1 Relating plant height to demographic rates and extinction vulnerability

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Summary

To prioritize conservation efforts, it is important to know which plant species are most vulnerable to extinction. Intrinsic extinction vulnerabilities depend on demographic parameters, but for many species these demographic parameters are lacking. Body size has been successfully used as proxy of such parameters to estimate extinction vulnerability of birds and mammals. For plants, not all necessary demographic parameters have been related to size yet.

Here, we derived allometric relationships with maximum plant height for the intrinsic population growth rate and the carrying capacity. Furthermore, for the first time, we derived a relationship between the variance in population growth rate due to environmental stochasticity and plant height. These relationships were used to relate extinction vulnerability to maximum plant height.

Extinction vulnerability was found to be most sensitive to fluctuations in the population growth rate due to environmental stochasticity. Large plant species were less susceptible to environmental stochasticity, resulting in a lower vulnerability to extinction than small plant species. This negative relationship between plant size and extinction vulnerabilities is in contrast to previous results for mammals and birds.

These results increase our theoretical understanding of the relationship between plant functional traits and extinction vulnerabilities and may aid in assessments of data deficient species. The uncertainty in the allometric relationships is, however, too large to quantify true extinction vulnerabilities. Further investigation in the relationship between demographic parameters and plant traits other than height is needed to further enhance our understanding of plant species extinction vulnerabilities.

Highlights

- We derived relationships between demographic rates and maximum plant height
- Large vascular plants are less susceptible to environmental stochasticity
- Plant growth form does not explain intrinsic population growth rates
- Plant height has a weak negative relationship with extinction vulnerability

Keywords: environmental stochasticity, intrinsic population growth rate, mean time to extinction, plant allometry, population viability analysis, probability of extinction

1 Introduction

Over the past few hundred years human activities have increased species extinction rates as much as 100-1000 times the historical background rates (Steffen et al., 2015). Especially high proportions of endangered species have been found for specific groups of vascular plants, e.g. about two thirds of cycads and one third of the world's conifers are currently threatened with extinction (IUCN, 2016). As vascular plant communities form the structural basis of many ecosystems and food webs, preservation of plant species diversity is of vital importance (Díaz et al., 2016).

Effective prioritization of plant populations for conservation depends greatly on our knowledge of species extinction risks (Pacifi et al., 2015). Understanding the factors that make some species more vulnerable to extinction than others, such as low reproductive rates and high susceptibilities to environmental disturbances (Dawson et al., 2011), may help to prioritize populations for conservation. However, the demographic data that may explain extinction vulnerabilities in plants are not available for many populations (Menges, 2000; Pacifi et al., 2015). Given the strongly increased extinction rates, and the large number of 'data-deficient' and not assessed plant species on the Red List (IUCN, 2016; Pimm and Raven, 2017), it is important to find new methods to increase the number of populations that can be quickly assessed (Darrah et al., 2017).

One of the ways this may be achieved is by relating demographic parameters to functional traits. The use of these traits to estimate demographic rates has previously been demonstrated for various taxonomic groups including plants (Adler et al., 2014; Visser et al., 2016). One of the key traits may be the size (body size or plant size) of an organism. Recently, Hilbers et al. (2016) introduced an extinction vulnerability framework based on allometric relationships between demographic variables and body size of mammal and bird species. Allometric theory predicts that species-specific demographic parameters are related to body size through allometric scaling of metabolic rates (West et al., 1999; Hendriks, 2007). Allometric relationships have also been reported in vascular plant species (Enquist et al., 1998; Hendriks and Mulder, 2008). For example, Marbà et al. (2007) found a positive relationship between life span and plant size and Enquist et al. (1999) showed that relative growth rates are negatively related to plant size. This scaling of plant demographic parameters and size suggests that for vascular plants extinction vulnerabilities may also be related to plant size.

The goal of this study was to develop allometric relationships between plant size and demographic rates related to extinction vulnerabilities in plants. Furthermore, we investigated whether the relationship between plant size and demographic rates is strong enough to inform estimates of intrinsic extinction vulnerabilities. Large plants may have a higher extinction vulnerability than smaller plants because they are expected to have smaller intrinsic population growth rates through allometric scaling of growth and reproduction rates (Hendriks and Mulder, 2008; Mace et al., 2008). On the other hand, populations of large species with a long life span are less sensitive to environmental stochasticity (Morris et al., 2008) which may decrease their extinction vulnerability.

Extinction vulnerabilities were estimated using two extinction risk indicators: the probability of extinction (PE; Ginzburg et al., 1982) and the mean time to extinction (MTE; Foley, 1994). We used a large database of plant population matrices (Salguero-Gómez et al., 2015) combined with a plant trait database (Kattge et al.,

111 2011) to relate maximum plant height to the intrinsic population growth rate (r_m) and
112 the variance in population growth rate due to environmental stochasticity (σ_r^2). To our
113 knowledge, the latter relationship has never been derived from empirical data for
114 plant species. These relationships were then combined to correlate maximum plant
115 height to the probability of extinction and mean time to extinction for vascular plants.

2 Methods

2.1 Extinction indicators

Two indicators of extinction risk were calculated: the probability of extinction (PE) and the mean time to extinction (MTE). Both extinction indicators are based on logistic population growth models in which the population size is assumed to fluctuate only due to environmental stochasticity.

2.1.1 Probability of extinction (PE)

Probability of extinction is defined as the probability of a population falling below a critical population level (N_c) after which extinction is imminent. In general, this probability is based on many stochastic population simulations. The extinction probability is defined as the proportion of simulations reaching extinction or quasi-extinction (Menges, 2000). An analytical version of the probability of quasi-extinction was developed by Ginzburg et al. (1982):

$$PE = \left(\frac{N_c \left(1 - \frac{N_0}{K}\right)}{N_0 \left(1 - \frac{N_c}{K}\right)} \right)^{2r_m / \sigma_r^2} \quad \text{eqn 1}$$

where PE is the quasi-extinction probability, N_c is the critical population size (in number of individuals), N_0 is the initial population size (in number of individuals), K is the carrying capacity (in number of individuals), r_m is the intrinsic density-independent per-capita population growth rate (per year) and σ_r^2 represents the variance in the population growth rate due to environmental stochasticity (per year).

2.1.2 Mean time to extinction (MTE)

The mean time to extinction is usually measured from stochastic population simulations as the mean time observed until a population reaches a threshold level of 1 individual or less. Instead of simulations we used the analytical solution derived by Foley (1994):

$$MTE = \frac{\sigma_r^2}{2r_m^2} \left[e^{2r_m \ln K / \sigma_r^2} \left(1 - e^{-2r_m \ln N_0 / \sigma_r^2} \right) - \frac{2r_m \ln N_0}{\sigma_r^2} \right] \quad \text{eqn 2}$$

where MTE is the mean time to extinction (in years) and all other variables are the same as for the probability of quasi-extinction.

2.2 Parameters

Our extinction indicators rely on several population demographic parameters: the intrinsic population growth rate (r_m), variance of the population growth rate (σ_r^2), the carrying capacity (K), the current population size (N_0) and the critical population size (N_c). These parameters, together with plant size, were derived from 4 datasets: the COMPADRE plant matrix database for r_m and σ_r^2 (COMPADRE Plant Matrix Database, v4.0.1), empirical data on maximum plant density ($N_{\max}$) from Enquist et al. (1998) and data on plant mass (M) and height (H) from the Biomass Allocation and Growth Data of Seeded Plants data set (Niklas and Enquist, 2004) to calculate K and the TRY Plant Trait Database for data on maximum plant heights (Kattge et al., 2011). More details on these data sets can be found below and in Table 1.

2.2.1 Maximum plant height (H)

Data on plant height was obtained from the TRY Plant Trait Database version 3.0. For each species, the maximum height was calculated as the average of the maximum heights reported (Kattge et al., 2011). When height data for a species was

not available from the TRY database, we searched literature underlying the COMPADRE database, including cross-references, and available online and physical floras for maximum plant heights (Supplemental material).

2.2.2 Intrinsic population growth rate (r_m)

The intrinsic population growth rate (r_m , yr^{-1}) for a density dependent population can be calculated from time series of the population size or from transition matrices from low-density populations. As we are not aware of any datasets containing either type of data for a large number of plant populations, we estimated r_m from field-based population growth rates (r , yr^{-1}). While r_m is determined only by intrinsic limits, environmental conditions and resource availability, r calculated from field-based population matrices also depends on population density (Fagan et al., 2010). Because r_m is by definition larger than r , we approximated r_m as the maximum calculated r for each species. Population growth rates were calculated from population matrices in the COMPADRE Plant Matrix Database (version 4.0.1, see Table 1 for a short description). All available population matrices were included except those with an annual periodicity different from 1 year to ensure that only population growth rates per year were derived. Annual population matrices included mean, individual and pooled matrices. For each population matrix, we calculated r as the natural logarithm of the dominant eigenvalue of the matrix. To arrive at an estimate of r_m , we took the maximum positive value of r for each species (Fagan et al., 2010). We were able to relate r_m to maximum plant height for a total of 339 plant species, with a height range of 0.02 – 110 m.

2.2.3 Variance in population growth rate (σ_r^2)

Assuming that demographic stochasticity in large-enough populations is negligible compared to environmental stochasticity (Mace et al., 2008), the variance in the population growth rate (σ_r^2) due to environmental stochasticity can be estimated using time series of population growth rates (Ginzburg et al., 1982; Brook et al., 2006). Growth rates were calculated from population matrices from the COMPADRE Plant Matrix Database (version 4.0.1). We selected all time series of at least 9 consecutive years from the same population (Brook et al., 2006). As with the intrinsic population growth rate, we included only population matrices with an annual periodicity equal to one. In addition, we excluded time series from managed populations to ensure that the calculated variance in population growth rate is indeed mainly due to environmental stochasticity. For each selected population time series, we calculated the variance in population growth rate (σ_r^2) from the annual population growth rates. This led to a total of 51 time series from populations of 23 species with a maximum height range of 0.25 – 4 m. These populations consisted of an average of 822 (100 – 3487) individuals (estimated population sizes were only available for 24 time series) which should be enough to make the effect of demographic stochasticity on population growth rates negligible (Mace et al., 2008). The vast majority of these time-series were recorded in Europe and North America. Because the selected data showed a nested structure of multiple populations of each species and because we expected populations from the same species to be more similar than populations from different species, we used mixed-effects models with species identity included as a random intercept effect (Zuur, 2009).

2.2.4 Carrying capacity (K)

Scaling relationships for the carrying capacity of plant species have, to our knowledge, not been investigated before. However, scaling relationships between the maximum density of plants and plant mass have been studied (Enquist et al.,

1998). To include this relationship in our analysis, we derived the allometric regression between maximum density (N_{max} , individuals m^{-2}) and total above-ground biomass (M, kg) using digitized data from Enquist et al. (1998). A total of 230 data points were retrieved with a mass ranging from 0.3 μg to 42438 kg. Maximum plant density scaled with plant mass with a scaling exponent of -0.72 ($p < 0.0001$; 95% confidence interval: -0.74 to -0.70; Appendix A Fig. 1a). To arrive at a relationship between maximum density and maximum plant height, we derived the relationship between plant aboveground (shoot) dry biomass (M, kg) and height (H, m) using the Biomass Allocation and Growth Data of Seeded Plants data set (Niklas and Enquist, 2004). In total, 876 observations with heights ranging from 9 mm to 49.9 m were included. Plant mass scaled with plant height with an average scaling exponent of 2.34 ($p < 0.0001$; 95% confidence interval: -2.30 to -2.37; Appendix A Fig. 1b). The carrying capacity was then calculated by multiplying the maximum plant density with the size of the populated area (A).

2.2.5 Populated area size (A)

The populated area size (A) is estimated as the area needed to support the initial population size ($N_0 = 10.000$) using a population density (N_d) that is below the maximum density to reflect the occurrence of populations of different species in the same area ($A = N_0/N_d$). This area was adjusted to plant size as larger plants have larger area requirements than smaller plants, and using a constant area size for all plants will disadvantage larger plants. We expected the current population density to be related to maximum plant height with a scaling exponent similar to the scaling exponent found for the maximum population density. However, the scaling intercept of the relationship between current population density and H is expected to be lower than that found for the maximum population density because an area is rarely occupied by just one species. Therefore, we estimated the current population size as the carrying capacity divided by the species richness (S) (Hendriks, 2007). Species richness, in turn, is often estimated from a power law, $S = cA^z$ in so-called species-area relationships (SAR; Rosenzweig, 1995). In summary, we estimated the available area from the current population size, the scaling relationship between maximum plant height and maximum density and a species-area relationship:

$$A = \left(\frac{N_{max}}{c * N_0} \right)^{\frac{1}{(z-1)}} \quad \text{eqn 4}$$

Where z is the scaling exponent of the SAR, c is the intercept of the SAR, N_{max} is the maximum plant density and N_0 is the current population size. SARs are often developed for specific vegetation types and generalization across these systems in terms of average species richness is difficult (Drakare et al., 2006). Alternatively, using maximum plant species richness, Wilson et al. (2012) were able to develop a SAR across vegetation types. In our calculations of we used the SAR found by Wilson et al. (2012) which has an intercept c of 65 individuals m^2 and a slope z of 0.25.

2.2.6 Critical population size (N_c)

The critical population size (N_c) was defined as the minimum population size that is necessary for a population to survive effects of genetic drift and demographic stochasticity. As we are not aware of any datasets containing critical population sizes per plant species we decided not to rely on allometric relationships. Instead, we assumed the critical population size to be independent of maximum plant height and lognormally distributed as values found in literature range from 50 to 5000 individuals

with a few hundred individuals being most frequently reported (Menges, 1992; Lande, 1995; Schultz and Lynch, 1997; Whitlock, 2000). We approximated N_c using a lognormal distribution with a mean of 500 individuals and the 95% confidence interval between 50 and 5000 individuals.

2.3 Regression models

To be able to estimate extinction risk for a large set of populations of vascular plant species for which demographic parameters are unknown, we derived relationships to estimate r_m , σ_r^2 , and K as a function of maximum plant height (H):

$$\log(D) = \log(\gamma) + \beta * \log(H) \quad \text{eqn 3}$$

where D is the demographic parameter of interest, $\log(\gamma)$ is the intercept and β the slope of the regression (Hendriks and Mulder, 2008).

For the intrinsic population growth rate and the variance in population growth rate we investigated the effect of plant growth form on the regressions by comparing a set of models in which growth form was included in various model structures. Two classification systems were tested based on the organism types in the COMPADRE database. The first classification system contained 8 classes defined as: annuals, ferns, palms, herbaceous perennials, trees, shrubs, epiphytes and succulents. In the second classification system, plants were classified as either annual/biennial herbs, perennial herbs or woody plants (Supplemental material S1). These two classification systems were included because growth form is generally associated with different life history strategies. For example, trees have longer generation times than herbs while shrubs typically have a higher reproductive output than herbs (Salguero-Gómez et al., 2016). For both classification systems, models were tested with growth form included only as intercept effect, and with growth form included as interaction with maximum plant height. The models were compared based on the Akaike Information Criterion (AIC) and the Bayesian Information Criterion (BIC). For each demographic parameter, the model with the lowest AIC and BIC was used to calculate the extinction indicators.

All data was checked for outliers using Cook's Distance tests. Data points with a Cook's distance above $4/N$, with N the number of observations, were re-evaluated on and removed from the analysis when found incorrect. All observations removed this way and the reasons for doing so are reported in the supplementary species list (Supplemental material S1).

2.4 Uncertainty analysis

We calculated the PE and MTE at a range of plant heights between 0.08 and 4 m using the above-described regression models and parameter distributions. To account for uncertainty in the parameterization of the regression models, we used parametric bootstrapping to generate 1000 parameter predictions at each prediction height using the 'boot' package (Canty and Ripley, 2016) for the linear regression models and using the 'lme4' package (Bates et al., 2016) for the mixed effect models. This parametric bootstrapping gave a distribution of possible values within the confidence intervals of our regression models for r_m and σ_r^2 at different heights. Next, at each height, 10.000 estimations of the PE and MTE were generated in which the various parameters were randomly sampled from their respective distributions. Lastly, relationship between plant height and PE and MTE was quantified by fitting a non-linear regression line through the generated data points

To assess which parameter has the largest contribution to the uncertainty in the extinction risk indicators, we calculated the Spearman rank correlation coefficient between each parameter and the corresponding extinction risk indicator along the range of maximum plant height.

All analyses were performed using the statistical software environment R, version 3.3.1 (R Core Team, 2016).

3 Results

3.1 Allometric regressions

A summary of the selected allometric regressions and databases used can be found in Table 1. Intrinsic population growth rates (r_m) for 339 species calculated from the COMPADRE database show a negative relationship with maximum plant height with a scaling exponent of -0.32 (95% CI: -0.43: -0.20, $p < 0.01$, $r^2 = 0.08$) when growth form is not accounted for (Fig. 1a). Including growth form, either using 3 or 8 classes, did not improve the model as the lowest AIC and BIC were found for the height only model (Appendix B Table 1).

Variance in population growth rate was calculated from 51 selected time series from 23 different species. These included only shrubs and herbaceous perennials because time series matching our selection criteria were not available for plants with other growth forms. Including growth form in the fixed effects part of the regression model did not improve the regression models (Appendix B Table 2). The fixed effects part of the selected model shows that variance in population growth rate (σ_r^2) is negatively related to maximum plant height with a scaling exponent of -1.24 (95% CI: -2.16: -0.32, $p < 0.01$, $r^2_{\text{marginal}} = 0.17$, $r^2_{\text{conditional}} = 0.78$) (Fig. 1b). The random effects part of the model shows a within-species covariance (τ_{00}) of 0.34 and a within-species variance (σ^2) of 0.13 leading to an intraclass correlation coefficient ($\text{ICC} = \tau_{00}/(\tau_{00} + \sigma^2)$) of 0.72.

3.2 Extinction vulnerability

We found a negative relationship between the median probability of extinction (PE) and maximum plant height and a positive relationship of maximum plant height with the median mean time to extinction (MTE) (Fig. 2a, b). Uncertainty in the extinction indicators increased as a function of maximum plant height with large uncertainties for larger plants.

To estimate the effect of the uncertainty in the regression parameters on the extinction indicators we calculated the Spearman rank correlation coefficient between the parameters and the extinction indicators at various plant heights. The PE at intermediate maximum plant heights was most correlated to uncertainties in the critical population size (N_c), with a Spearman rank correlation coefficient of 0.78 (Fig. 3a). The MTE was most strongly correlated to the variation in the population growth rate due to environmental stochasticity (σ_r^2) with a Spearman rank correlation coefficient of -0.92 (Fig. 3b). For the PE, a strong correlation with σ_r^2 was also present ($\rho = 0.55$). Both the PE and MTE were only moderately correlated to the intrinsic population growth rate (r_m) at intermediate maximum plant heights ($\rho = -0.12$ and $\rho = 0.29$ respectively). At a maximum plant height of 0.1 m, the correlation between r_m and both the MTE and PE disappears. Furthermore, higher correlation coefficients are found for σ_r^2 at both ends of the height scale while for the PE the correlation with N_c is highest at intermediate maximum plant heights.

4 Discussion

The goal of this study was to develop allometric relationships that can be used to relate the extinction vulnerability of vascular plants to maximum plant height. We found a negative relationship between maximum plant height and extinction vulnerability. However, while the relationships between the demographic parameters and plant height were significant, the uncertainty in these relationships was too large to reliably quantify extinction vulnerabilities from maximum plant height only.

4.1 Allometric regressions

Allometric theory predicts the intrinsic population growth rate (r_m) to have a negative relationship with plant size (Enquist et al., 1999; Hendriks and Mulder, 2008). This is a result of the expected positive relationship between generation time and life span and plant size based on allometric scaling of biomass production rates (Enquist et al., 1999; Hendriks and Mulder, 2008). This is consistent with the negative relationship between maximum plant height and r_m found in this study. While plant species with different growth forms have been shown to have somewhat different life histories (Franco and Silvertown, 2004; Salguero-Gómez et al., 2016), in our analyses growth form did not improve the explanative power of the model. This indicates that plant growth form does not explain much variation in r_m that is not already explained by maximum plant height.

Although we found a significant relationship between maximum plant height and intrinsic population growth rate, maximum plant height explained only a small part of the variation in r_m ($r^2 = 0.08$). Other functional traits that are related to plant energy trade-offs such as wood density and leaf mass per area may be included to explain parts of the variance in intrinsic population growth rates (Adler et al., 2014; Díaz et al., 2016). Additionally, in allometric theory, total body mass is used as a measure of organism size instead of height or length which do not account for variation in, for example, stem diameter (West, 1997). However, estimates of maximum or average adult biomass were not available for many plant species.

Variation in population growth rate (σ_r^2) due to environmental stochasticity gives an indication of the susceptibility of a species to environmental fluctuations. Species with a high susceptibility are expected to be more affected by environmental change and will have a higher intrinsic extinction vulnerability than less susceptible species (Ginzburg et al., 1982; Lande, 1993). We found a strong negative relationship between maximum plant height and the susceptibility to environmental fluctuations. High sensitivity to environmental fluctuations has been associated with short-living species for both plants and mammals (Morris et al., 2008). Life span, in turn, has a positive relationship with maximum plant height (Enquist et al., 1999; Marbà et al., 2007). This would imply that larger plants should be less sensitive to environmental fluctuations than their smaller counterparts which is consistent with the results of our study. Similar to the intrinsic population growth rate, we found no improvements of the σ_r^2 model performance by including growth form. However, for this parameter, we were only able to include herbaceous plants and a very limited ($n=3$) number of shrubs.

To account for the variation of σ_r^2 between population of the same species we used a mixed-effects regression model. We found a high intraspecies covariation compared to the intraspecies variation leading to a high intraclass correlation coefficient. These results indicate that populations from the same species are more similar than populations from different species and show that within-species variability is smaller

than between-species variability. Unexplained variability between species may be reduced by adding additional functional traits. For example, wood density may be a good indicator of the structural strength and mortality rates of plants (Visser et al., 2016).

To our knowledge, this is the first time that variance in the population growth rate of plant populations is related to maximum height across various plant species. However, time series of population growth rates in plant population are scarce and our model may be significantly improved by including more estimates of the variance in population growth rate for species larger than 2 m. We should also note here that all time series, except two, used for this analysis were recorded in either North America or Europe. As climate effects play a major role in environmental stochasticity, the derived allometric regression for the variance in population growth rate are expected to be valid only for temperate climates, thus limiting the geographical representability of our study. This further highlight the importance of long-term demographic research on shrubs and trees.

4.2 Extinction vulnerability

The derived allometric relationships were combined to calculate two indicators of extinction risk (PE and MTE) as a function of maximum plant height. The fit through the median estimations of both the MTE and PE showed a negative relationship between maximum plant height and extinction vulnerability. Furthermore, for both the MTE and PE the fitted slope became steeper with increasing plant heights. While we found significant relationships between the demographic parameters and plant height, the uncertainty in these relationships was too large to directly estimate extinction vulnerabilities from maximum plant height. The uncertainty analysis showed that the uncertainty in the extinction indicators is mainly due to the uncertainty in the regression model of σ_r^2 . This explains why uncertainty increases with plant height (Figure 1b). The fact that this parameter contributes so strongly to the uncertainty in our estimates of the extinction indicators can be explained by the fact that the regression model for this parameter is based on a limited number of observations (51) which are not evenly spread across the height range.

Our results are contradictory to those found for mammals and birds by Hilbers et al. (2016). They found that larger animals were more vulnerable to extinction than their smaller counterparts mainly due to their lower intrinsic population growth rates (r_m) and lower carrying capacities. In mammals and birds, σ_r^2 is thought to be related to size with the same scaling exponent as r_m (Sinclair, 2003; Hilbers et al., 2016). This suggests that small species are able to sustain in changing environments due to high reproduction rates while large species are able to sustain to due to their high survivorship in such a way that the coefficient of variation in population size is independent of body size. However, our results show a higher scaling exponent for r_m than for σ_r^2 so that for plants scaling σ_r^2 does not fully offset scaling of r_m as in mammals and birds. We hypothesize that this difference may be due to the fact that larger plant species generally have a larger number of seeds per reproductive event than their smaller counterparts while maintaining a high survivorship. For mammals, no relationship, or the opposite, is generally observed (Hendriks and Mulder, 2008). This can offset the relationship between size and intrinsic population growth rate in favour of larger species as we found in our results where the scaling exponent of -0.32 for r_m is higher than the expected scaling exponent of -1 based on allometric theory (Enquist et al., 1999; Niklas and Enquist, 2001).

The extinction vulnerabilities estimated in our approach should be used with caution. First of all, maximum plant height is not the only trait that matters; other functional traits, such as wood density or seed mass, are critical to the survival and reproduction of plants and may be related to extinction risks as well (Díaz et al., 2016; Visser et al., 2016). Furthermore, the extinction vulnerabilities calculated in this study are based on populations with an initial population size of 10.000 individuals, while the relationship with height is not influenced by this choice, absolute values of the MTE and PE are (see appendix C for a calculation of the MTE using an initial population size of 100 individuals). Lastly, estimations of extinction vulnerability may be improved by including other life history parameters such as life span and age of maturity and number of offspring. However, many of these life history parameters are in turn also expected to be related to organism size. For example, a strong relationship between generation time and size has been reported for plants and animals (Hendriks, 2007).

4.3 Relevance

To conserve plant biodiversity, conservation biologists and policy makers often have to prioritize which species to protect from extinction. In many regions there are, however, no reliable estimates of extinction risk for the vast majority of species, making prioritizing difficult. For intensively studied populations of which population structures are known, extinction risks can be estimated from detailed matrix population models (Crone et al., 2011). For species of which the population structure is unknown, the extinction risks can be estimated from species-specific demographic parameters such as the intrinsic population growth rate (r_m), the carrying capacity (K) and the sensitivity of the population to environmental stochasticity (σ_r^2). As it is impossible to gather these demographic parameters for each vascular plant species, we developed allometric relationships to estimate species-specific demographic parameters based on maximum plant height. Such allometric scaling relationships of demographic rates can be used to explain various ecological processes such as successional dynamics, population response to stochastic environmental events, population persistence (Rees et al., 2001; Enquist et al., 2009; Hilbers et al., 2017) and may be used to estimate extinction vulnerabilities.

Although smaller plant species have higher reproductive rates compared to larger plant species, this does not fully compensate their higher sensitivity towards environmental stochasticity. This result is in line with Morris et al. (2008) who found that short lived (small) plant species are more negatively affected by increasing variability in their vital rates making them more vulnerable to climate change and environmental disturbances than long lived (large) plant species. Similarly, Burns and Neufeld (2009) found that plant populations of larger individuals on islands are less prone to extinction. Similarly, small plant species may be more vulnerable to human disturbances than their larger counterparts. For example, wildfires, both naturally occurring and human induced, may lead to an increased mortality of trees as a function of plant height in tropical forests (Brando et al., 2012). However, for such specific disturbance regimes, other traits, such as the potential for seedling recruitment after a fire, may be more important for population persistence (Pausas and Keeley, 2014).

However, extinction risks depend on a combination of intrinsic traits, environmental factors and interactions with other species. An approach based solely on functional traits is therefore not applicable to derive actual extinction risks of populations. Instead our approach may be used to compare the extinction vulnerability of

populations for which no detailed population-level demographic data is available and that exist under similar levels of environmental stress. For example, we found that plants that can reach heights of about 4 m can be expected to be less vulnerable to environmental disturbances than smaller plants. As such, all other things being equal, populations of small plant species may be under greater risk of extinction than larger species because they are more vulnerable to environmental fluctuations.

While plant height was found to be related to the demographic parameters used in this study, the explanative power of the derived allometric regressions was low. Plant height alone is not enough to reliably compare the extinction vulnerabilities of different populations. Other species traits, such as seed mass and stem diameter, may help to better estimate plant extinction vulnerabilities. However, these additional trait data are not available for many species. Several initiatives have already substantially increased the availability and reachability of plant functional trait data, such as the TRY initiative (Kattge et al., 2011) and plant life history data, such as the COMPADRE database (Salguero-Gómez et al., 2015). Despite these efforts, the overlap between these databases is relatively small, making it especially difficult to combine these different datasets. New databases including both functional traits and time series of population structures are needed to better understand the relationships between functional traits and demography. Additionally, they can help to better investigate the contribution of different life history components to the scaling of demographic rates and extinction vulnerabilities.

In the absence of more detailed demographic information, the results of our study can help conservation managers to prioritize conservation efforts among populations of different species under equal external pressures. Additionally, the relationships presented in this study, with additional traits, may be combined with environmental indicators such as habitat size and connectivity. For example, combining the framework with species distribution models (SDMs) may give insights in the changes of extinction vulnerabilities under climate change or landscape fragmentation (Keith et al., 2008; Tian et al., 2014; Evans et al., 2016; Zurell et al., 2016). Lastly, combining demographic rates with global species occurrence maps can help obtain estimates of the vulnerability of a species to global extinction (Hilbers et al., 2016). This may be used to obtain first estimates of the extinction vulnerability of data deficient species. Given the large percentage of data-deficient species for vascular plants as compared to mammals and birds (IUCN 2016), this would be an important methodological advance.

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6 Supporting information

Data S1: Spreadsheet containing an overview of all species used in this study and digitized data on maximum density and average biomass.

Appendix A: Relationships derived between the maximum population density ($N_{\max}$) and plant mass (M).

Appendix B: Results of regression model selection for the intrinsic population growth rate and variance in population growth rate

Appendix C: Supplementary results: MTE as a function of maximum plant height using an initial population size of 100 individuals.

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713 Table 1: Allometric regressions of demographic parameters with maximum plant height (H , m) with 95%
714 confidence interval between brackets and descriptions of the datasets used to estimate them. Asterisks
715 indicate significance levels: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Parameter	Estimate	Dataset	Dataset description
Intrinsic population growth rate (r_m , yr ⁻¹)	$\log(r_m) = \gamma_r + \beta_r * \log(H)$ $\gamma_r = -0.80 (-0.89, -0.72) ***$ $\beta_r = -0.32 (-0.43, -0.20) ***$ $r^2 = 0.08$ $N = 339$	COMPADRE Plant Matrix Database Version 4.0.1	The COMPADRE Plant Matrix Database Version 4.0.1 contains 7024 matrix population models of 695 taxonomically accepted plant species. Matrix population models and metadata are compiled mostly from published literature. Where possible, separate matrix models are compiled corresponding to only survival, only sexual reproduction and only clonal reproduction. (Salguero-Gómez et al., 2015)
Variance in population growth rate (σ_r^2 , yr ⁻¹)	$\log(\sigma_r^2) = \gamma_\sigma + \beta_\sigma * \log(H) + 1/\text{Species}$ $\gamma_\sigma = -1.29 (-1.62, -0.97) ***$ $\beta_\sigma = -1.24 (-2.16, -0.32) **$ <i>Random effects</i> $T_{00} = 0.34$ $\sigma^2 = 0.13$ $r^2_{\text{marginal}} = 0.17$ $r^2_{\text{conditional}} = 0.78$ $N = 51$ $\#\text{Species} = 23$	COMPADRE Plant Matrix Database Version 4.0.1	
Maximum monospecific plant density ($N_{\max}$, ind m ⁻²)	$\log(N_{\max}) = \gamma_r + \beta_r * \log(M)$ $\gamma_r = -0.61 (-0.68, -0.54) ***$ $\beta_r = -0.72 (-0.74, -0.70) ***$ $r^2 = 0.96$ $N = 230$	Enquist et al. (1998)	This data was digitized from a figure published in Enquist et al. (1998). We were able to retrieve 230 of the 251 data points.
Plant mass (M , kg)	$\log(M) = \gamma_M + \beta_M * \log(H)$ $\gamma_M = -0.84 (-0.88, -0.80) ***$ $\beta_M = 2.34 (2.30, 2.37) ***$ $r^2 = 0.95$ $N = 876$	Biomass allocation and growth data of seeded plants	This data set of leaf, stem, and root biomass for various plant taxa was compiled from the primary literature of the 20th century. Recent allometric additions include measurements made by Karl J. Niklas, Brian J. Enquist, and colleagues (Niklas and Enquist, 2004)

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Fig. 1: (a) Allometric relationships between plant height and intrinsic population growth rate (r_m) and (b) variance in population growth rate (σ_r^2) derived in this study. A total of 339 species (individual data points) were used in the regression of model of r_m . A total of 23 species and 51 observations, multiple data points per species (indicated by symbols), were used for σ_r^2 . Dashed lines represent the 95% confidence interval of the regressions.

Fig. 2: The probability of extinction (PE, a) and mean time to extinction (MTE, b) as a function of plant height calculated using the relationships between demographic rates and plant height derived in this study. Non-linear regression line is shown in black (also given in text), shading shows the 90% confidence interval of the Monte Carlo simulations of the PE and MTE as a function of height.

Fig. 3: Spearman rank correlation coefficients between the critical population size (N_c), plant mass (M), maximum population density (N_{max}), intrinsic population growth rate (r_m) and variance in population growth rate (σ_r^2) and the probability of extinction (PE; a) and the mean time to extinction (MTE; b) at maximum plant heights of 0.1, 0.5 and 4 m.