

Do plant reproductive traits influence species susceptibility to decline?

Sandrine Godefroid^{1,2,3,*}, Steven Janssens¹ & Thierry Vanderborght¹

¹Botanic Garden Meise, Domein van Bouchout, Nieuwelaan 38, BE-1860 Meise, Belgium

²Laboratory of Plant Biology and Nature Management (APNA), Vrije Universiteit Brussel, Pleinlaan 2, BE-1050 Brussels, Belgium

³Laboratory of Systems Ecology and Resource Management, CPI 264/1, Université libre de Bruxelles, Avenue F.D. Roosevelt 50, BE-1050 Brussels, Belgium

*Author for correspondence: sandrine.godefroid@br.fgov.be

Background and aims – Habitat destruction, eutrophication and fragmentation are the main drivers of plant extinctions. In addition to these environmental factors, it has been suggested that features related to intrinsic characteristics of the species play a role in their decline, however leading to widely divergent results. This paper aims at exploring whether intrinsic factors (species traits) can play a role in the decline of plant species, by specifically asking whether: (1) plant reproductive traits are significantly different between declining species and species that are doing well; and (2) these traits are related differently to species trend in different countries, suggesting context-dependent relationships.

Methods – Species traits and trend indices were compared for large datasets from UK (1136 species) and Northern Belgium (1055 species) using multiple trait analysis (GLM) and single trait analysis (Kruskal-Wallis analysis of variance).

Key results – Of the ten traits considered, type of reproduction and pollen vector showed by far the strongest association with species trend, although differently in each of the datasets considered. Species trends were also associated to flower class, floral reward, diaspore type, dicliny and breeding system, but patterns were not consistent among countries confirming a context-dependence of these findings.

Conclusions – The relationships between decline and plant traits likely depend primarily upon extrinsic (environmental) factors, which might explain the difficulty in recognising consistent patterns. Consequently, environmental degradation (e.g. habitat destruction) is likely the main driver of plant decline and may cause extinctions irrespective of species traits. This context-dependence of the findings indicates that reliably identifying those species most prone to extinction based on their reproductive traits is problematic. We therefore recommend great caution when interpreting patterns emerging from the study of species traits.

Key words – Change index, functional traits, life-history traits, reproductive biology.

INTRODUCTION

Plant extinctions are a growing threat to biodiversity worldwide. To minimise this threat, it is critical to understand what factors are influencing plant extinction rates (Hahs et al. 2009). In Western Europe, the loss or degradation of appropriate habitat and eutrophication are apparent causal factors (e.g. Thompson & Jones 1999, Godefroid 2001, Van Landuyt et al. 2008). Habitat fragmentation is also recognised as a main issue responsible for plant species loss (e.g. Godefroid & Koedam 2003, Van Geert et al. 2010). In addition to these environmental factors, it might be possible that features related to intrinsic characteristics of the species play a role in their decline. It is for instance expected that habitat fragmentation select for a predictable suite of species that carry traits related to metapopulation persistence or persistence despite

small population size (Williams et al. 2009). For example, species with limited dispersal capacity, low seed production or no seed bank are more vulnerable to loss via failed recolonisation (Williams et al. 2009). Species that are dependent on specialised pollinations are also at greater risk of loss through fragmentation (Pauw 2007).

Even though autecological studies unveil important aspects of species' biology, it is actually impossible to carry out such studies for every rare species (Murray et al. 2002). Indeed, in Europe alone, according to the latest and most detailed list, there are almost 2000 threatened plant species, representing 15% of the European flora (Sharrock & Jones 2009). Comparative studies of a large number of plant species can reveal crucial features of life history that influence species' susceptibility to extinction (Farnsworth & Ogurcak 2008). Such knowledge is crucial for providing a scientific

basis for the development of strategies aimed at conserving species in the long term (Kunin & Gaston 1997, Murray et al. 2002, Kolb & Diekmann 2005). Determining which factors increase the probability of a species becoming extinct can for instance help to predict future extinctions. It can also potentially reduce the need for large numbers of expensive and time-consuming autecological studies (Murray et al. 2002).

Several studies have examined the distribution of rare vs. common species across a variety of ecological and life-history traits, such as competitive ability, habitat specialisation, growth form, plant height, dispersal mode, seed size, seed number, clonality, specific leaf area, flowering period (Lahti et al. 1991, Cadotte & Lovett-Doust 2002, Lavergne et al. 2004, Pilgrim et al. 2004, Bekker & Kwak 2005, Kolb & Diekmann 2005, Farnsworth 2007, Stehlik et al. 2007, Farnsworth & Ogurcak 2008, Gargano et al. 2009, Cornwell & Ackerly 2010, Duncan et al. 2011). Some traits have been shown to correlate with extinction risk in plants, such as plant height, longevity, growth form, seed mass, and the size and persistence of the seed bank (Pimm et al. 1988, Leach & Givnish 1996, Stöcklin & Fischer 1999, Williams et al. 2005). However, according to other comparative studies, no clear differences between the traits of rare and common plant species have emerged (Bevill & Louda 1999, Murray et al. 2002, Lozano et al. 2003). Trying to untangle the relationships between life-history traits and species threat status through a review of 54 studies, Murray et al. (2002) have shown that most studies are characterised by small sample size, with often very little replication at the level of rare-common species contrasts. They therefore stressed the need for more comparative studies incorporating a large number of rare vs. common species if we want to make robust generalisations in relation to rare-common differences or similarities. Furthermore, it has been demonstrated that the outcome of the studies was overwhelmingly to differ from each other, which might be due to differences in the way in which rarity is measured between studies (Murray et al. 2002), i.e. abundance (density, percentage canopy cover, biomass, number of individuals, area of occupancy), distribution (extent of occurrence, number of populations, area of occupancy), or threatened status (rare species listed as endangered or vulnerable by relevant authorities particular to each study). These weaknesses highlighted by Murray et al. (2002) are still present in some recent studies where a limited number of species is taken into account (e.g. Farnsworth 2007, Cornwell & Ackerly 2010). However, one must emphasize the recent work of Duncan et al. (2011) who compiled data on eleven plant traits for 8269 species. Nevertheless, even with such a large number of species, the main finding of this study was that few traits reliably predicted extinction probability.

In the present study, we want to revisit the topic, using an approach that eliminates some drawbacks of previous studies. We chose not to use a measure of rarity but an index of decline. Indeed, we believe that the trend of a species (decline or increase) will be more consistent across regions compared to its rarity. As species may be rare but not threatened (stable trend), analysing their trend is more relevant from a conservation perspective because it focuses on their degree of endangerment, what the rarity does not necessarily

do. Comparing species of varying trend index may therefore be an interesting way to identify factors that promote decline and extinction in plants. Such trend indices were analysed for a large dataset and compared between two regions: Britain (1136 species) and Northern Belgium (1055 species). As there is still fragmentary information about which role reproductive biology can play in the current loss of species, we focus on those traits that are related to floral and reproductive biology, using some features that were so far scarcely explored (e.g. dichogamy, pollen vector, flower class, diaspore type). The fact that reproduction processes cannot cope with changes in the environment could be the main reason for species extinction (Moza & Bhatnagar 2007). By using these features in combination with trend indices, we can potentially advance our understanding of the role played by life-history traits in plant extinctions.

The aim of this paper is therefore to explore whether intrinsic factors (unfavourable species traits) can play a role in the decline of plant species, by specifically asking whether: (1) plant reproductive traits are significantly different between declining species and species that are doing well; and (2) these traits are related differently to species trend in different countries, suggesting context-dependent relationships.

MATERIALS AND METHODS

Contrary to previous comparative studies investigating relationships between plant traits and species rarity, we used in the framework of this study a measure of species decline instead of rarity. Since the latter does not predict the probability of extinction, focusing on species decline instead of rarity will be more relevant from a conservation point of view because it can help to understand the mechanisms that underlie extinctions. Focusing on species trend instead of rarity allows to link traits with species dynamics, what rarity does not. Rarity reports species abundance while the trend reveals how that abundance has changed in the recent past. Another advantage of using species trend is that it is a quantitative variable that can be treated as a continuous variable, whereas rarity is most often a qualitative variable (rare vs. common) implying the use of cut-offs or thresholds. Rarity was once the only criterion used to allocate species status, but increasingly there is a focus on decline (Telfer et al. 2002). For instance, the IUCN threat categories are based on five quantitative criteria, three of which include an assessment of decline in either range or population size. In order to quantify species' decline, we used the change index developed by Telfer et al. (2002). This index measures the relative magnitude of change in range size using atlas data from two different periods. The method allows for the effect of variations in the geographical coverage and intensity of recorder effort. For the earlier and later periods, a weighted linear regression model is fitted to the relationship between counts of grid cells (as logit-transformed proportions). An index of the relative change in species' range size is provided by the standardised residual for each species (Telfer et al. 2002).

In order to test the robustness of the outcome, we wanted to compare the results obtained from two geographical areas with different environmental contexts. We chose two regions having intensive flora recording and accessible databases,

UK and Northern Belgium (Flanders), where the species trend is very-well known. This knowledge makes them valuable study cases for analysing patterns of regional declines. For the British flora, the change index was taken from the PLANTATT database (Hill et al. 2004), comparing the period 1930–1960 with 1987–1999. For the Belgian flora, the change index was gathered from the *Atlas of the Flora of Flanders and the Brussels Capital Region* (Van Landuyt et al. 2006), comparing the period 1939–1971 with 1972–2004. It ranges from -4.78 to 4.70 for the whole British flora, but since we focused only on native species, this index ranges from -2.68 to 3.66 for those species used in the British dataset ($n = 1136$). In the case of the Belgian flora, the change index varies from -3.13 to 6.06 for the whole flora, and from -2.58 to 4.62 for those species used in the Belgian dataset ($n = 1055$).

Information on species traits was obtained from the BiolFlor database (Klotz et al. 2002). We focused on those traits that are related to floral and reproductive biology as they may significantly influence extinction risks: type of reproduction, dicliny, dichogamy, self-compatibility, pollen vector, breeding system, amount of floral reward, flower class, fruit type, and diaspore type (table 1). Species' dispersal ability can be affected by the type of reproduction, pollen vector, fruit type and diaspore type, whereas self-incompatibility, breeding system, dicliny and dichogamy are known to influence outcrossing rate (e.g. Routley & Husband 2003, Adam et al. 2011) and therefore reproduction success. We may also expect that the amount of floral reward influences insect visitation having therefore an impact on the quantity and quality of seeds. Since flower classes are often specific to a particular type of pollinators, we can assume that the decline of some of them might affect plant survival. Certain species show various attributes within one trait, e.g. some individuals of a plant which is most often hermaphrodite may have been recorded as gynomonocious, or individuals of a plant normally pollinated by insects can sometimes develop selfing at failure of outcrossing. For these species, we selected only those attributes whose frequency was recorded as 'always' or 'the rule' in the BiolFlor database, discarding those that were categorised as 'possible' or 'rare'. Traits with a high number of attributes that could obscure some patterns have been pooled into a smaller number of functional categories (table 1).

To control for the non-independence of species data, we first checked whether trend indices showed any phylogenetic signal that would prevent us from using traditional linear regression (Blomberg et al. 2003). For doing this, we calculated the lambda metric, a maximum-likelihood-based measurement of phylogenetic signal (Pagel 1999), after constructing a phylogenetic tree for each dataset (UK and BE) based on the recently published phylogeny dated supertree for Central European angiosperms (Durka & Michalski 2012). This analysis was carried out using the *phylosig* function as implemented in the *Phytools* package (Revell 2012) in R version 3.0.2 (R Core Team 2013). Pagel's lambda is equal to 0 when the trait is evolving independently of the phylogeny, while a value of 1 indicates the presence of a phylogenetic structure (Pagel 1999, Freckelton et al. 2002). The lambda metric indicated that there was no phylogenetic signal in the

Table 1 – Species traits and their attributes used in the framework of this study.

n = number of species in each dataset (UK and BE). Similar categories were pooled in order to provide sufficient power for the analyses: flower classes were pooled according to the type of pollinator (long proboscis = butterfly or moth flowers; short proboscis = bee, bumble bee, hymenoptere, ichneumonide or syrphid flowers); fruit types were pooled according to their ability to open at maturity (dehiscent = legume, lomentum, capsule or siliqua; indehiscent = berry, drupe, nut, pome, aggregate nutlets, aggregate drupelets).

Trait	Attributes	n (UK)	n (BE)
Type of reproduction	only or mostly by seed	414	488
	by seed and vegetatively	468	422
	only or mostly vegetatively	64	64
Dicliny	dioecious	86	53
	hermaphroditic	701	754
	monoecious	169	169
Dichogamy	protandrous	186	220
	homogamous	276	289
	protogynous	259	257
Self-compatibility	self-compatible	605	646
	self-incompatible	135	136
Pollen vector	insects	418	448
	selfing	169	199
	wind	250	246
Breeding system	obligate or mainly allogamous	387	392
	mixed mating	183	187
	obligate or mainly autogamous	202	227
Amount of floral reward	none	214	217
	little	18	24
	present	367	402
Flower class	plenty	42	31
	long proboscis	20	15
	short proboscis	544	603
Fruit type	water flowers	6	7
	wind flowers	274	269
	dehiscent	412	408
Diaspore type	indehiscent	420	464
	fruit	515	561
	infructescence	10	19
	seed	356	350

trend index for the British dataset ($\lambda = 0.088$) and a low phylogenetic signal for the Belgian dataset ($\lambda = 0.489$). This lambda test indicated that no phylogenetic correction is needed for the UK dataset, which makes sense since we do not expect that trend indices are correlated with the phylogeny. However, given the ambiguous lambda value of the Belgian dataset, we nevertheless wanted to check whether a phylogenetic adjustment would substantially alter our results, using the *pgls* function in the *caper* R package

Table 2 – Summary of GLM analysis on the effect of plant reproductive traits on species' trend for both datasets (Belgium and UK).

Source	Belgium				UK			
	SS	df	F	P	SS	df	F	P
reproduction type	6.714	2	6.404	0.002	2.304	2	2.739	0.066
dicliny	2.257	2	2.153	0.117	1.337	2	1.589	0.206
dichogamy	0.172	2	0.164	0.848	0.047	2	0.056	0.945
self-compatibility	0.007	1	0.014	0.907	0.328	1	0.779	0.378
pollen vector	0.392	2	0.374	0.688	0.064	2	0.076	0.926
breeding system	1.743	2	1.663	0.191	0.021	2	0.025	0.975
amount of floral reward	3.888	3	2.472	0.061	1.804	3	1.430	0.234
flower class	0.26	2	0.248	0.781	0.589	3	0.467	0.705
fruit type	0.398	1	0.759	0.384	0.592	1	1.408	0.236
diaspore type	0.062	1	0.118	0.731	0.766	1	1.820	0.178

(Orme et al. 2013). The comparison between phylogenetically corrected and uncorrected models showed that phylogenetically corrected models did not result in any change in the significance patterns observed.

To evaluate the effects of reproductive traits (explanatory variables) on species decline (response variable), we first used General Linear Models. For this multiple trait analysis, data reduction was required prior to model development since each explanatory variable contained a different set of missing values. As a consequence, the model was run on 518 and 405 species for the Belgian and British flora, respectively.

In a second step we analysed all traits separately by means of Kruskal-Wallis tests because we were also interested in detecting the range of reproductive traits - and therefore the range of mechanisms - associated to species decline, rather than finding the best model predicting performance from traits (Pywell et al. 2003). Here we could use the entire datasets (1055 species for Belgium and 1136 species for UK). Post-hoc comparisons were done with the Scheffé test.

GLM's, Kruskal-Wallis and Scheffé tests were performed using SYSTAT 8.0 (Wilkinson 1998). The 0.05 level of probability was accepted as threshold of significance throughout this work.

RESULTS

Multiple trait analysis

Of the ten variables considered for multivariable modelling, only one significantly contributed to the species change index in both countries (type of reproduction) although marginally in the UK dataset (table 2).

Single trait analysis

The type of reproduction showed a significant association with species trend (fig. 1A). Patterns however, were not consistent from one dataset to the other. In the British flora, species reproducing by seeds were declining while species reproducing vegetatively were extending (Kruskal-Wallis test: $H = 8.812$, $P = 0.012$, $df = 2$). This pattern is reversed for the

Belgian flora (Kruskal-Wallis test: $H = 26.885$, $P < 0.001$, $df = 2$).

Species trends were correlated with dicliny only in Belgium (Kruskal-Wallis test: $H = 6.380$, $P = 0.041$, $df = 2$), with monoecious species showing a small decline, differing significantly from the slightly extending hermaphroditic ones (fig. 1B).

In both datasets, dichogamy and self-compatibility had no effect on species trend (fig. 1C & D).

In the British dataset, we found self-pollinated species and insect-pollinated species to be prone to decline whereas wind-pollinated species increased (Kruskal-Wallis test: $H = 49.942$, $P < 0.001$, $df = 2$). In the Belgian flora, self-pollinated species were characterised by a significant extension of their range size (Kruskal-Wallis test: $H = 13.909$, $P = 0.001$, $df = 2$, fig. 1E).

Species trend was related to breeding system only in the Belgian dataset (Kruskal-Wallis test: $H = 9.080$, $P = 0.011$, $df = 2$), with allogamous characterised by their decline while autogamous increasing their range size (fig. 1F).

In UK, species with floral reward were affected by a stronger decline compared to those offering no reward (Kruskal-Wallis test: $H = 15.559$, $P = 0.001$, $df = 3$). In Belgium, those species whose flowers provide the largest amount of reward were affected by the most pronounced decline (Kruskal-Wallis test: $H = 9.072$, $P = 0.028$, $df = 3$, fig. 2A).

Flower class was also significantly related to species trend (fig. 2B). In UK, wind flowers showed an increase in their range size whereas insect flowers (long or short proboscis) showed a decline (Kruskal-Wallis test: $H = 50.264$, $P < 0.001$, $df = 3$). With the Belgian flora, pairwise comparisons showed no differences while the overall tests was significant (Kruskal-Wallis test: $H = 10.179$, $P = 0.017$).

Species trend was related to fruit type only in the British dataset (Mann Whitney test: $U = 73887.0$, $P < 0.001$, $df = 1$), with most declining species characterised by dehiscent fruits (fig. 2C).

When looking at diaspore type (fig 2D), patterns were similar in both countries although marginally significant in the British flora (Kruskal-Wallis test: $H = 6.645$, $P = 0.036$,

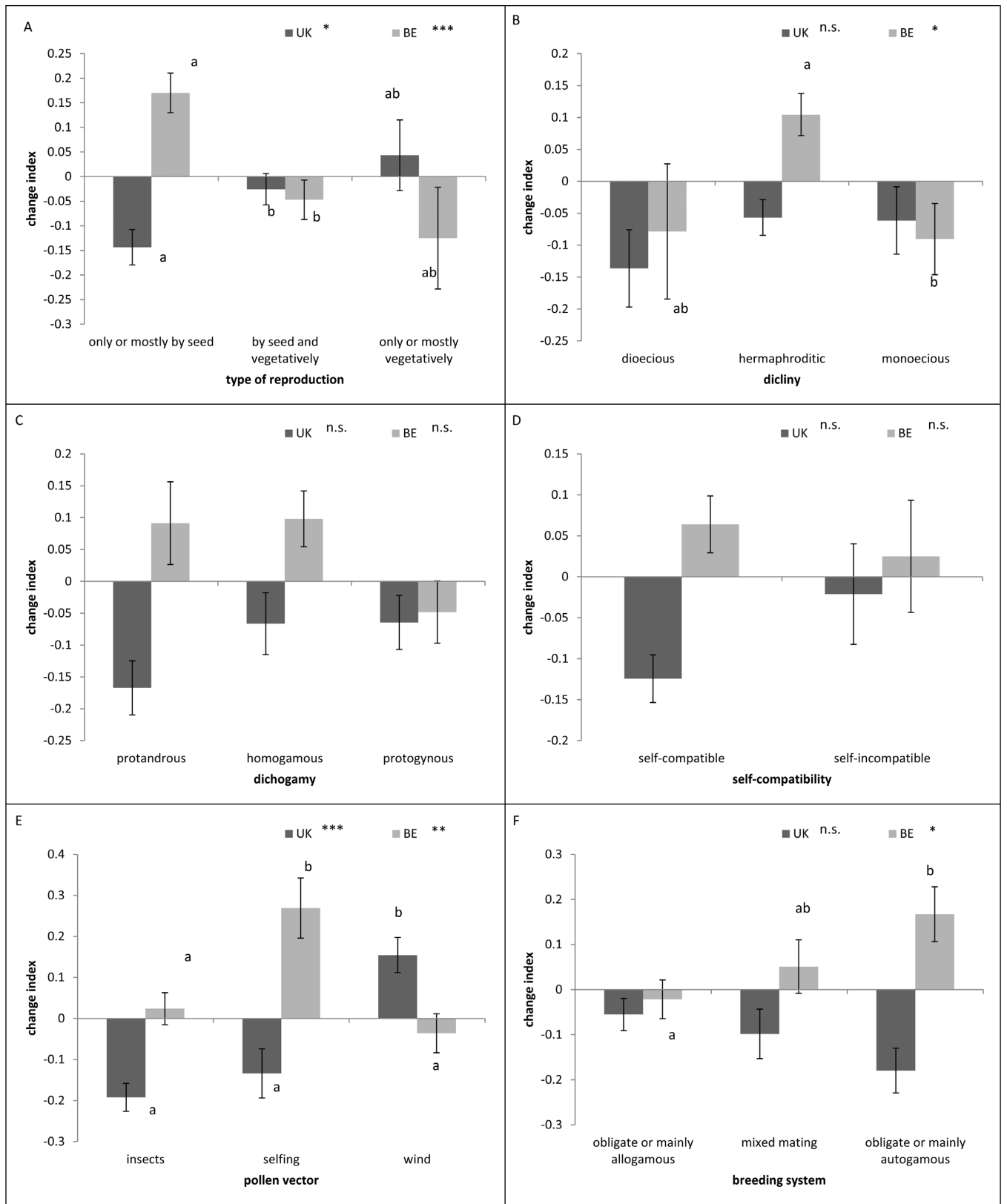


Figure 1 – Relationship between species’ trend in Great Britain (UK) and Belgium (BE) and their type of reproduction, dicliny, dichogamy, self-compatibility, pollen vector and breeding system. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; n.s. = not significant (see text for details). Different letters within each country show significant differences among groups ($P < 0.05$).

df = 2). In both countries, species dispersed as infructescence, showed an increasing trend (Kruskal-Wallis test: $H = 7.303$, $P = 0.026$, $df = 2$).

DISCUSSION

Plant reproductive traits and species decline

Of the traits that have been examined in previous studies, seed size and competitive ability have by far received most attention (Murray et al. 2002), while traits considered in the present study have rarely been investigated. In both approaches (single-trait vs. multi-trait analyses), reproduction type emerged as a (marginally) significant explanatory variable in relation to species decline. In the British dataset, we found that vegetatively-reproducing species were expanding while species that lack this ability were declining. When environmental conditions do not allow species to produce seeds, the ability to spread vegetatively may be important for

the long-term persistence of populations. This was illustrated by a meta-analysis of grassland restoration experiments, showing that species using vegetative reproduction had higher performance than species relying on seasonal regeneration by seed production (Pywell et al. 2003). Vegetative reproduction is advantageous for long-term persistence in undisturbed or moderately disturbed sites (McIntyre et al. 1995). In an urban-rural gradient in Australia, Williams et al. (2005) found that the lack of vegetative reproduction increased the probability of local extinction in all landscapes. The Belgian flora however behaves differently, with species reproducing only or mostly vegetatively being affected by a significant decline. According to Kunin (1997), a vegetatively reproducing species cannot easily adapt to changing conditions. It also gradually accumulates deleterious mutations (Müller 1964) leading to a further deterioration of its performance (Kunin 1997). Asexuality might therefore cause species to become gradually less fit, and thus, presumably, rarer (Kunin 1997).

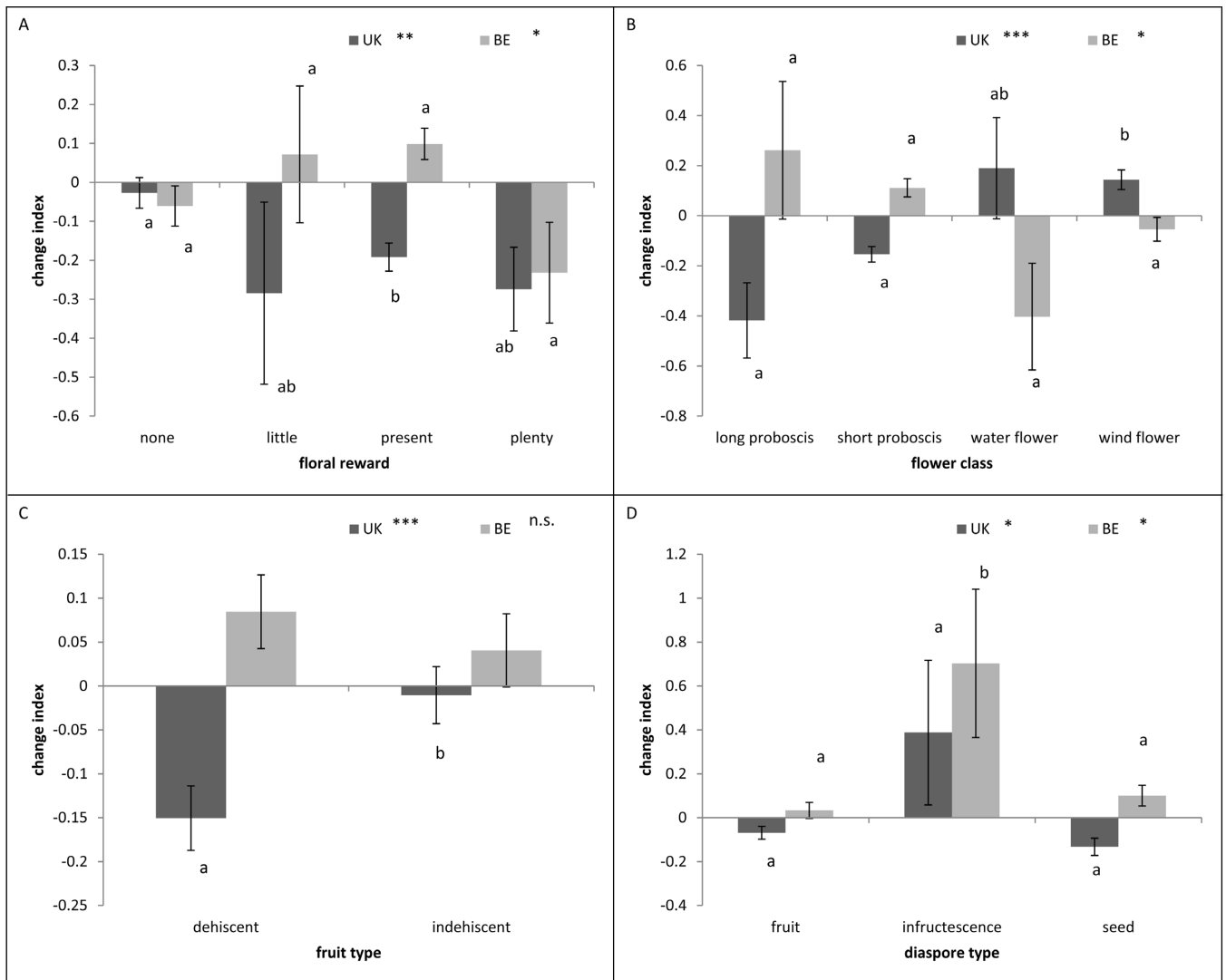


Figure 2 – Relationship between species' trend in Great Britain (UK) and Belgium (BE) and amount of floral reward, flower class, fruit type and diaspore type. *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; n.s. = not significant (see text for details). Different letters within each country show significant differences among groups ($P < 0.05$).

In the multi-trait model, all other traits did not affect species' trends, whereas in the single-trait approach, some significant patterns emerged. Several reasons might explain that. First, the multi-trait analysis examines all correlations simultaneously and gives a complete representation of all interdependencies between traits, whereas the simple-trait analysis produces pairs of correlations and ignores the possible contribution of other related traits in each correlation pair. Then, one must keep in mind that the multi-trait model was run with twice fewer species than the single-trait analysis since the former does not accept missing values, with possible consequences for the obtained patterns.

Concerning dicliny, we found that species decline was unrelated to whether or not species were monoecious or dioecious. We were therefore unable to confirm patterns emerging from previous studies. For instance, Cadotte & Lovett-Doust (2002) found that rare species were less likely to be dioecious while comparing 1398 rare and common native plants of southern Ontario. When examining correlates of extinction proneness in 1884 plant species from Singapore, Sodhi et al. (2008) found that dioecious species have a lower extinction probability compared to monoecious or hermaphrodite species.

There were three traits related to selfing (pollen vector, self compatibility and breeding system), but not all were significant. However, if we compare the significant results with each other, we see that they are consistent, e.g. in the Belgian flora both self-pollinated and autogamous species show an increasing trend, which obviously makes sense. For the British flora, insect-pollinated species appeared to be more in decline than wind-pollinated ones. This result is in accordance with previous works having found wind-pollination to be under-represented among rare species (Kelly & Woodward 1996, Cadotte & Lovett-Doust 2002, Pilgrim et al. 2004, Carvell et al. 2006, Farnsworth & Oğurcak 2008) and it supports the "cost of mutualism" hypothesis proposed by Kelly (1996), that association with a specific pollinator constrains the range a plant species may colonise. Anemochory enables dispersal over greater distances (Lososová et al. 2006), increasing the likelihood that wind-dispersed species reach favorable habitats. Kolb & Diekmann (2005) also demonstrated that insect-pollinated species are more negatively affected by habitat fragmentation. In the Belgian flora, self-pollinated species increased in comparison with those pollinated by insects or wind, but possible reasons for this pattern remain obscure.

With respect to breeding system or self-compatibility, no consistent pattern emerged. This confirms previous studies (Anderson 1980, Mehrhoff 1983, Fiedler 1987, Karron 1987, Byers & Meagher 1997, Kunin & Schmid 1997, Bosh et al. 1998, Young & Brown 1998), the vast majority of which only exploring one rare-common contrast. This finding is rather astonishing, as we could have expected that self-fertilization would be favoured via natural selection in geographically restricted species that receive little or unreliable pollinator visitation (Karron 1987). Using the British dataset, it appeared that autogamous species show a (non significant) tendency to be more prone to decline than allogamous species, which is in accordance with some experimental data (Fréville et al. 2007) and genetic models suggesting that selfing species

may be more prone to extinction than outcrossing species (e.g. Barrett & Kohn 1991, Lennartsson 2002). Self-fertilisation can lead to a deterioration of a species' performance, due to a rapid loss of genetic diversity in heavily inbred individuals (Kunin 1997). Selfing therefore causes species to become gradually less fit, and thus, presumably, rarer (Kunin 1997). The opposite pattern found with the Belgian dataset remains puzzling.

Concerning the access to floral rewards, no consistent pattern became apparent, probably because open access increases the number of pollinator visits but may decrease their quality (e.g. through inappropriate pollen brought by a generalist pollinator), whereas restricted access limits the range of pollinators liable to visit but increases incentives for floral constancy, i.e. the tendency of individual pollinators to exclusively visit certain flower types (Kunin & Schmid 1997).

When looking at the flower class, the most significant differences emerged from the British dataset. To our knowledge, it is the first time that relationships between species decline and flower class are described. Interestingly, species with flowers adapted to long-proboscis (pollinated by butterflies and moths) were found to be the most declining in UK. These pollinator groups are precisely those that are most in decline globally and especially in Western Europe (Rasmont & Mersch 1988, Fitzpatrick et al. 2007, Kosior et al. 2007, Patiny et al. 2009, Grunewald 2010, Potts et al. 2010, Brereton et al. 2011, van Swaay et al. 2011). In Britain and the Netherlands, Biesmeijer et al. (2006) also reported parallel declines in pollinators and the plants that rely upon them.

Concerning the diaspora type, the fact that species whose dispersal unit is (a section of) the infructescence are doing better than species dispersed by fruits or seeds might be due to the presence of a hard or hook-like beak (e.g. *Arctium* spp., *Hordeum* spp.) that can attach to animal fur, making dispersion therefore more efficient.

Context-dependence of the findings

We have seen that the traits that predict species decline may substantially vary among locations, indicating a context-dependence of these findings, as already suggested by Pilgrim et al. (2004). Comparing the trends of plant species in Britain and the Netherlands, Biesmeijer et al. (2006) also found a reverse pattern in insect-pollinated outcrossing plants that were declining in Britain and increasing in the Netherlands.

Detecting patterns in differences between rare and common plants is exceedingly difficult given the incongruous nature of the data (Bevill & Louda 1999). For this reason we have considered here standardised parameters in order to allow potential generalisations while avoiding this bias. Using the change index (instead of rarity) for both datasets ensures that the same calculation method was used for obtaining species trends. Differences among regions can therefore not be explained by data from different origin. The same is valid for species traits that are taken from the same database for both case studies. In a review of studies addressing similar questions, it was apparent that conflicting results could emerge when different special scales or very different floras were considered (Murray et al. 2002). Even if Northern Belgium is infinitely small compared to UK, values reported in both

datasets are expressed at large scale (10 × 10 km squares are employed for biological recordings in the British Isles, while 4 × 4 km squares are used in Belgium). Moreover, both species lists do not differ greatly from each other (717 taxa were common to both datasets), which allows us to exclude the flora as a cause of divergence in the outcome. However, some inconsistencies have been detected when looking at the species' trend indices in each of the studied region. Some species indeed show opposing trends, i.e. are increasing in one country and declining in the second and vice versa. For instance, *Dryopteris affinis*, *Puccinellia distans* or *Nymphoides peltata* are strongly increasing in the UK, while they are declining in Belgium. The opposite appears for e.g. *Epilobium parviflorum*, *Solanum dulcamara* or *Galium aparine*. This might be due to the fact that drivers of plant range may vary geographically, as recently shown by Powney et al. (2014) in a trait-based analysis of range change in the flora of Britain. For instance, nitrogen deposition is higher in Northern Belgium than in Great Britain (Sutton et al. 2011). This can explain why some nitrophilous species increase in Belgium and decrease in the UK. Furthermore, the different patterns obtained in both regions may be due to the time spans taken into consideration. For Belgium, both periods are 33 year long, while for UK the first period of 31 year is compared to a second of 13 years. However, threshold dates are likely more important than time spans, and in both countries the first time interval corresponds to a period of stability of the flora, while the second period is characterized by many changes in land use and local extinctions.

The lack of consistent plant trait-decline relationships may also arise because extinction is more about being in the wrong place than possessing a particular suite of traits (Duncan et al. 2011). Recognising consistent patterns can therefore be difficult also because the relationships between decline and plant traits are likely to depend upon extrinsic (environmental) factors (Fréville et al. 2007). This could mean that environmental degradation (e.g. habitat destruction) might be the main driver of plant decline and may cause extinctions irrespective of species traits. This is what emerges from several other studies. For instance, after having examined a wide variety of traits in 1884 plants from Singapore, Sodhi et al. (2008) highlighted that only a relatively small amount of variation in extinction probability could be explained by life history correlates. Since they carefully chose traits based on previous studies, one can doubt that the poor explanatory power was due to inappropriate traits being used. They concluded that the loss of plant species in their study area was largely due to habitat destruction irrespective of life-history traits, and that the extinction process is more random than previously thought and mainly due to stochastic forces operating after population reduction. Similarly, Duncan et al. (2011) compiled data on eleven plant traits for 8269 species and found that few traits reliably predicted the pattern of plant extinction. They concluded that the complexity of environmental changes most likely obscure simple trait responses because there are multiple drivers affecting multiple traits which may not be independent.

Implications for conservation

The identification of traits associated with species that have become endangered or vulnerable is of critical importance (Murray et al. 2002). Approaches based on species traits may aid in the assessment of the endangerment of plant species and ultimately in the conservation of biological diversity (Kolb & Diekmann 2005). For this reason, one of the main goals of this study was to provide useful biological information for management strategies aiming at the long-term conservation of species. Because extinction is often delayed (extinction debt), it is important to assess which species are likely to go extinct in a near future. Despite the fact that the multi-trait model highlighted a (marginally) significant link between species' trend and the type of reproduction in both countries, the single-trait approach revealed patterns that are not directly exploitable because of discrepancies between both countries. There were however patterns that deserve to be further explored. For instance in the British flora, we have seen that threat seems to be clumped within particular functional groups (e.g. insect-pollinated, reproducing only or mostly by seeds, long proboscis flowers), which may require special attention in the future. In UK, species like *Anacamptis pyramidalis*, *Daphne laureola* or *Lychnis viscaria* share these three attributes while currently not (yet) declining. We have not been able to prove the same patterns for the Belgian flora, but if it turns out that this tendency can be confirmed for other floras, special attention should then be paid to those plant species within these functional groups that are not presently threatened (Lockwood et al. 2002) as these species may have a higher chance than expected of becoming endangered. The implementation of such approach could enable conservation efforts, which are limited by resources and funds, to be more focused and proactive (Pilgrim et al. 2004). Plant trait-based analyses may also provide a useful approach for identifying those areas most in need of conservation. Indeed, areas containing a high proportion of species with traits that predispose them to decline may have high extinction rates.

The outcome of this study could potentially inform the ongoing process of conserving plant species in UK and Belgium. However, an important conclusion of this work is that the relationships between plant traits and species decline can vary from one area to another, implying that these results are not necessarily transposable to other Western European regions. This context-dependence of the findings indicates that reliably identifying those species most prone to extinction based on their reproductive traits is problematic. We therefore recommend great caution when interpreting patterns emerging from the study of species traits.

ACKNOWLEDGMENTS

The authors thank Quentin Groom and Filip Vandeloos for statistical advice and constructive recommendations. Pierre Meerts and three anonymous reviewers provided valuable comments on an earlier draft of this paper.

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Manuscript received 13 Mar. 2013; accepted in revised version 24 Mar. 2014.

Communicating Editor: Pierre Meerts.