Using Encyclopedia of Life's TraitBank to identify plant traits associated with vulnerability

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Abstract

Certain biological traits seem to predispose some species to greater extinction risk than others and, when vulnerability information is limited, could be used as proxies to identify understudied species likely in need of protection. In the past, identifying broadly applicable traits associated with extinction risk has been hampered by the difficulty of collecting information for a broad range of species (both geographically and taxonomically), with most comparative analyses focusing on regional and/or taxon specific patterns. However, efforts to collect and compile existing trait information from regional and taxon specific datasets into a single repository are making it possible to analyze patterns between traits and vulnerability on ever broader scales. We compared trait information from one such repository, the Encyclopedia of Life (EOL) TraitBank, to information on threat status from the International Union for the Conservation of Nature (IUCN) Red List to determine whether such consolidated data can help either clarify

PeerJ PrePrints | http://dx.doi.org/10.7287/peerj.preprints.491v1 | CC-BY 4.0 Open Access | rec: 8 Sep 2014, publ: 8 Sep 2014

previously identified associations or identify new associations between plant traits and threat risk. Using generalized linear mixed effects models (GLMM's) we found five plant traits that could be used to predict whether a species is threatened or not: 'plant growth form', 'life cycle habit', 'low temperature tolerance', 'soil depth' and 'foliage porosity in winter'. Threatened plant species tend to be trees rather than shrubs or grasses, live for more than one season (i.e. perennials), be less tolerant of cold temperatures, require deep soil for good growth, and have less dense foliage in the winter. Both 'plant growth form' and 'life cycle habit' have been identified as correlates of vulnerability in past studies and both are relatively easy to use as diagnostic characters, which is ideal for identifying understudied species of potential conservation concern. However, how these two traits relate to vulnerability seems context dependent, with opposite relationships in past regional or taxon specific studies. Unfortunately we could not identify further traits that could add explanatory power to those relationships with the existing data on EOL's TraitBank but the repository is still growing and the inclusion of additional traits and/or species from other datasets could clarify these relationships further.

Introduction

Human activities are resulting in the loss of alarming numbers of species both regionally (extirpations) and globally (extinctions), with some scientists referring to the current era as the 'sixth mass extinction event' in history (Pimm et al., 1995; Stork, 2010). The fossil record indicates that there have been fewer mass extinction events for plants than animals in the past (Willis & Bennett, 1995). However, since the arrival and settlement of humans, a combination of direct exploitation, habitat change (loss, degradation and/or fragmentation), invasive species introductions, and climate change has led to plant species declines, extirpations and extinctions worldwide (Thomas et al., 2004; Hahs et al., 2009; Stork, 2010). Given limitations in money and time for conservation, it would be impossible to implement conservation measures for the 298,000 plant species estimated worldwide (Mora et al., 2011), only a small proportion of which have been studied (Vié et al., 2009). To best conserve the plant species remaining, strategies are needed to identify and focus efforts towards those species that are likely to disappear fastest and therefore need help most urgently.

Certain life history, ecological, and morphological traits appear to make some organisms more vulnerable to human activities than others and, where direct vulnerability information is limited, could be used as proxies to identify understudied plant species in need of conservation action. Although relationships between plant traits and vulnerability have not been studied as well as in other taxa, at least 80 of 118 plant traits assessed seem to have some relationship with at least one metric of vulnerability (plant species abundance, distribution, threatened status, or rarity) (reviewed in Murray et al., 2002; Walker & Preston, 2006; Stork et al., 2009; Neel & Che-Castaldo, 2013; Musters et al., 2013; Bradshaw et al., 2008; Mcintyre et al., 2014). Many of these identified traits were only examined in a single study and, among those examined in multiple studies (e.g. plant height, seed size, growth form), their relationships with vulnerability seem to depend on the scale and context of the study (Murray et al., 2002). For example, shorter plant species were more likely to go extinct than taller species after European settlement in New Zealand (Duncan & Young, 2000), but taller species are more likely to have a threatened status among legumes (family Fabaceae) on a global scale (Bradshaw et al., 2008). Establishing general relationships between plant traits and vulnerability has been difficult partly because studies tend to be limited in scope either geographically (e.g. Duncan & Young, 2000; Walker & Preston, 2006; Neel & Che-Castaldo, 2013; Musters et al., 2013), taxonomically (e.g. Bradshaw et al., 2008), or both (e.g. Sodhi et al., 2008). A further difficulty is that most studies have only analysed relationships with a single trait in isolation (reviewed in Murray et al., 2002), with some more recent notable exceptions (e.g. Duncan & Young, 2000; Walker & Preston, 2006; Neel & Che-Castaldo, 2013; Musters et al., 2013) and, therefore, may have missed important relationships among traits. The limited scope of past studies likely stems from the difficulty of collecting sufficient amounts of information about multiple traits for species from a broad taxonomic range and on a global scale.

Efforts such as the Encyclopedia of Life's (EOL) TraitBank are making it possible to compare a broader range of species (both geographically and taxonomically) and traits than was possible in the past, allowing for more thorough analyses of plant traits associated with vulnerability. The EOL TraitBank is "a searchable, comprehensive, open digital repository for organism traits, measurements, interactions and other facts for all taxa across the tree of life" (http://eol.org/info/516; Parr et al., 2014). The depository currently includes trait information for thousands of plant species, compiled from published studies (e.g. Chave et al., 2009), regional databases (e.g. the U.S. based USDA plants database (http://plants.usda.gov) and the Mediterranean based BROT Database (http://www.uv.es/jgpausas/brot.htm)), as well as databases specific to particular taxa (e.g. Shaw Nature Reserve Lily Database - http://www.missouribotanicalgarden.org/visit/family-of-attractions/shaw-nature-reserve.aspx) or biomes (National Wetland Plant List - http://rsgisias.crrel.usace.army.mil/NWPL/). Our goal in this paper is to assess whether the consolidated data in EOL's TraitBank can help clarify previously identified associations between plant species traits and their vulnerabilities and/or identify relationships with previously untested traits.

Methods

Compiling plant trait and vulnerability data

For plant species trait data we relied on EOL's TraitBank (accessed on 15 July 2014), transforming and/or combining some of the traits to make analyses easier. We manually searched the TraitBank repository for all life history, morphological, or ecological traits that included information for any plant species (Kingdom Plantae). Three traits contained information about seed size ("seed mass", "seeds per pound", and "seeds per unit") so we converted each into weight per seed (in grams) and combined them into a single "seed weight" trait, using averages for any species with more than one value. We also combined two traits that indicate whether a plant species has some commercial use ("commercial availability" and "uses") into a single "commercially used" trait, assigning each species to a category of either "used" or "not used" based on their original categories. Lastly, we converted the categorical "active growth period" trait (indicating the seasons in which plant growth occurs for a given species), into a numeric trait: "active growth duration", that indicates instead the number of seasons in the year (1-4) with active growth.

For our metric of plant species vulnerability, we categorized each plant species as either "threatened" or "lower risk", using the IUCN Red List extinction risk categories (IUCN, 2014; accessed on 01 August 2014). The IUCN Red List assigns each evaluated species to one of nine ordered risk categories, using the best data available and standard, rigorous criteria: Data Deficient (DD), Least Concern (LC), Lower Risk (LR), Near Threatened (NT), Vulnerable (VU), Endangered (EN), Critically Endangered (CR), Extinct in the Wild (EW), or Extinct (EX). We searched the Red List for all assessed plant species and compiled information on their threat status and taxonomy (kingdom, phylum, class, order, family, genus, species), removing any species assessed as Data Deficient, since extinction risk is uncertain for those species. Since all traits did not have representatives from each of the eight remaining extinction categories, we re-assigned each species to one of two categories: "threatened" (VU, EN, CR, EW, EX), and "not threatened" (LC, LR, and NT). The IUCN Categories and Criteria manual (IUCN, 2012), indicates that three categories are "threatened" (VU, EN, CR). Although there were few species within the two extinct categories (EW and EX), we also assigned those to our "threatened" category, assigning all others to a "not threatened" category (LC, LR, NT).

Analyzing relationships between plant traits and extinction risk categories

To identify relationships between species plant traits and the probability of being in a threatened Red List category we used generalized linear mixed effects models (GLMM's) and a stepwise model building approach. GLMM's have been used to test relationships between plant traits and vulnerability in several previous studies (e.g. Bradshaw et al., 2008; Sodhi et al., 2008). One of its advantages is that GLMM's can be used to test which combination of traits explain the most variance in extinction risk among plant species while controlling for the effect of phylogeny. Phylogenetically paired contrasts are another popular regression based method for comparing traits and vulnerability (Purvis, 2008), but are less appropriate when categorical variables are included in the analysis, as is the case for many plant traits in TraitBank.

We fitted GLMM's to the plant trait and vulnerability data using the 'lmer' function from the lme4 package in R (Bates et al., 2014). For each GLMM, we coded "threat" as a binomial response variable and each plant trait as a fixed effect, with a logit link function (Bates, 2010). To control for the fact that closely related species can have similar traits through shared evolutionary histories, we controlled for pseudoreplication stemming from phylogenetic influences by including taxonomy as a nested random factor in each GLMM (phylum/class/order/family). We did not have sufficient replication within genera to include genus in the nested random factor.

To identify individual plant traits associated with threat risk that should be considered in more complex models, we compared models with and without each trait. In each case, we compared full models (including the trait with taxonomy as a random factor) with reduced models (including only taxonomy as a random factor) using the 'anova' R function (R Core Team, 2013). We calculated the percent deviance explained by inclusion of each trait in the model and retained traits if their addition significantly reduced model deviance according to a Chi-squared test and false discovery rate corrected significance levels to account for multiple comparisons (Zuur et al., 2009). To further assess the relative strength of each full model, we calculated conditional and marginal R^2 values according to Nakagawa & Schielzeth (2013). Other studies have used Akaike's Information Criteria (AIC) or Bayesian information criteria (BIC) to compare the strengths of evidence for competing models (e.g. Bradshaw et al., 2008; Sodhi et al., 2008). However, those criteria are less suitable for comparison among models built using different datasets and many of the EOL TraitBank traits had information for different subsets of species (Nakagawa & Cuthill, 2007).

To test whether combined traits explain more of the deviance than any individual trait, we built GLMM's with combinations of traits retained from the individual analyses and compared those with GLMM's with individual traits. Starting with pairs of traits with the highest significance (i.e. lowest P-values), we used the 'anova' R function (R Core Team, 2013) to test for differences in deviance between models with and without each trait in combination (Zuur et al., 2009; Bates, 2010). Variables were only retained if they were not correlated with a trait already in the model and their inclusion significantly reduced model deviance according to a Chi-square test.

To determine whether there were any relationships among traits that could confound comparisons with threat risk, we tested for correlations/independence using Spearman rank tests or Chi-square tests, depending on the trait. For traits with continuous and/or ordered categorical values we tested for covariance using Spearman correlations in the ‘rcorr’ function from the Hmisc package in R (Harrell, 2014). To test for associations among categorical traits (ordered or unordered), we used Chi-square tests of independence (‘chisq.test’ function in R; R Core Team, 2013).

Results

We found 92 life history, ecological, morphological, and usage traits on EOL’s TraitBank that include information for plant species, 47 of which were useful for our comparisons with threat risk (i.e. had a plausible relationship with threat risk and sufficient sample sizes). Several traits were management-based with no clear hypothesis for how they could relate to species vulnerability (e.g., garden persistent range, germination treatment). The number of records returned by our EOL TraitBank search ranged from 1 to 48973 for each of the plant traits we identified, with an average (mean) of 2917 records. Our search of the IUCN Red List returned 19381 species, 1526 of which were assessed as Data Deficient, leaving 17856 species assessed in one of the categories informative for our analyses (i.e. could be assigned to a “threatened” or “not threatened category”. However, far fewer species (2340) had both threat risk information from the IUCN Red List and information for at least one of the 47 plant traits from EOL useful for our analysis, with each trait having information for a subset of those species (range = 1-1307 spp.; mean = 316 spp.). Consequently, several traits had information for too few species for analysis (e.g. ‘submergence tolerance’). It was possible to fit GLMM’s using traits with information for as few as 14 species (i.e. ‘seed ripening date’). However, it was not possible to combine traits with such small sample sizes in more complex GLMM’s.

According to GLMM analyses with individual traits, only five of the 47 traits we analyzed were significantly associated with variation in threat risk among plant species (Table 1). In comparisons of GLMM’s with and without each trait, ‘plant growth habit’, ‘low temperature tolerance’, ‘life cycle habit’, ‘foliage porosity in winter’, and ‘soil depth’ reduced between 2.7 and 16.8% of the deviance in whether a plant species was threatened or not, significant even after correcting for multiple comparisons using the false discovery rate ($P < 0.01$). ‘Plant growth habit’ had the most significant influence on reduction in deviance (i.e. lowest P-value) and resulted in the GLMM with the highest relative strength in predicting threat risk (marginal and conditional R^2 values > 0.98), indicating that trees have higher threat risk than shrubs and shrubs have higher threat risk than forbs/herbs or graminoids (Fig. 1a). However, low temperature tolerance explained more of the deviance in threat risk (17%) compared to its null model, indicating that plants that can withstand colder temperatures are less likely to be threatened (Fig 2a). Furthermore, plants that survive multiple seasons (perennials) were more often categorized as threatened than annual species (Fig. 1b) and those that have denser foliage in the winter were at greater risk than those with sparse foliage at that time of year (Fig. 1c). Finally, plants that need deeper soil for good growth had higher probabilities of being in a threatened IUCN Red List category (Fig 2b).

None of the GLMM models with multiple traits performed significantly better than individual models, except for those containing correlated traits. The combination of foliage porosity in winter and soil depth explained significantly more deviance than without either of those traits ($p < 0.02$). However, those two traits are linked. Plants that require deeper soil tend to have less foliage in the winter (Spearman rank test; $p < 0.0001$). Likewise, a combined model including life cycle habit and low temperature tolerance explained significantly more deviance in threat risk than without either trait ($p < 0.005$), but those two traits are negatively correlated: perennial species tend to have lower temperature tolerances than annual or biennial species (Spearman rank test; $p < 0.0001$).

Discussion

By comparing EOL TraitBank plant traits and IUCN Red List threat status information, we found evidence supporting associations between five traits and threat risk, two of which have been identified as correlates of vulnerability in the past: ‘plant growth habit’ and ‘life cycle habit’. Plant growth habit (or plant growth form, as it is sometimes termed), has been found to be associated with several metrics of vulnerability including distribution/rarity (reviewed in Murray et al., 2002), extinction proneness (Sodhi et al., 2008), and threatened status (Bradshaw et al., 2008), so it is perhaps not surprising that we found such a strong relationship, with a conditional R^2 value of 0.99. However, the direction of the relationship between plant growth form and vulnerability has differed somewhat among past studies. Our results are consistent with patterns reported for plants in central Australia and Sydney, where shrubs and trees were found to be rarer than herbs (Oakwood et al., 1993) and results among legume species, within which trees had higher probability of being threatened than shrubs or herbs and shrubs had higher probabilities of being threatened than herbs (Bradshaw et al., 2008). In contrast, our results differ from those reported for British plants, where trees are less likely to be rare (Kelly & Woodward, 1996), and for Australian *Eucalyptus* species in which trees are more common than shrubs (Murray et al., 2002). Our results for 'life cycle habit' (sometimes referred to as 'longevity') also differ from results reported for rarity in grassland plants, among which annuals and biennials were less abundant with narrower distributions than perennials (Eriksson & Jakobsson, 1998). Our hope was to clarify previously identified relationships between plant species traits and their vulnerabilities but it appears that these two traits may be context dependent. Since we were unable to find any associations with the other traits in our analysis that might account for some of this context, further analyses may be needed to explore additional factors.

In addition to the two previously identified traits, we found associations between threat risk and three apparently untested traits: 'low temperature tolerance', 'soil depth' and 'foliage porosity in winter'. Although we were unable to find any comparative analyses that examine relationships between low temperature tolerance and vulnerability, bioclimatic models predict that plant species with narrower tolerance ranges (including temperature tolerances) will be more vulnerable to anthropogenic climate change (Midgley et al., 2002). High temperature tolerance may be more important as warming continues, but low temperature tolerance may also impart some resilience to the increase in stochastic events predicted to occur with climate changes. Unfortunately we did not have access to high temperature tolerance data but it would be interesting to compare the two to determine their relative and combined influence on vulnerability. 'Soil depth' is essentially another measure of abiotic tolerance; plants requiring deeper soil should be more vulnerable as it could limit the possible range of environments they can inhabit, thus limiting their ability to spread into new areas when habitats are disturbed or altered through climate change. Possible mechanisms linking foliage porosity in winter and threat risk are less clear. In general, plants that can go through periods of dormancy can also withstand dramatic changes (Stork et al., 2009). High porosity in winter could be linked to a plant's ability to shed leaves during periods less suitable for growth. However, if that were the case we would expect to find a relationship between 'shedability' (deciduous or evergreen) and threat risk, but we did not. Since foliage porosity is correlated with soil depth, it could also be that it is this indirect connection that is responsible for the relationship with threat risk.

Interestingly, we did not find significant relationships among other traits previously hypothesized to be predictive of plant vulnerability. In particular, plant height has been linked to vulnerability in at least three separate studies, with some indicating short plants are more vulnerable (Mitchley, 1988; Duncan & Young, 2000; Walker & Preston, 2006), and another indicating tall species are at greater risk (Bradshaw et al., 2008). However, these studies were either regionally based (Mitchley, 1988; Duncan & Young, 2000; Walker & Preston, 2006) or focused on specific plant taxa (Bradshaw et al., 2008). If the direction of the relationships between plant height and vulnerability depends on the context, as suggested by these past studies, we may not have found a relationship with this trait because it is not generalizable on broader geographic and taxonomic scales. Seed production is another trait that has been linked to vulnerability in several studies but, unlike relationships with plant height, results have been consistent with more productive species being less vulnerable (reviewed in Murray et al., 2002). We did not find a significant relationship between the associated EOL trait 'fruit/seed abundance' and threat risk. However, our analysis was hampered by the limited number of species from a threatened category with this information (only 15 spp.).

There are several possible reasons why we may not have found more significant relationships between extinction risk and the plant traits we used, including (1) choosing inappropriate traits, (2) biases or inconsistencies in either the predictive variables (traits) or the response variable (threat risk), or (3) insufficient sample sizes for each trait and their combinations. We included a large number of potential traits, many of which were hypothesized to have an influence on vulnerability in previous studies. However, it is possible that we missed some other important traits or other related variables in our analysis. One of the drawbacks of our analysis (and many other similar analyses) is that we only had one trait value for each species. It could be that the variability in traits within a species is as important or more than the mean value for a species (e.g. phenotypic plasticity). However, trait databases rarely include intra-specific variability. In addition to intrinsic traits such as those that we used, other comparative analyses are including extrinsic factors (e.g. rainfall, human population density, invasive species) to identify correlates of vulnerability and extinction risk in other taxa (Murray et al., 2011; Tingley et al., 2013). While these extrinsic factors have proven useful for regional analyses, it could be difficult to summarize such spatially explicit factors for species with large ranges. In all broad comparative analyses of extinction risk, such as this one, there are also concerns about whether the data represent an unbiased sample (González-Suárez et al., 2012). In our data, for example, there could be more information for species that are more conspicuous or have commercial uses. However, as part of our analysis we examined the spread of the data among groups and found no obvious skew in the data. In addition to biases, there could be important differences in the way variables are measured. For instance, other comparative analyses have included more categories in their ‘plant growth form’ trait than used in the EOL TraitBank (e.g. epiphytes: Sodhi et al., 2008; climbers: Bradshaw et al., 2008). Lastly, our analysis could have been limited by small sample sizes for each trait. It is interesting that the traits we found to be significant in our analysis tended to have information for more species than traits which were not significant (means = 631 spp. vs. 211 spp.), but the difference was not significant (t-test, P>0.05).

The EOL TraitBank has information for a large variety of traits, covering a broad range of organisms (both taxonomically and geographically) but, unfortunately, that was not always the case for individual traits and when focusing on species with threat risk information from IUCN. The 47 traits we were able to use for our analysis is greater than almost all other comparative analyses of extinction risk for plant species (with the notable exception of Musters et al., 2013). Furthermore, even though the numbers of species with both trait and threat risk information was far fewer than the number for each, the mean number of species for each trait in our analyses (316 spp.) was still greater than used in many similar past studies (reviewed in Murray et al., 2002). If we had included regional endangered species in our analyses we might have been able to increase the sample size. However, including regional categorizations could have been problematic because some species can be endangered in one region and not in another. We believed that using the IUCN Red List was the most appropriate method to assess whether a species is assessed throughout its range. Since there were more plant species with threat risk data from IUCN than for most traits, it would also make more sense to look for additional trait information rather than additional threat status information, especially since one of the ultimate goal of this research was to identify relationships that could be used to guide further conservation assessments. There are other plant trait databases that contain information for more species than used in our analyses (e.g. TRY Plant Trait Database: http://www.try-db.org/TryWeb/Home.php; GLOPNET Global Plant Trait Network: http://bio.mq.edu.au/~iwright/glopian.htm). Fortunately, the EOL TraitBank is still adding new datasets such as these to their repository, with the potential for even stronger analyses in the future. Perhaps the greatest potential for using the EOL TraitBank repository, though, is in even broader scale analyses than in this study, such as those searching for general trends even among kingdoms (e.g. Stork et al., 2009; Musters et al., 2013).

Conclusions

Since only a small proportion of known plant species have been studied enough to know their risk of extinction, and there are insufficient resources available to protect them all, strategies are needed to focus efforts towards those species are most in need of conservation. This is particularly important given that human activities represent some of the greatest risks to thee species. Our study adds to the growing body of evidence showing that certain life history, ecological, and morphological traits predispose species to higher vulnerabilities. By comparing EOL TraitBank plant traits with IUCN threat risk categories, we were able to identify five such traits: 'plant growth habit', 'life cycle habit', 'low temperature tolerance', 'soil depth' required for good growth, and 'foliage porosity in winter'. Threatened plant species tend to be trees rather than herbs or grasses, live for more than one season (perennials), are able to withstand colder temperatures, can live in shallower soil depths, and have less foliage during the winter. In the absence of direct vulnerability information, these traits, among others found in past studies, could be used to guide further conservation assessments towards those most likely at risk. Ideally, such traits should be easy to measure and generalizable. Fortunately, two of the traits we identified (plant growth habitat, and life cycle habit) seem to satisfy both of these requirements, although their specific relationships may be context dependent. Further analyses using other plant trait databases could clarify these relationships further.

Acknowledgements

This research was supported through participation in a "NESCent-EOL-BHL Research Sprint" event co-hosted by the National Evolutionary Synthesis Center (NESCent), the Encyclopedia of Life (EOL), and the Biodiversity Heritage Library (BHL). We would especially like to thank CS Parr and CR McClain for their leadership and advice during the event. We would also like to thank JP Balhoff for his help and advice with data management solutions, KS Schulz for her assistance gathering appropriate data from TraitBank and CD Caldwell for his advice and feedback on earlier drafts of the paper.

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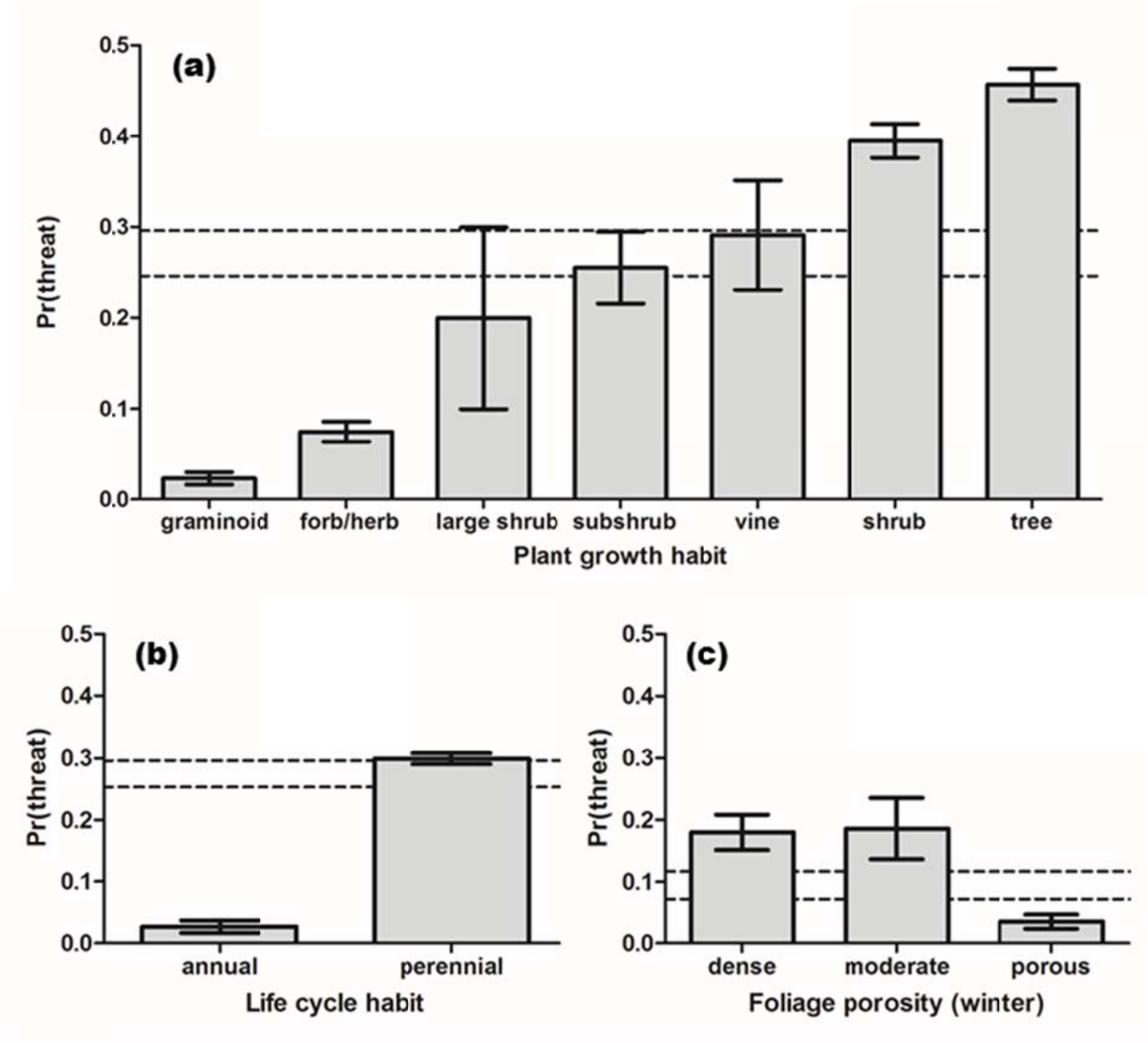

Figure 1: Probabilities of plant species being classified as 'threatened' (Pr(threat)) for each level of the three categorical traits found to significantly reduce deviance when added to GLMM's that only consider taxonomy as a nested random factor. Error bars represent standard deviations of bootstapped probabilities (10 000 iterations using 70% of the data). Dotted horizontal lines represent the range in fitted values from the associated GLMM with each trait.

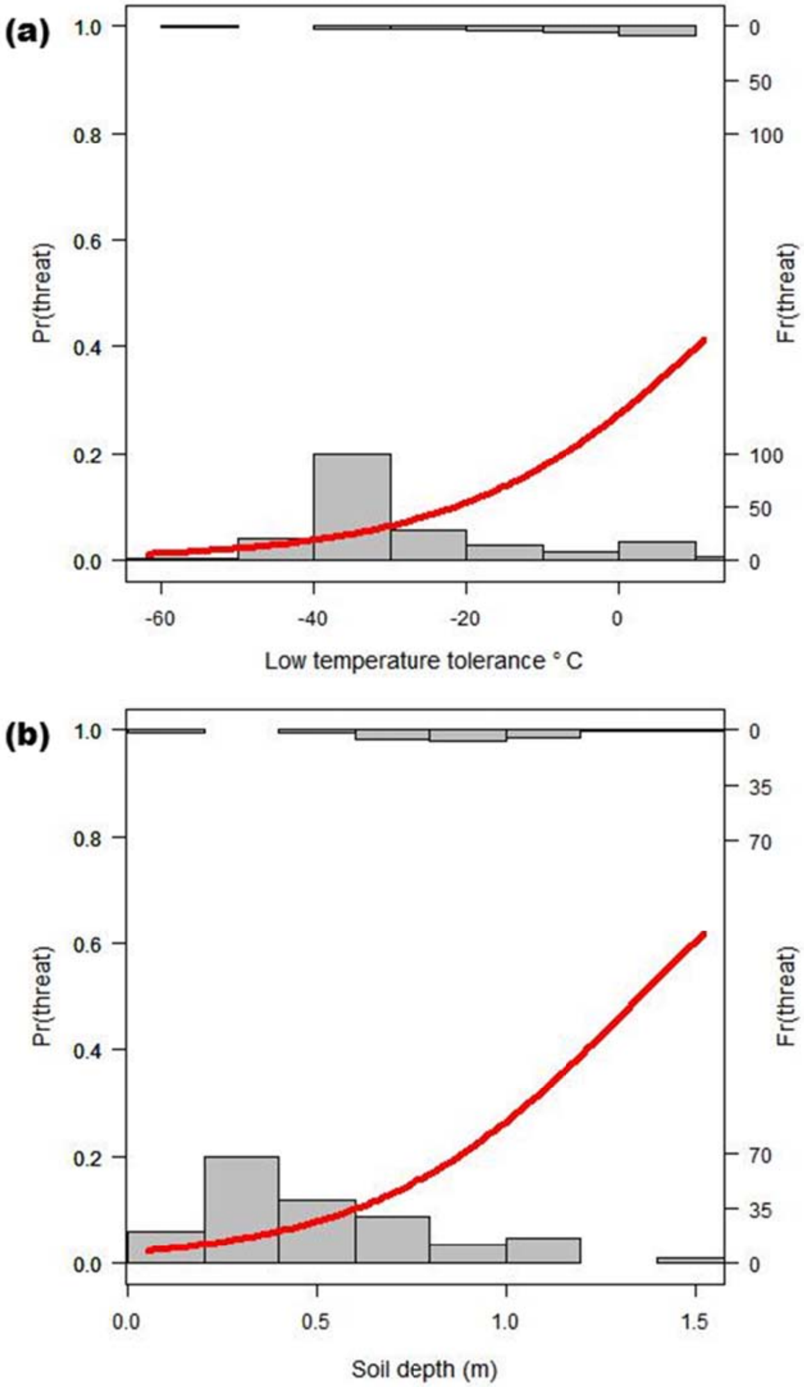

Figure 2: Binned frequencies showing how often plant species are classified as either ‘threatened’ (=1) or ‘not threatened’ (=0) (Fr(threat); gray bars), and modelled probabilities of a plant species being ‘threatened’ (Pr(threat); red line) for each of the two continuous traits found to significantly reduce deviance when added to GLMM’s that only consider taxonomy as a nested random factor.

Table 1: Generalized linear mixed effects model (GLMM) results for the five plant traits that significantly reduced deviance in threat risk (i.e. whether a species is listed in a threatened IUCN Red List category or not) when added to null models that only include the effect of taxonomy. Results shown include numbers of species used in each model (*Spp*), maximum log-likelihoods (*LL*), marginal R^2 values ($R^2_{GLMM(m)}$), conditional R^2 values ($R^2_{GLMM(c)}$), percent deviance explained (*%DE*), and results from chi-square tests comparing models with and without the trait (*Chi-square* and *P*).

Trait	*Spp*	*LL*	$R^2_{GLMM(m)}$	$R^2_{GLMM(c)}$	*%DE*	*Chi-square*	*P*
Plant growth habit	1192	-396.442	0.982	0.996	9.468	82.917	1.26×10^{-14}
Life cycle habit	1307	-479.457	0.154	0.894	2.740	27.016	1.36×10^{-06}
Low temperature tolerance	222	-57.651	0.273	0.878	16.803	23.287	1.40×10^{-06}
Soil depth	213	-63.162	0.215	0.717	8.057	11.070	0.0008777
Foliage porosity (winter)	219	-60.911	0.279	0.856	9.232	12.391	0.002039