



## Relating plant height to demographic rates and extinction vulnerability

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### ABSTRACT

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.

### 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

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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., 2011) to relate maximum plant height to the intrinsic population growth rate ( $r_m$ ) and the variance in population growth rate due to environmental stochasticity ( $\sigma_r^2$ ). To our knowledge, the latter relationship has never been derived from empirical data for plant species. These relationships were then combined to relate maximum plant 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):

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

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  $\sigma_r^2$  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):

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

where MTE is the mean time to extinction (in years) and all other variables are the same as for the probability of 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 ( $\sigma_r^2$ ), 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  $\sigma_r^2$  (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 (Data S1).

#### 2.2.2. Intrinsic population growth rate ( $r_m$ )

The intrinsic population growth rate ( $r_m$ ,  $\text{yr}^{-1}$ ) 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 ( $r$ ,  $\text{yr}^{-1}$ ). 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 ( $\sigma_r^2$ )

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 ( $\sigma_r^2$ ) 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

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