

## LETTER

# Opposing macroevolutionary and trait-mediated patterns of threat and naturalisation in flowering plants

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## Abstract

Due to expanding global trade and movement of people, new plant species are establishing in exotic ranges at increasing rates while the number of native species facing extinction from multiple threats grows. Yet, how species losses and gains globally may, together, be linked to traits and macroevolutionary processes is poorly understood. Here, we show that, adjusting for diversification rate and clade age, the proportion of threatened species across flowering plant families is negatively related to the proportion of naturalised species per family. Moreover, naturalisation is positively associated with range size, short generation time, autonomous seed production and interspecific hybridisation, but negatively with age and diversification, whereas threat is negatively associated with range size and hybridisation, and positively with biotic pollination, age and diversification rate. That we find such a pronounced signature of naturalisation and threat across plant families suggests that both trait syndromes have coexisted over deep evolutionary time and counter to intuition, that neither strategy is necessarily superior to the other over long evolutionary timespans.

## Keywords

Angiosperms, comparative study, flowering plants, naturalised, phylogenetic regression, rarity, threatened.

*Ecology Letters* (2021) **24**: 1237–1250

## INTRODUCTION

Ongoing habitat loss, degradation and fragmentation (Vitousek *et al.*, 1997; Saar *et al.*, 2012; Corlett 2016), disruption of historic disturbance regimes (Alstad *et al.*, 2016), increased invasion success of alien species (Winter *et al.*, 2009) and climate change (Willis *et al.*, 2008, 2010) are driving plant extinctions at accelerating rates (Alstad *et al.*, 2016; Yessoufou & Davies 2016). At the same time, global trade has increased the pace at which alien plants are introduced and become established outside their native ranges (Seebens *et al.*, 2017). Yet, while a broad body of work suggests threatened and invasive species contrast sharply in traits (Table 1) and have distinct phylogenetic distributions (Davies *et al.*, 2011), our understanding of global patterns of threat and naturalisation as potentially interrelated macroecological and macroevolutionary phenomena remains lacking (Colautti *et al.*, 2017).

Extinction risk at broad scales appears to be strongly structured on plant phylogeny (e.g. Lozano & Schwartz 2005; Vamوسي & Wilson 2008; Davies *et al.*, 2011; Thuiller *et al.*, 2011; Vamوسي *et al.*, 2018) with the frequency of threatened angiosperms highest within speciose clades (Schwartz & Simberloff 2001; Pilgrim *et al.*, 2004; Yessoufou *et al.*, 2012) and generally young, rapidly diversifying lineages (Lozano & Schwartz 2005; Davies *et al.*, 2011; Duncan *et al.*, 2011). Critically, extinction risk may be more related to evolutionary

dynamics (Sodhi *et al.*, 2008; Davies *et al.*, 2011) than to traits, and contingent on extinction drivers such as habitat loss, exploitation, etc. (Godefroid *et al.*, 2014; Freville *et al.*, 2007; Davies 2019). That extinction risk correlates strongly with clade age and richness suggests that the defining characteristics of rarity – endemism, limited range and small population sizes (Rabinowitz 1981; Rabinowitz *et al.*, 1986) – may simply follow from high rates of speciation (Lozano & Schwartz 2005; Davies *et al.*, 2011). Yet, contradicting this, Vamوسي & Wilson (2008) found extinction risk to be elevated in species-poor families, and, moreover, in some habitats, phylogenetically distinct species may be more threatened (Daru *et al.*, 2013). Perhaps, then, in old and species-poor families, remnants of formerly large and diverse clades, extinction risk may be linked to life-history features that are sensitive to extinction drivers (Yessoufou & Davies 2016), while diversification dynamics may dominate in young, species-rich families, implying that the drivers of extinction differ between old vs. young clades (Vamوسي *et al.*, 2018; Davies 2019).

Successful plant invasions are, of course, conditioned on context-specific factors that include use (van Kleunen *et al.*, 2020) and transport by humans (Kueffer 2017), degree of climate matching (Thuiller *et al.*, 2005), residence time (Wilson *et al.*, 2007), propagule pressure (Simberloff 2009), geography of habitat alteration and anthropogenic disturbance (Lembrechts *et al.*, 2016) and the invasibility of particular

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**Table 1** Broad summary of findings from studies of rare/threatened and naturalised/invasive species by traits and taxonomy from comparative studies, surveys and literature reviews

Category	Correlates	Contrast	Geographic scope	Taxonomic scope	# species compared	Study type	Phylogenetically controlled	Source
Naturalised	Positively with specific leaf area, but negatively with maximum height and seed mass	Naturalised alien species to co-occurring native species	Global	Angiosperms	4473	Comparative study	Yes	Ordonez et al. (2010)
Naturalised	Competitive ability	Naturalisation success among introduced species	Global	Vascular plants	3004	Comparative study	Yes	Guo et al. (2018)
Naturalised	Autofertility	Mainland species, island colonists, island endemics	Global	Angiosperms	1752	Comparative study	Included random effect of family	Razanajatovo et al. (2016)
Naturalised	Large native range size, broad climate range	Naturalised species among introduced Central European species	Global	Seed plants	1218	Comparative study	Yes	Pysek et al. (2009)
Naturalised	Positively with native range size, height, number of subtaxa	Naturalised species among species introduced from southern Africa	Global	Iridaceae	1036	Comparative study	Taxonomic groupings used as covariates	Van Kleunen et al. (2007)
Naturalised, Invasive	Naturalised species more likely to produce seeds autonomously than native species, but less likely to reproduce asexually	Native, naturalised, invasive	U.S.	Angiosperms	141	Comparative study	Yes	Burns et al. (2011)
Naturalised, Invasive	Propose hybridisation as a means by which invasiveness can evolve, providing many examples in plants	NA	Global	Angiosperms	24	Survey	NA	Schierenbeck and Ellstrand (2009); Ellstrand and Schierenbeck (2000)
Naturalised, Invasive	Families with more hybrids do not produce more invasive species	Hybrids to non-hybrid naturalised and invasive taxa by family	Global	Vascular plants	256 families	Comparative study	Yes	
Invasive	Polyploid, broad environmental tolerances, large native range size	Invasive among naturalised species	U.S.	Angiosperms	4953	Comparative study	Family included as covariate	Schmidt et al. (2012a)
Invasive	Broad environmental tolerances	Invasive (high impact environmental or agricultural weeds) among naturalised species	Australia	Angiosperms	146 congeneric pairs	Comparative study	Yes	Gallagher et al. (2015)

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Table 1 (continued)

Category	Correlates	Contrast	Geographic scope	Taxonomic scope	# species compared	Study type	Phylogenetically controlled	Source
Agricultural weeds, Invasive	Families with at least some abiotically pollinated species had higher proportions of natural area invaders and agricultural weeds than biotically pollinated species; species primarily aquatic or semi-aquatic, grasses, nitrogen-fixers, climbers, and clonal trees have some of the highest risk of becoming natural area invaders globally	Taxonomic	Global	Angiosperms	1348	Comparative study	Comparison by family	Daehler (1998)
Invasive	Small seed mass and high specific leaf area positively associated with invasion success	Invasiveness among non-native species as measured by abundance at regional and continental scales while controlling for residence time	eastern Australia	Angiosperms	152	Comparative study, field survey	N	Hamilton <i>et al.</i> (2005)
Invasive	Self-compatibility, autonomous seed production	Introduced range size among invasive Asteraceous species in China as a function of autofertility and autofertility of invasive species relative to Asteraceae globally	China	Asteraceae	12, 36	Comparative study with empirical data collection on self-compatibility and autonomous seed production	N	Hao <i>et al.</i> (2011)
Invasive; Threatened	Invasive disproportionately polyploid; threatened disproportionately diploid	Invasive and non-invasive congeneric species; threatened and non-threatened congeneric species	Global	Angiosperms	2437; 9645	Comparative study	Congeners compared	Pandit <i>et al.</i> (2011)
Rare; Pest	Pests disproportionately polyploid, tend to multiple life histories and growth forms, and to occur in wetland habitats; rare disproportionately diploid, tend to single life history and growth form, and non-wetland	Rare species across flora; native pest species across flora	North America	Angiosperms	15 213	Comparative study	Yes	Schmidt <i>et al.</i> (2012b)

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Table 1 (continued)

Category	Correlates	Contrast	Geographic scope	Taxonomic scope	# species compared	Study type	Phylogenetically controlled	Source
Threatened; Invasive	Invasive climbing, herbaceous, native to multiple floristic kingdoms, broad habitat range; threatened tall, tree-like and range restricted	Threatened species within Fabaceae	Global	Legumes	8906	Comparative study	Yes	Bradshaw <i>et al.</i> (2008)
Threatened; Invasive	"Polyploidy can be an important factor in species invasion success through a combination of (1)'pre-adaptation', whereby polyploid lineages are predisposed to conditions in the new range and, therefore, have higher survival rates and fitness in the earliest establishment phase; and (2) the possibility for subsequent adaptation due to a larger genetic diversity that may assist the 'evolution of invasiveness'. Alternatively, polyploidisation may play an important role by (3) restoring sexual reproduction following hybridisation or, conversely, (4) asexual reproduction in the absence of suitable mates."	NA	Global	Angiosperms	NA	Review	NA	teBeest <i>et al.</i> (2012)
Threatened	"Taxonomic distribution of extinction risk differs significantly between regions, inconsistent with a simple, trait-based model of extinction. Extinction risk is higher for young and fast-evolving plant lineages"	Extinction risk between geographic regions and plant families	Cape of South Africa, Great Britain	Vascular plants	NA	Taxonomic distribution of extinction risk based on IUCN Redlist data	Yes	Davies <i>et al.</i> (2011)
Threatened	Small range size, low population size, low abundance	Extinct and extirpated species among the California flora	California	Angiosperms	5280	Survey	NA	Rejmánek (2018)

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Table 1 (continued)

Category	Correlates	Contrast	Geographic scope	Taxonomic scope	# species compared	Study type	Phylogenetically controlled	Source
Threatened	Small population size, low seedbank survivorship, large plant size	Extinction probability	southeastern France	Rare and common weeds of cereal fields	24	Field surveys, comparative study	No	Saatkamp <i>et al.</i> (2018)
Threatened	Species more prone to local population extinction were characterised by shorter lifespan, self-pollination, a lack of clonal growth, fewer seeds per shoot, lower average height, lower soil nitrogen preference and higher requirements for light, indicating a limited ability to tolerate the range of changes in biotic and abiotic conditions of the sites. Locally extinct populations were also characterised by wind-dispersed seeds, lower seed weight and lower terminal velocity of seeds, suggesting that species strategies for long-distance dispersal are not favoured in highly fragmented landscapes	Extinction probability among species characteristic of calcareous grasslands	Estonia	Species occurring on European calcareous grasslands (a highly fragmented habitat)	122	Field surveys, comparative study	Yes	Saar <i>et al.</i> (2012)
Threatened	Species least able to cope with habitat loss were poor competitors, abiotically dispersed and perennial, clonal species	Species richness of habitat patches and by species traits	Central, Northern Europe	Herbaceous specialist species of European grassland fragments	NA	Field surveys, comparative study	No	Marini <i>et al.</i> (2012)
Threatened	Habitat specialism, short life-cycle, poor dispersal	Species richness of habitat patches and by species traits	Norway	Species occurring in European calcareous grasslands	158	Field surveys, comparative study	No	Olsen <i>et al.</i> (2018)
Threatened	Extinction risk negatively related to range size and positively to traits associated with habitat specialisation: poor competitors (i.e. short stress-tolerators) of open habitats with very low or high pH and soil moisture particularly at risk	Species traits of extirpated threatened species compared to regional flora	Bedfordshire, Northamptonshire, England	Regional flora	94 extinct/threatened	Comparative study, analysis of historical and contemporary records	No	Walker and Preston (2006)

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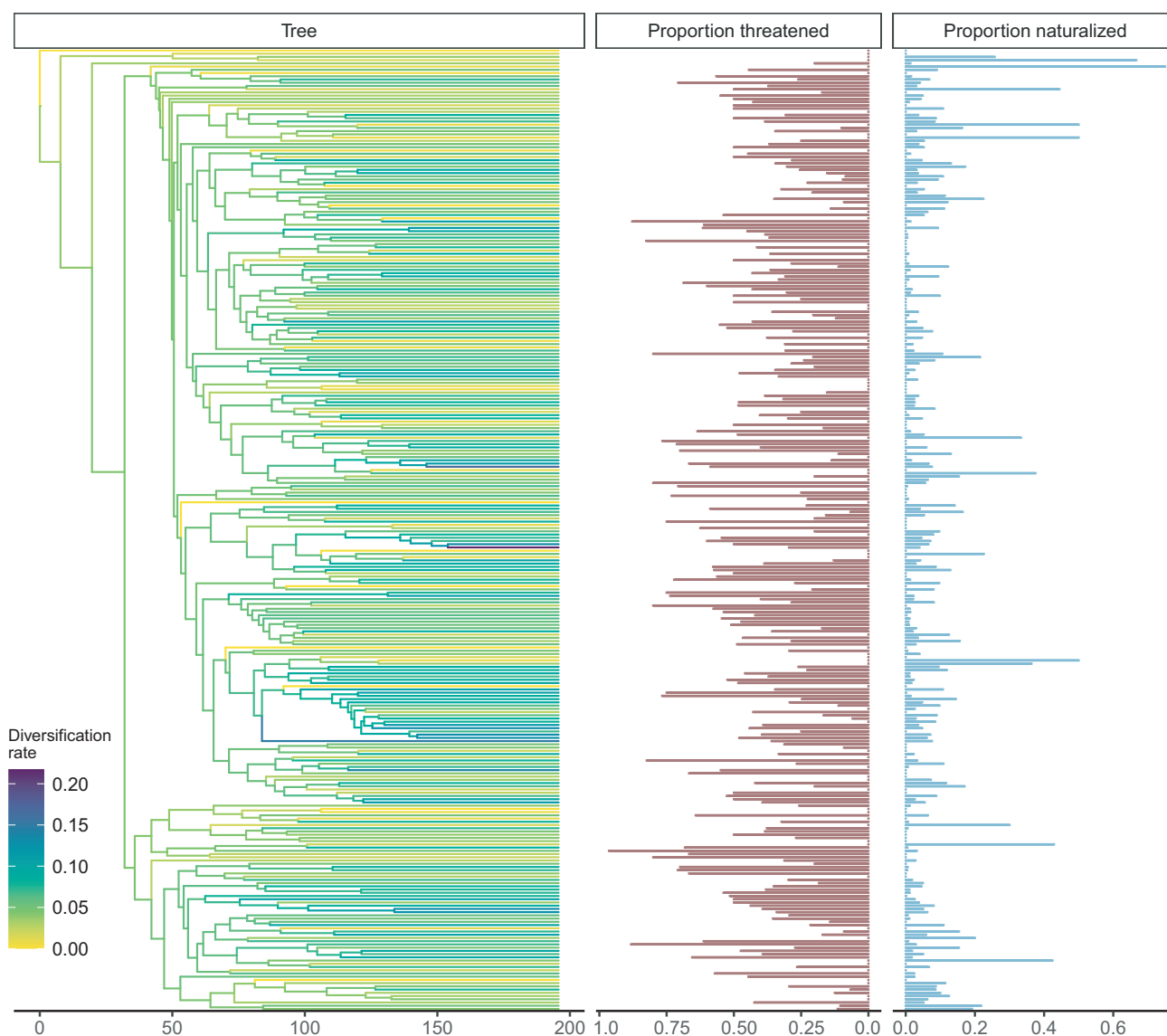
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Category	Correlates	Contrast	Geographic scope	Taxonomic scope	# species compared	Study type	Phylogenetically controlled	Source
Threatened	Monoccy, dry, indehiscent fruits	Rare and threatened species to entire native flora	Australia	Terrestrial plants	18 822	Comparative study	Threatened species clustered in some clades, small families less likely to contain threatened species	Sjöström and Gross (2006)
Threatened	Epiphytic, monococious, hermaphroditic, mammal pollination, restricted to inland forests	Rare and threatened species to entire native flora	Singapore	Terrestrial angiosperms	1884	Comparative study	Yes	Sodhi <i>et al.</i> (2008)
Threatened	Diploid rather than polyploid	Grassland plant species	South-central Sweden	Angiosperms	116	Field surveys, comparative study	Yes	Plue <i>et al.</i> (2018)
Threatened	Populations lost and decline in range greater for insect-pollinated, non-wetland and locally dispersed taxa	Degree of threat among rare species	New England	Angiosperms	71	Occurrence records	No	Farnsworth and Ogurcak (2008)
Rare	Endemic species likely to be either herbs or shrubs and plastic in growth form, whereas suffusively rare species more likely to occur in wetland habitats.	Endemic (large local populations but small geographic ranges, 22.6%) vs. suffusively rare (small local population sizes but large geographic ranges, 2%)	U.S., Canada	Vascular plants	NA	Comparative treatment of patterns	Most rare species are Eudicots, but suffusively rare species more likely to be monocots or seedless vascular plants, and less likely to be Eudicots.	Mills and Schwartz (2005)
Rare	Rare species smaller and produced fewer and shorter lived diaspores than common species	Rare and common species occurrence across habitat patches by species traits	north western Germany	Herbaceous angiosperms pre-dominantly growing in closed forests, at forest edges or in gaps, or in the forest as well as in the open landscape	82	Field surveys, comparative study	No	Kolb and Diekmann (2005)

communities and biogeographic regions (Richardson & Pyšek 2006). Nonetheless, successful invasions have been correlated in comparative studies with a suite of traits – autofertility (Burns *et al.*, 2011; Razanajatovo *et al.*, 2016), self-compatibility (Hao *et al.*, 2011), height (van Kleunen *et al.*, 2007; Ordonez *et al.*, 2010), small seeds (Hamilton *et al.*, 2005; Ordonez *et al.*, 2010), high specific leaf area (Hamilton *et al.*, 2005; Ordonez *et al.*, 2010), large native range size (van Kleunen *et al.*, 2007; Schmidt *et al.*, 2012a), broad climate and habitat tolerances (Bradshaw *et al.*, 2008; Pyšek *et al.*, 2009; Schmidt *et al.*, 2012a; Gallagher *et al.*, 2015), competitive ability (Guo *et al.*, 2018), variability and perhaps plasticity in growth form and life history (Schmidt *et al.*, 2012b), abiotic pollination (Daehler 1998; Hao *et al.*, 2011), polyploidy (Pandit *et al.*, 2011; Schmidt *et al.*, 2012a; Schmidt *et al.*, 2012b) and

hybridisation (Ellstrand & Schierenbeck 2000; Schierenbeck & Ellstrand 2009) – that appear consistently advantageous (Table 1). Thus, while naturalised species may also be non-randomly distributed among angiosperm families (Pyšek 1998; Daehler 1998; Pyšek 2017) and benefit from historical factors extrinsic to ecological features, trait syndromes across clades appear to strongly influence invasion success.

Here, adjusting for phylogenetic relatedness, clade size and geographic range, we ask whether (1) the representation of globally threatened species by flowering plant family is related to that of naturalised species (Fig. 1); (2) the frequency of species in either category tends towards the opposite extremes of broad trait axes captured by readily available data related to life history and dispersal – autonomous seed production, abiotic pollination and animal-dispersed fruits, large range size



**Figure 1** Phylogeny of angiosperm families with at least one species vetted by the IUCN, and with less than 100% of species categorised as either threatened or naturalised ( $n = 298$ ). Internal branches (*left*) show family-level diversification rate,  $\log(\text{species richness})/\text{clade age}$ . For illustrative purposes, we used ancestral state reconstruction via the *fastAnc* in the *phytools* R package to paint the diversification rates onto the branches of the tree. Proportion IUCN-vetted species classed as globally threatened in red (*middle*) and proportion of all species in the family naturalised in blue (*right*).

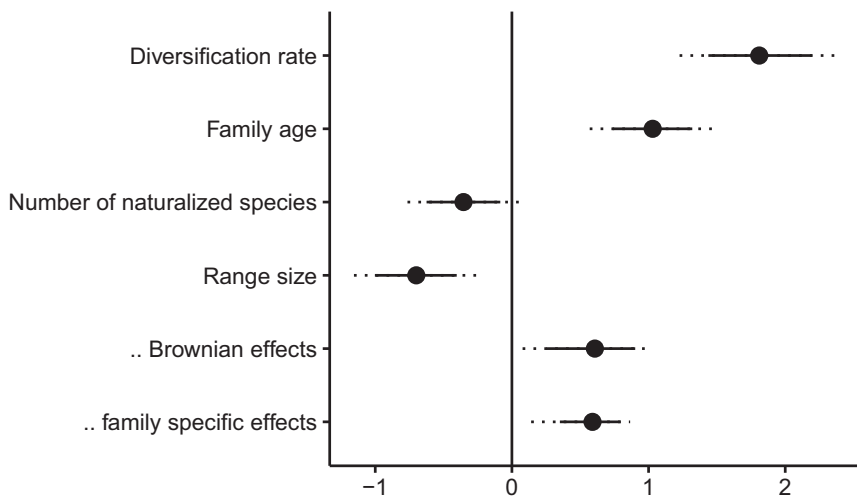
and climate generalism, hybridisation, growth form and generation time, and (3) the relative importance of traits vs. evolutionary history as explanatory variables differs for threat vs. naturalisation. We evaluate these hypotheses in a hierarchical Bayesian regression framework – allowing us to quantify uncertainty in analyses and to better compare effect sizes among predictors.

**RESULTS**

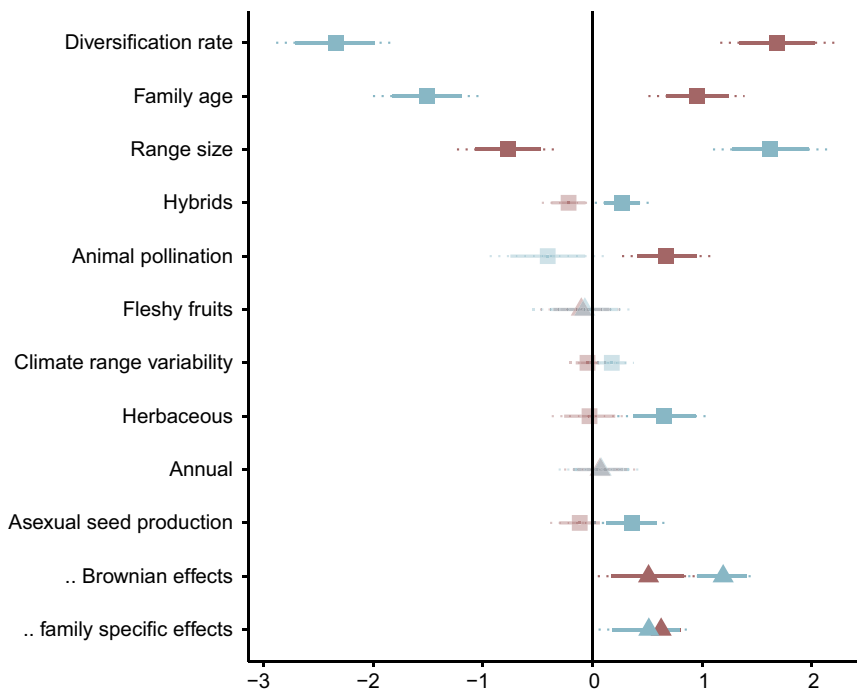
Across angiosperm families, the proportion of vetted species classed as threatened was negatively related to the proportion of naturalised to total species (Fig. 2) – although the 95% credible interval of the effect of naturalised species richness includes 0. In separate models predicting the proportion by family of threatened to vetted species or naturalised to total species as a

function of traits and evolutionary history, the proportion threatened was positively related and the proportion naturalised negatively related – to family age and diversification rate. However, the pattern was opposite for range size. Notably, the negative effects of diversification rate and family age, and positive effect of range size, on proportion naturalised were greater in magnitude than the opposite effects of these same factors on proportion threatened (Fig. 3).

Trait covariates also showed opposing patterns in threatened vs. naturalised models. Threat decreased with the number of interspecific hybrids and was higher in families that included animal pollinated species (Fig. 3). In contrast, proportion naturalised per family was positively related to the number of interspecific hybrids, and negatively to animal pollination. Herbaceous growth form and presence of species with asexual seed production were also positively related to



**Figure 2** Estimated model parameters (regression coefficients and standard deviations for hierarchical effects) for the proportion threatened by family among the 317 families with IUCN-vetted species as a function of the number of naturalised species, while adjusting for diversification rate ( $\log(\text{family size})/\text{family age}$ ) and the estimated standard deviation parameters ( $\sigma$ ) for the family level effects: Brownian (phylogenetic) effects and the (non-phylogenetic) family-specific effects. Mean parameter estimates are indicated by points, 80% credible intervals as solid lines and the 95% credible intervals as dotted lines.



**Figure 3** Estimated model parameters (regression coefficients and standard deviations for hierarchical effects) for both the proportion threatened by family (*red*) among the 317 families with IUCN-vetted species and the proportion naturalised (*blue*) among all species per family for all 395 families included in the study. Squares (rather than triangles) indicate variables with opposite effects on naturalised vs. threatened status, pale symbols indicate credible intervals overlapping zero. Mean parameter estimates are indicated by points, 80% credible intervals as solid lines and the 95% credible intervals as dotted lines.



proportion naturalised per family but did not affect proportion threatened. While annual life history, climate variability (number of climate zones occupied) and presence of fleshy fruits had no clear effect on proportion either threatened or naturalised per family (Fig. 3), results overall suggest family level trait syndromes.

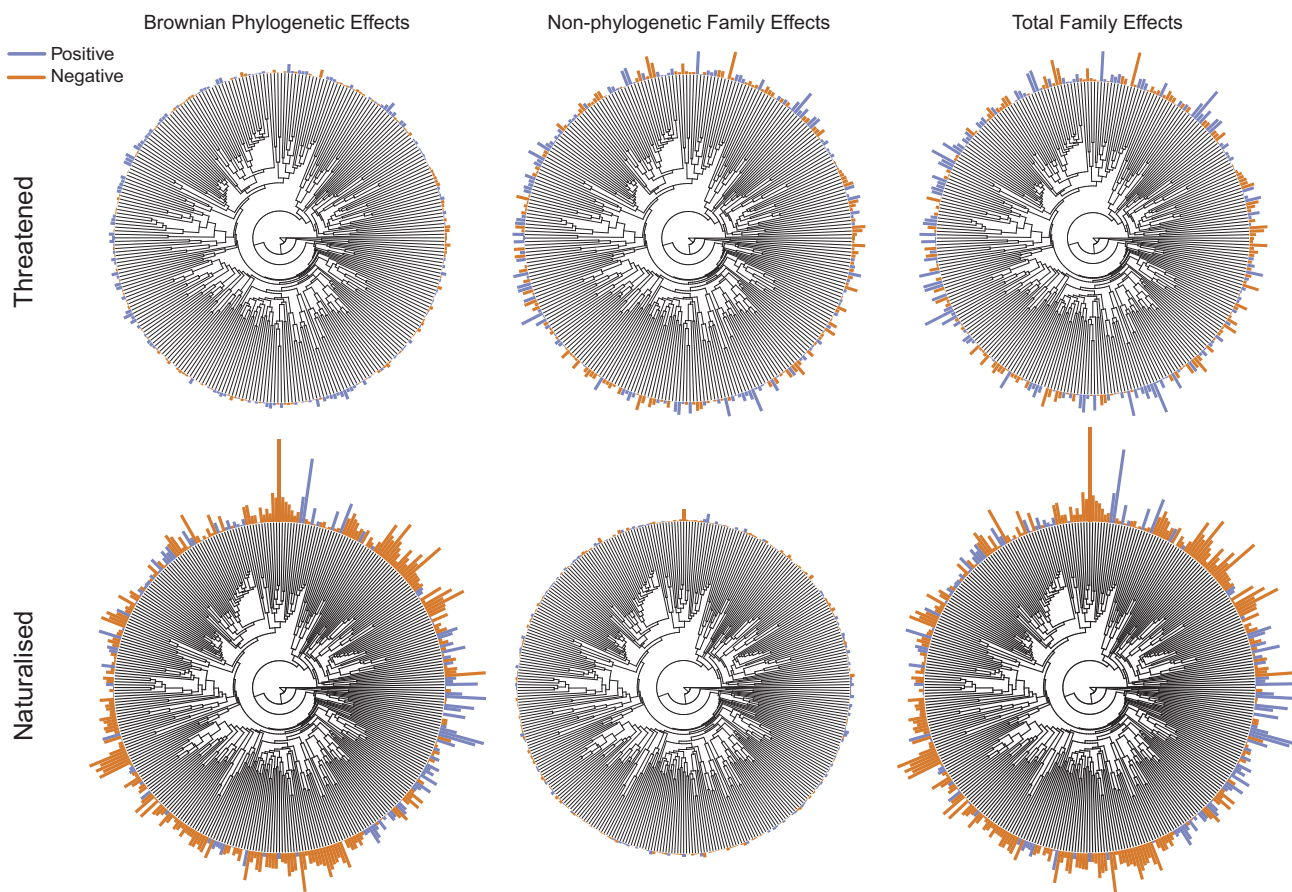
Model fit (normalised root mean squared error: *NRMSE*) for threat (*NRMSE* = 0.31, *SD* = 0.04) was better than for naturalisation (*NRMSE* = 0.51, *SD* = 0.07). And, contrary to expectations, the proportion of the total variance in family level effects explained by the Brownian phylogenetic component (phylogenetic heritability, Lynch's  $\lambda$ ) was higher for naturalisation ( $\lambda$  = 0.81, *SD* = 0.15) than threat ( $\lambda$  = 0.40, *SD* = 0.27, Fig. 4). Sensitivity analyses using the total number of species per family rather than IUCN-vetted species in the binomial response (*NRMSE* = 0.47, *SD* = 0.05, S3.3) and excluding all family level effects (*NRMSE* = 1.14, *SD* = 0.05, S3.2) both reduced threat model fit, demonstrating the importance of controlling for data deficiencies and family-level variation not accounted for by trait data. Sensitivity analyses using the Methods of Moments diversification rate estimates (0.97 correlation with the simple diversification rate) resulted in nearly identical results (S3.4).

## DISCUSSION

At the global scale, we show that the drivers of threat and naturalisation across angiosperms are opposing, and that this can be explained by divergent macroevolutionary and ecological trait relationships. We note that models excluding family-specific effects or phylogeny were poorer fits, indicating that a large component of the variation among families still remains unexplained; and family-level estimates of age and diversification rate (not entirely separable) may not optimally capture the signature of macroevolutionary processes towards the present.

Nonetheless, our results provide the first quantitative support at a global scale across angiosperms for the hypothesis that naturalisation and threat represent “two sides of the same coin” (van Kleunen & Richardson 2007; Bradshaw *et al.*, 2008; Jeschke & Strayer 2008; Pandit *et al.*, 2011; Schmidt *et al.*, 2012).

Consistent with previous studies (Lozano & Schwartz 2005; Davies *et al.*, 2011), diversification rate was positively related to proportion threatened per family. In contrast, naturalisation was negatively related to both diversification rate and family age. Fast diversifying clades are often associated with



**Figure 4** Family-level hierarchical effects for the full model of the proportion IUCN-vetted species threatened per family (*top row*), and the proportion naturalised (*bottom row*) among all species per family, separated into Brownian phylogenetic, non-phylogenetic (termed family-specific effects in the models) and total family effects (the addition of Brownian phylogenetic and non-phylogenetic effects). Purple bars indicate positive effects, orange bars indicate negative effects and bar lengths indicate the relative magnitude of the mean estimated effect per family.

localised radiations that give rise to many endemics with narrow ranges that are restricted to particular habitat types (e.g. many plant lineages in the Fynbos, South Africa, have diversified rapidly, and are characterised by a high diversity of narrowly distributed species, frequently restricted to particular soil types, Davies *et al.*, 2011). This high ecological specialisation likely restricts geographical expansion and naturalisation outside the native range, resulting in a negative correlation between diversification and naturalisation. More established lineages, and those in older families may have had more time to spread and thus have had more opportunities to become naturalised outside their native range. However, as species age, they may also contract in their geographic extent, especially if the environmental conditions which favoured their initial expansion change (c.f. taxon cycle: Ricklefs & Bermingham 2002). Species experiencing range contraction are also less likely to become naturalised elsewhere. As only old families can contain old species, this could lead to a negative correlation between naturalisation and family age. The negative relationship we find between diversification and naturalisation is in apparent contradiction to the findings of Lenzner *et al.*, (2020), who found a positive relationship between diversification and “naturalisation success” in angiosperm families. In fact, we are modelling quite different responses such that the results of the two studies might be harmonised (Naturalisation success was calculated by dividing naturalised species per family in GLoNAF by total species per family in The Plant List then multiplying by the “number of regions where each species of the family is naturalised in to characterise invasion success by both the number of species that have successfully naturalised in at least one region and the total size of the area colonised by these species”). In our study, the magnitude of the negative effects of diversification rate and family age on naturalisation was also somewhat greater than those of the positive effects on threat. Contrary to initial expectations, after adjusting for macroevolutionary and life-history predictors, we also found that in the naturalisation model, a larger fraction of variance in total family level effects was attributable to Brownian phylogenetic effects compared to the equivalent model for threat. We suggest that one possible explanation for the weaker signature of macroevolutionary process on threat is the mixing of threatened taxa found within both young and old clades such that observed threat captures two independent processes.

The opposing relationship between threat and naturalisation was also manifested in the trait syndromes that characterise either status. Naturalisation was positively related to herbaceous growth form, range size (but not necessarily the breadth of climate tolerance), frequency of interspecific hybrids and asexual seed production, and negatively related to animal pollination, whereas threat was negatively related to range size and frequency of interspecific hybrids, and positively to animal pollination. The correlations we detect among angiosperm families match closely to expectations from theory and existing comparative studies across various scales (Table 1) – with naturalisation characterised by habitat/climatic generalism and large native range size (van Kleunen *et al.*, 2007; Schmidt *et al.*, 2012a), abiotic pollination (Daehler 1998; Hao *et al.*, 2011), asexuality (Burns *et al.*, 2011; Razanajatovo *et al.*,

2016) and polyploidy and perhaps hybridisation (Schmidt *et al.*, 2012b; Schierenbeck & Ellstrand 2009, but see Whitney *et al.*, 2009) and threat by habitat specialism and endemism (Rejmánek 2018; Olsen *et al.* 2018), dependence on mutualists (Farnsworth & Ogurcak 2008; Sodhi *et al.*, 2008) and diploidy (Plue *et al.* 2018; Pandit *et al.*, 2011).

That we recover such strong associations at higher taxonomic levels and at a global scale is notable and suggests that the trait signatures characterising threat and naturalisation in the present day extend back over deep evolutionary time. Thus, while particular trait syndromes appear to predispose some species to higher risk of extinction and others to ecological expansion, this might not translate straightforwardly to long-term macroevolutionary dynamics. For example, the traits characteristic of threatened species today may be features that permit chronically rare species to persist (e.g. the directed movement of pollen by an animal vector) and, by limiting outcrossing, allow adaptation to spatially restricted environmental conditions (Vermeij & Grosberg 2018). An alternative strategy – promoting colonisation and expansion at range margins – relies on features such as abiotic pollination, asexual seed production, and, to enable rapid niche shifts in the face of novel climatic conditions or sudden environmental change, hybridisation and polyploidy (Vanneste *et al.*, 2014; Baniaga *et al.*, 2019). Both strategies may thus represent successful macroevolutionary syndromes, but under contrasting selective regimes.

## METHODS

### Data

To estimate species richness, from The Plant List (TPL, <http://www.theplantlist.org/>) we tabulated the number of species (including interspecific hybrids, but excluding infraspecific taxa) within each of 395 angiosperm families (per APG3, Angiosperm Phylogeny Group 2009) present in the Ramirez-Barahona *et al.*, (2020) supertree for which trait values were also available – counting only the 302 733 species with ‘Accepted’ names. To determine the number of species in each class, we compiled a list of all angiosperms labelled as (1) ‘naturalised’ (11 146 species) in any region, globally, from the GLoNAF database (van Kleunen 2019); and (2) as ‘threatened’ (12 367 species), if listed as globally ‘Vulnerable’ or more threatened by the International Union for the Conservation of Nature (<https://www.iucnredlist.org/>, accessed March 11, 2019). We labelled species as ‘not threatened’ if listed as ‘Least Concern’ or ‘Near Threatened’ by the IUCN. To control for study effort, we summed the number of species per family that have currently been assessed by the IUCN excluding those labelled ‘Data Deficient’, 31 345 species in all across the 395 families. In all cases (naturalised, threatened and vetted), we again counted only those species with accepted names per TPL. Of the 395 families, 235 included a naturalised species, 317 included an IUCN-vetted species and 240 vetted families included a threatened species.

To test the effect of broad climate tolerance and range size at the family level, we retrieved binary data on climate zones (tropical, subtropical, temperate and frigid zone) occupied

from the Watson & Dallwitz (1992 onwards) online key to angiosperm families. To capture variability in climate tolerance, we then summed the number of climate zones (1–4) reported across species within each family. For family range size, the combined extent of the ranges of all species in the family, we relied on data from Hawkins *et al.*, (2011).

We assembled data on traits related to life-history strategy (growth form, breeding system, dispersal, hybrid formation) from a variety of sources that provide tabular trait data by angiosperm family. From Watson & Dallwitz, animal pollination and fleshy fruits were coded for each family as 1 if biotic pollination (328 families) or fleshy fruits (73 families) was the sole mode, 0.5 if multiple traits (biotic and abiotic pollination (13 families) or fleshy and non-fleshy fruits, 131 families) and 0 if only abiotic pollination (44 families) or dry fruits (191 families) are known. From Watson & Dallwitz and data from the Plants National Database (<https://plants.sc.egov.usda.gov/>), we labelled families as known to include annual species (1, 98 families) or otherwise (0, 297 families). From Zanne *et al.*, (2014) and Hawkins *et al.*, (2011), we classified families as predominantly herbaceous (1, 151 families), predominantly woody (0, 188 families) or mixed (0.5, 56 families). From The Plant List, we tallied the number of interspecific hybrids per family (126 families contained at least 1 hybrid). To make statistical models less complex and more readily interpretable, rather than including multiple overlapping binary variables, we use 0.5 to indicate families that are polymorphic for a binary trait. Lastly, we used data from Hojsgaard *et al.*, (2014) to identify families in which apomixis or asexual seed production (1, 203 families) is known to occur vs. all other families (0, 322 families).

To control for family age and diversification rates, we used estimates of stem family ages extracted from the Ramirez-Barahona *et al.*, (2020) time tree of flowering plants. We use this phylogeny because it is well informed by the fossil record, and thus family ages are likely highly robust to sample completeness, tree resolution and included sequence data.

### Statistical analyses

We used Bayesian binomial-logit multilevel regressions to model the proportion of species threatened and naturalised per family. This approach allows us to model proportions on their natural scale, to partition family level hierarchical effects and trait effects and to propagate uncertainty in estimating parameters. To test the relationship between threat and naturalisation, we fit an initial model for each family with the proportion of all species naturalised as the response, and family age and diversification rate as continuous predictors, and as second model with the proportion of vetted species (those assessed by the IUCN) that have been classed as threatened as the response. To aid in the comparison of effect sizes across continuous and binary predictors, we log transformed, centred and scaled (to a standard deviation of 0.5) all continuous predictors prior to analyses (Gelman 2008). To identify traits associated with the proportion of species threatened and naturalised per family, we fit two additional models that included family-level traits, and family age and diversification rate. We first calculated diversification rate as  $\log(N)/\text{clade}$

age, which is the maximum-likelihood estimate of diversification rate assuming negligible extinction (eq. 3 in Magallon & Sanderson 2001). While previous work has shown that this metric provides robust family level diversification rate estimates for comparative analyses (Jansson & Davies 2008), it is nonetheless possible that high extinction rates could bias estimates for some families. To evaluate the robustness of our results, we also explored rate estimates with a relatively high assumed extinction fraction ( $e = 0.9$ ) by following the method of moments approach of Magallon & Sanderson (2001). To account for phylogenetic non-independence and family-level effects in each of these models, we included hierarchical effects by family separated into phylogenetic (assuming a Brownian motion model of evolution) and non-phylogenetic effects. To do this, we followed an additive quantitative genetic model adapted to interspecific data (Lynch 1991). We calculated the correlation matrix for determining family-level Brownian phylogenetic effects from the Ramirez-Barahona *et al.*, (2020) time tree of flowering plants pruned to a single representative species per family.

We fit all models in Stan version 2.18.0 (The Stan Development Team 2020) accessed using the R package *brms* version 2.7.0 (Buerkner 2017). We fit models with *brms* default priors, uniform for the regression coefficients, and half-Student's  $t$  distributions with three degrees of freedom and scale parameter of 10 for the variance components of the family-level effects. As these represent extremely weak priors, for the simplified and full threatened models, we also explored the use of alternative custom priors (normal (0, 1.5) for regression coefficients and normal (0,1) for family effect standard deviations), which reflect more realistic expectations (Figs S1 and S2). We found a negligible influence of each set of priors on posterior estimates (S2), and therefore applied the *brms* default priors for all other models. We ran models across four chains, with 10 000 iterations per chain. For each chain, the first 5000 iterations were used as burn-in and discarded. The remaining iterations were thinned to retain every fourth iteration, resulting in a total of 5000 posterior draws. We diagnosed convergence by visual inspection of traceplots and observation of Rhat values equal to 1.0 for all estimated parameters and assessed model fit using posterior predictive checks (see Data & Code supplement) and root mean square error (*RMSE*). To compare model fits across varying responses, we calculated the normalised *RMSE* (*NRMSE*) scaling by the interquartile range of the observed data, and across all posterior samples. To calculate phylogenetic heritability (Lynch 1991), we used the *hypothesis* function in *brms* with the hypothesis  $\sigma^2_{\text{Brownian}} / (\sigma^2_{\text{brownian}} + \sigma^2_{\text{family-specific}}) = 0$  across all posterior samples.

To explore the effect of including both Brownian and non-phylogenetic family-specific effects, we ran sensitivity models which fit the full threatened model with a) no family-level effects, b) non-phylogenetic family-specific effects only, and c) Brownian phylogenetic effects only. To determine the effect of using the number of IUCN-vetted species rather than the total number of species per family, we fit the full threatened model with total species richness per family as  $n$  (the denominator) in the binomial model. Lastly, we also explored the effect of using the Method of Moments diversification rate estimates.

## ACKNOWLEDGEMENTS

We thank the Macroecology of Infectious Disease Research Coordination Network, funded by NSF (DEB 1316223), for facilitating discussion among the authors and for supporting MJF as a postdoctoral research associate. We also thank several anonymous reviewers for quite helpful suggestions.

## AUTHOR CONTRIBUTIONS

JPS, MJF and TJD designed the study. JPS compiled the data. MJF conducted the analyses. JPS wrote the manuscript with input from TJD and MJF. The authors declare no conflicts of interest.

## DATA ACCESSIBILITY STATEMENT

All data and code necessary to reproduce the results are included in <https://figshare.com/s/6d032d41cf669f4bd6e1> (reserved <https://doi.org/10.6084/m9.figshare.11372037>). New data – family range size, newly calculated family age and diversification rates – accompany this revision.

## PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13740>.

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Editor, Tim Coulson

Manuscript received 25 January 2021

Manuscript accepted 27 February 2021