increases towards the tropics, probably because tropical areas contain a broader diversity of functional groups of pollinators including taxa such as bats, birds or primates (Ollerton *et al.*, 2006, but see Schleuning *et al.*, 2012). In addition, it has been shown that interactions with pollinators are more specialized in the tropics (Trojelsgaard & Oleson, 2013). These combined factors explain possible selection for a higher number of floral traits adapted to specific pollinators in the tropics. Among the many different pollination systems that have been described in Ericales, some are found across all latitudes (e.g. pollen/nectar collecting bees, flies), but many are indeed unique to the tropics (bats, Euglossini bees, squirrels/flying squirrels) or at least more diverse in the tropics (moths, birds, hummingbirds, mammals; Sazima *et al.*, 1993; Endress, 1996; Yumoto *et al.*, 2000; Kubitzki, 2004). Exceptions to this pattern might occur in biodiversity hotspots (South Africa, the Mediterranean area), although we do not observe a particular peak in floral disparity for the corresponding latitudes in our dataset (Fig 1). Note that wind pollination is of lesser importance in Ericales (it is found e.g. in Ericaceae -heath family- in the genus *Erica* and the tribe Empetreae, and in Actinidiaceae -kiwifruit tree family- in the genus *Actinidia*; Kubitzki, 2004).

The general increase in disparity towards tropical latitudes that we observe in our data may be partly due to the diverse pollination systems in the largely tropical families Lecythidaceae (bees, bats, beetles; Kubitzki, 2004), Sapotaceae (insects, bats, squirrels/flying squirrels; see below), Primulaceae p.p. (oil bees; Buchmann, 1987). In contrast to this, it has also been shown elsewhere that species-rich tropical lineages (or assemblages) can show very little floral variation if all or most of their species are pollinated by animals from the same functional pollinator group. This is for instance the case in the tropical trees from the large genus *Myrcia* (Myrtaceae, Myrtales; Vasconcelos *et al.*, 2018) bearing morphologically homogeneous, inconspicuous and unspecialized flowers pollinated by bees. Delmas *et al.* (2020) also showed that tropical and temperate/subtropical assemblages of woody species in Australia mostly produce small whitish generalist flowers probably pollinated by insects including thrips, flies and small beetles. In our dataset, Sapotaceae also mostly bear small white flowers (Kubitzki, 2004), but is one of the most variable families in the order when looking at other floral traits than color (Chartier *et al.*, 2017). As far as known, this family is pollinated by bats (Cleghorn, 1922; van der Pijl, 1936; Nathan *et al.*, 2009), squirrels and flying squirrels (Yumoto *et al.*, 2000), and insects (Basga *et al.*, 2018) and shows high variation in e.g. petal and petal whorl numbers, stamen and stamen whorl numbers, and types of staminodes.

The presence of generalist systems in the tropics, leading to the evolution of lineages bearing homogeneous (e.g. small and white) flowers is not incompatible with an overall pollination-driven increase of floral disparity in the tropics. In our dataset, the morphospace area occupied by

cold/temperate species and the area occupied by tropical species largely overlap, the area occupied by tropical species being larger (*SI* section 2.2). The morphological diversity of tropical ericalean flowers encompasses the diversity of the order as whole and exceeds that of non-tropical species. This is in agreement with the general observation that floral diversity is broadest in the tropics (e.g. Endress, 1996). It also implies that there are no specific floral morphologies related to cold/temperate zones, pointing towards the absence of large-scale patterns of morphological convergence. Our data rather indicate a release of constraints in the tropics, expressed in the occupation of large areas of the floral morphospace by certain phylogenetic lineages. In particular, two tropical families increase the total area of the ericalean floral morphospace: (i) Lecythidaceae, a medium-sized family presenting the highest floral disparity in Ericales, and (ii) Sapotaceae, a very speciose homogeneous group, but whose unique combinations of floral features place the family in the periphery of the morphospace (Chartier *et al.*, 2017).

The patterns of disparity variation that we observed at the order level were not significant or could not be properly tested within families or within factor categories with our sampling effort as some factor categories are distributed un-evenly across the order. For example, for some factors only one category is represented in a given family (e.g. all Sapotaceae and Lecythidaceae are tropical trees, all Marcgraviaceae are distributed in South America). In addition, some families are too small to observe any pattern even if sampled completely (seven families contain fewer than 12 species - e.g. Tetrameristaceae, Roridulaceae, and Fouquieriaceae). Nevertheless, even if in many cases Ericalean families are limited to a narrow range of strategies (with regard to the factors we investigated here), we observe broad trends in biodiversity variation that emerge from these patterns at a larger phylogenetic scale. This has also been shown for the latitudinal gradient in vascular plant species number (Wieser *et al.*, 2018). Even though we cannot test for the effect of phylogenetic relationships on disparity based on the present data because several deeper nodes of Ericales are presently unresolved or unsupported (Schönenberger *et al.*, 2005, Rose *et al.*, 2018), exploring such effects could be approached in the future by focusing on well-supported subclades (e.g. the ericoids or the primuloids, Rose *et al.*, 2018) or at individual families.

The drawback of working at large taxonomic scales is, unfortunately, the present lack of ecological information (particularly about pollination) that could help us to understand the mechanisms leading to these broad-scale patterns. Our data on Ericales, however, suggest that a well-suited clade for studying these mechanisms at a finer scale would be Primulaceae (primrose family), because of its large size (2,788 species) and high morphological variability. Primulaceae represent 22.1% of Ericales species, and contribute 14% to the order's floral disparity (Chartier *et al.*, 2017). In addition, the family presents sufficient variation in climate types, growth form, habitat, and is widely distributed (*SI* "Dataset.xlsx"). However, even at this scale, the lack of ecological data for most species would remain a limiting factor for these analyses.

In our data, the species displaying the highest degree of floral disparity are those with an arborescent form distributed in the African and South American tropical forests (Fig. 3). There is, however, no apparent link between growth form and floral disparity, and the slightly higher floral disparity of trees may be an artefact due to the strong association between the states *tree* and *tropics* (Fig. 3). Indeed, nearly sixty percent of the tree species included in our dataset grow in tropical forests, and within the tropics, over sixty percent of Ericales species are trees. This makes it difficult to disentangle the effects of growth type and climate type on the variation of floral disparity. In addition, we did not correct for a phylogenetic effect when studying the relationships between factors and disparity, which is a limitation of this study. There is no distinct pattern of disparity variation in Ericales, for example early diverging clades do not seem to show more or less disparity than later diverging clades; however, disparity varies greatly among Ericalean families (Chartier et al. 2017). The high disparity found for trees could for example be due to the contribution of the family Lecythidaceae. When Lecythidaceae are pruned from the dataset, our main results do not change but lose statistical significance as the category *tropical climate* then only tends to show the highest disparity. In these adapted analyses, there is also no more trend for any *growth form* to show different levels of morphological disparity. The effect of climate on floral disparity thus appears to be more robust than the effect of growth form. Further evidence for the importance of the effect of climate lies in the decrease in disparity from tropical to temperate climate categories. Categories cold and polar do not display significantly different disparity from any other climate category in our dataset (although they clearly tend to show lower disparity), most likely because these categories are very often associated to category *temperate* in the data (polymorphism).

In angiosperms, the flower is the structure dedicated to sexual reproduction, and a shift in floral features can provoke reproductive isolation by different mechanisms (Waser & Ollerton, 2006). We might thus expect floral disparity to be correlated with species number in a clade or a region. Our data shows that this is not always the case (Fig. 4c, *SI* section 2.4, Chartier *et al.*, 2017). For example, we find that African species tend to display the highest level of floral disparity although, in our dataset, species number is significantly higher for the South American and Indo-Pacific regions. The decoupling of disparity and species number in a clade, a region, or through time is quite common (Lupia, 1999; Roy *et al.*, 2001; Neige, 2003; Roy & Foote, 1997; Eble, 2000; Oyston *et al.*, 2015).

Clearly, disparity is an important component of biodiversity and is worth being considered in any attempt to measure biodiversity. When calculated on floral traits, disparity may also provide useful approximations for the diversity of ecological relationships (e.g., plant-pollinator interactions) and might help understand evolutionary patterns (e.g., pollination-mediated selection in a biogeographic context). Floral disparity in a given geographical area might also be a particularly

useful parameter for assessing the conservation value of the area, as disparity not only reflects an important part of the local plant community, but as it is, via plant-pollinator interactions, also a possible proxy for a community's ecological dynamics.

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Author's contribution

M.C., M.v.B. and J.S. designed the work, S.S., M.v.B., M.C., S.L., F.J. and J.S. generated the data, H.S. designed the online database (PROTEUS) used to record and store the data, M.C. analysed the data with help from T.P.; M.C., M.v.B. and J.S. wrote the paper with significant contributions from the other authors. All authors gave final approval for publication.

Material & correspondence

The dataset supporting this article is given in Supplementary Information (“Dataset.xlsx”). The data are also stored in the online database PROTEUS (<http://eflower.myspecies.info/>; Sauquet, 2019). Correspondence and material requests should be addressed to M.C. and J.S.

Competing interests

The authors declare no competing interests.

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Figure and table legends

Figure 1. Climate categories and latitudinal gradient. **a**, Köppen-Geiger climate classification simplified to five categories (figure adapted from Peel *et al.* (2007)). **b**, Estimated latitudinal distribution (number of species) of Ericalean species (grey bars) and the corresponding floral disparity (\bar{D} : yellow dots, SD shown in light blue) per ten-degree longitudinal categories.

Figure 2. Overall variation of floral disparity among categories of growth form (a), climate (b), habitat (c), and geographic region (d). D = mean pairwise differences. For each boxplot, sample size is given below each box and disparity ($\bar{D} \pm SD$) is indicated by orange dots and black error bars. Post hoc test results are depicted by red letters; categories that are significantly different are labelled with a different letter. The coloured barplots indicate the number of species sampled per family (according to APG IV; Stevens, 2001 onwards) in each factor category. For growth form (a), the category "root parasitic" was not included in the statistical analyses as it contains only two species.

Figure 3. Association network (a) and disparity for two clusters of associated categories (b). The graph in **a** is used to visualize the results of chi-square tests assessing the multiple associations among factor categories in our dataset. Factor categories that are significantly associated are linked by a line whose colour represents the strength and direction of the association (interpreted from the values of Pearson residuals). This representation is equivalent to a classical correlation table (*SI* section 1.3). Our results show that some categories are associated to each other, and form two distinct groups that we call Cluster 1 and Cluster 2. The disparity of these clusters is given in **b**: D = mean character differences between two taxa, sample size is given below each box, and disparity ($\bar{D} \pm SD$) is indicated by orange dots and black error bars.

Figure 4. Relationships among species richness, floral disparity, and latitude for 347 species of Ericales. Black lines: significant correlation, red dashed line: correlation only significant when the three latitudinal intervals containing 5 species or less (red dots) are included. Absolute values were used for latitude, to pool data from the northern (gray/light red dots) and the southern (black/red dots) hemispheres.

Table 1. Chi-squared tests for the association among the categories of factors *growth form*, *habitat*, *climate*, and *region*.

Comparison	χ^2	df	p-value
Growth form-climate	80,99	9	$1,03 \cdot 10^{-13}$
Growth form-region	100,12	15	$1,24 \cdot 10^{-14}$
Growth form-habitat	49,34	6	$6,39 \cdot 10^{-09}$
Climate-region	263,29	15	$< 2,20 \cdot 10^{-16}$
Climate-habitat	64,13	6	$6,49 \cdot 10^{-12}$
Region-habitat	47,52	10	$7,59 \cdot 10^{-07}$

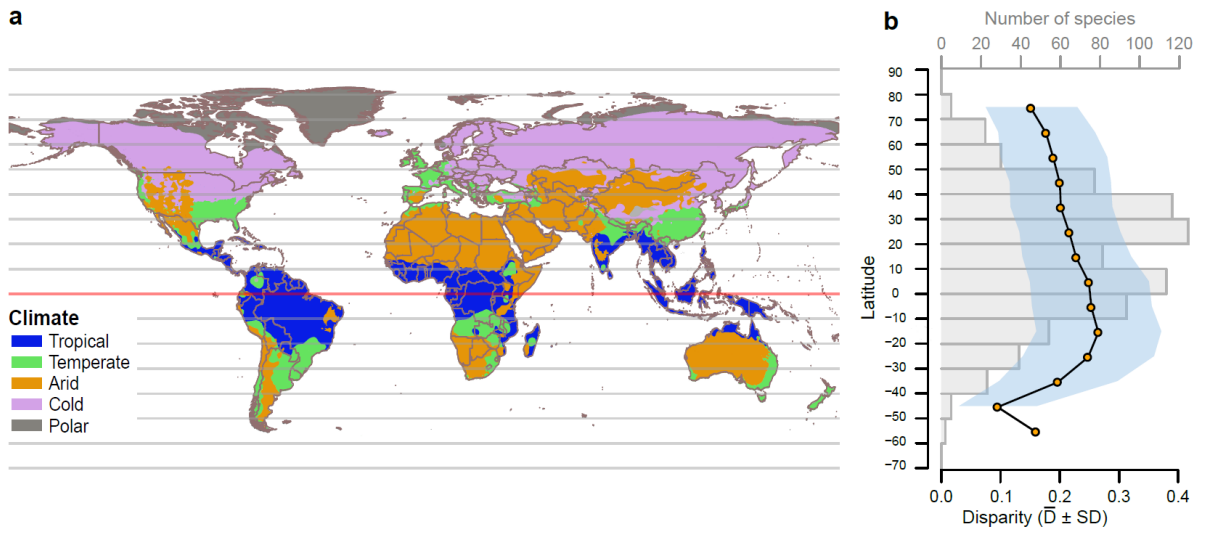


Figure 1

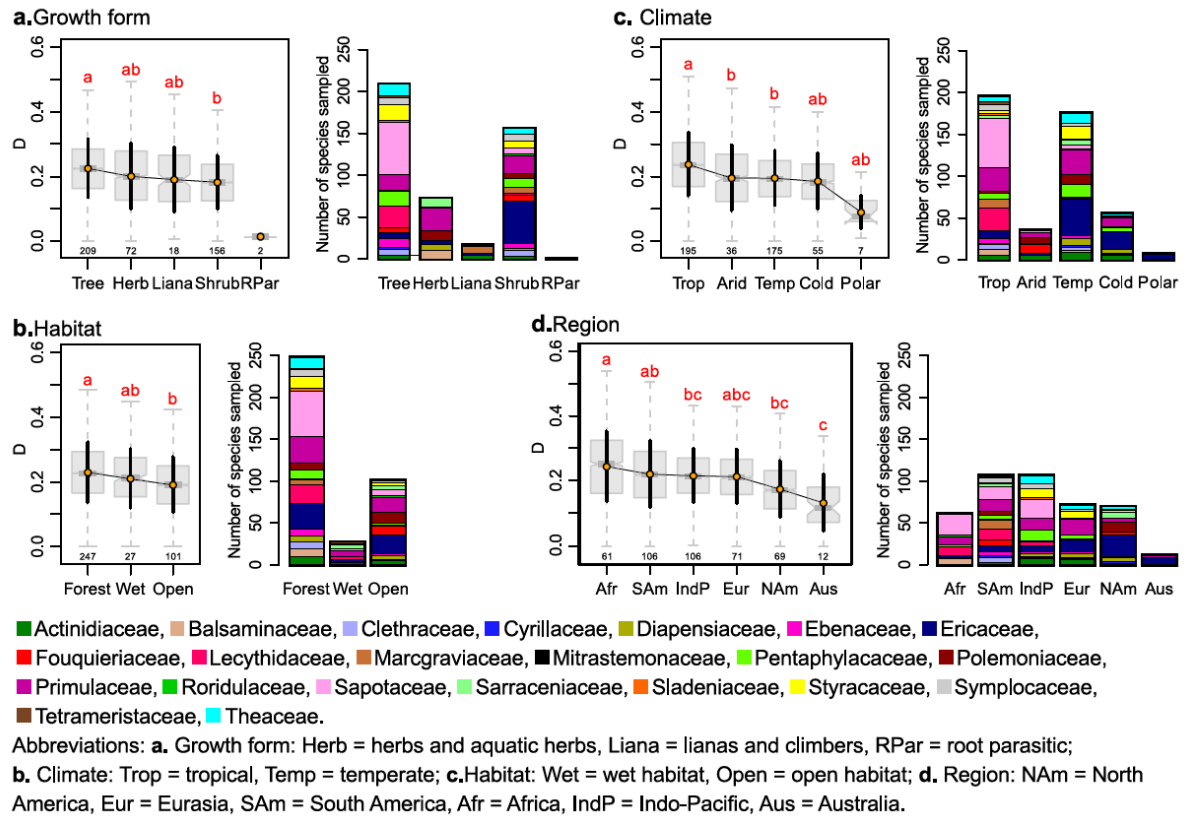


Figure 2

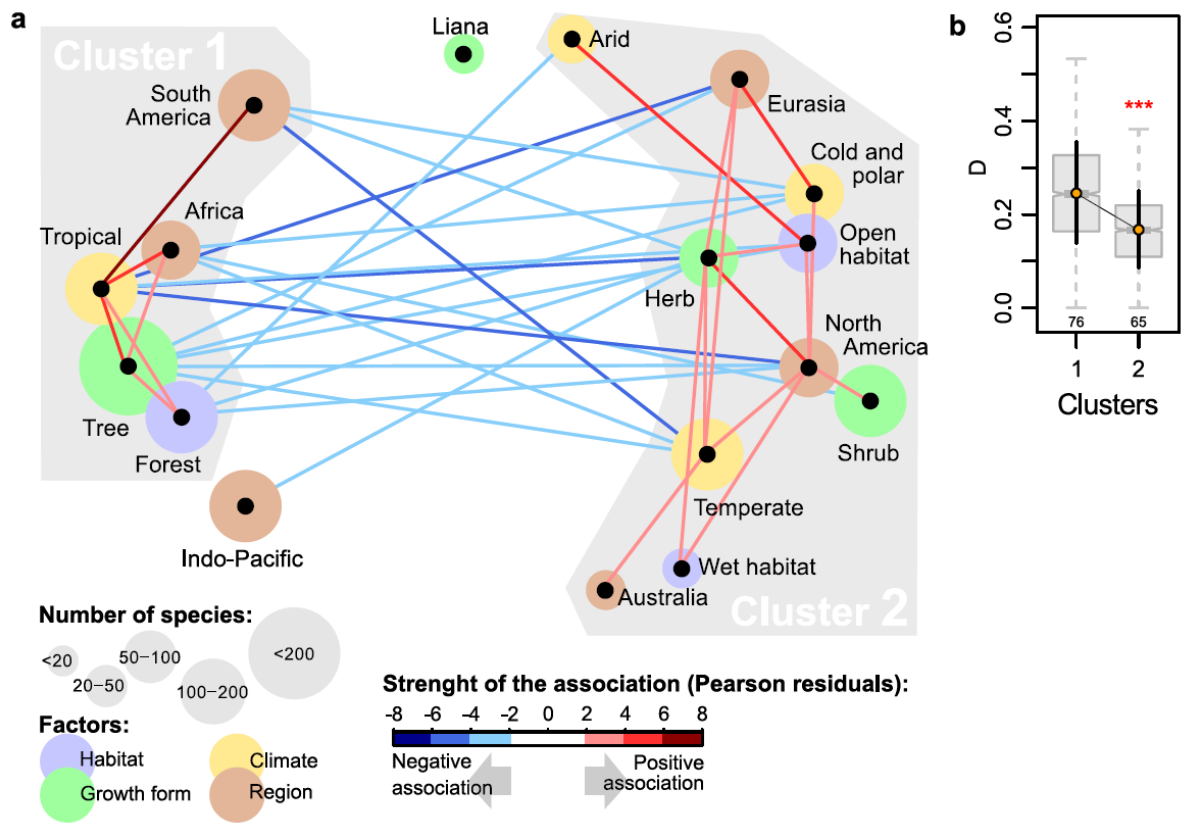


Figure 3

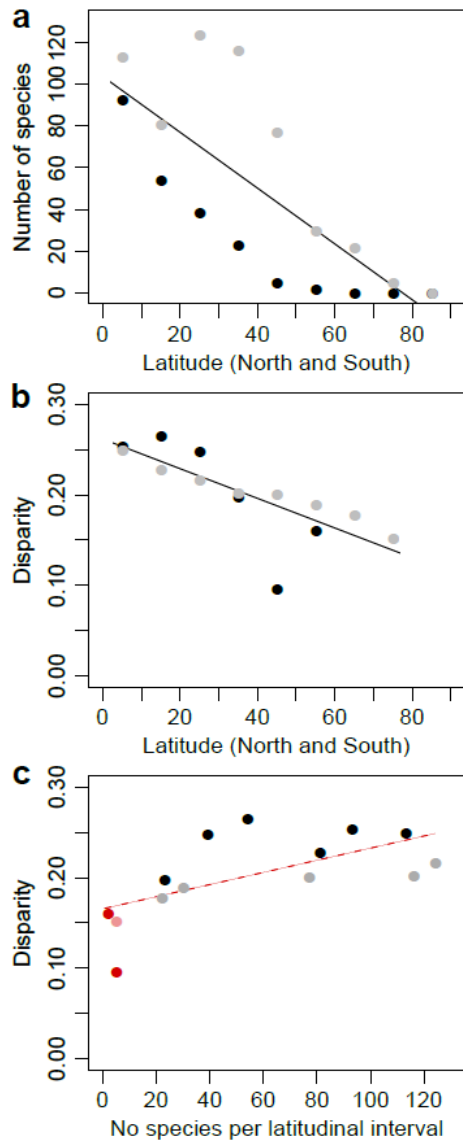


Figure 4