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1 Relating plant height to demographic rates and extinction vulnerability

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3 A manuscript for Biological Conservation

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5 Melinda M.J. de Jonge<sup>1\*</sup>, Jelle P. Hilbers<sup>1</sup>, Eelke Jongejans<sup>2</sup>, Wim A. Ozinga<sup>3,4</sup>,

6 A. Jan Hendriks<sup>1</sup>, Mark A.J. Huijbregts<sup>1</sup>

7

8 <sup>1</sup> Department of Environmental Science, Institute for Water and Wetland Research,  
9 Radboud University, P.O. Box 9010, NL-6500 GL, Nijmegen, The Netherlands

10 <sup>2</sup> Department of Animal Ecology and Physiology, Institute for Water and Wetland  
11 Research, Radboud University, P.O. Box 9010, NL-6500 GL, Nijmegen, The  
12 Netherlands

13 <sup>3</sup> Team Vegetation, forest and landscape ecology, Wageningen Environmental  
14 Research (Alterra), Wageningen UR, P.O. Box 47, NL-6708 AA, Wageningen, The  
15 Netherlands

16 <sup>4</sup> Department of Experimental Plant Ecology, Institute for Water and Wetland  
17 Research, Radboud University, P.O. Box 9010, NL-6500 GL, Nijmegen, The  
18 Netherlands

19

20 \* Corresponding author: [m.dejonge@fnwi.ru.nl](mailto:m.dejonge@fnwi.ru.nl), [phone: + 31 \(0\)24 365 32 81](tel:+31243653281)

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31

## 32 Summary

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

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

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

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

## 55 Highlights

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

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

## 63 1 Introduction

64 Over the past few hundred years human activities have increased species extinction  
65 rates as much as 100-1000 times the historical background rates (Steffen et al.,  
66 2015). Especially high proportions of endangered species have been found for  
67 specific groups of vascular plants, e.g. about two thirds of cycads and one third of the  
68 world's conifers are currently threatened with extinction (IUCN, 2016). As vascular  
69 plant communities form the structural basis of many ecosystems and food webs,  
70 preservation of plant species diversity is of vital importance (Díaz et al., 2016).

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

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

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

107 Extinction vulnerabilities were estimated using two extinction risk indicators: the  
108 probability of extinction (PE; Ginzburg et al., 1982) and the mean time to extinction  
109 (MTE; Foley, 1994). We used a large database of plant population matrices  
110 (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 ( $\sigma_r^2$ ). 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.

## 116 2 Methods

### 117 2.1 Extinction indicators

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

#### 122 2.1.1 Probability of extinction (PE)

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

$$129 \quad PE = \left( \frac{N_c \left(1 - \frac{N_0}{K}\right)}{N_0 \left(1 - \frac{N_c}{K}\right)} \right)^{2r_m / \sigma_r^2} \quad \text{eqn 1}$$

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

#### 135 2.1.2 Mean time to extinction (MTE)

136 The mean time to extinction is usually measured from stochastic population  
137 simulations as the mean time observed until a population reaches a threshold level of  
138 1 individual or less. Instead of simulations we used the analytical solution derived by  
139 Foley (1994):

$$140 \quad MTE = \frac{\sigma_r^2}{2r_m^2} \left[ e^{2r_m \ln K / \sigma_r^2} \left( 1 - e^{-2r_m \ln N_0 / \sigma_r^2} \right) - \frac{2r_m \ln N_0}{\sigma_r^2} \right] \quad \text{eqn 2}$$

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

## 143 2.2 Parameters

144 Our extinction indicators rely on several population demographic parameters: the  
145 intrinsic population growth rate ( $r_m$ ), variance of the population growth rate ( $\sigma_r^2$ ), the  
146 carrying capacity ( $K$ ), the current population size ( $N_0$ ) and the critical population size  
147 ( $N_c$ ). These parameters, together with plant size, were derived from 4 datasets: the  
148 COMPADRE plant matrix database for  $r_m$  and  $\sigma_r^2$  (COMPADRE Plant Matrix  
149 Database, v4.0.1), empirical data on maximum plant density ( $N_{max}$ ) from Enquist et  
150 al. (1998) and data on plant mass ( $M$ ) and height ( $H$ ) from the Biomass Allocation  
151 and Growth Data of Seeded Plants data set (Niklas and Enquist, 2004) to calculate  $K$   
152 and the TRY Plant Trait Database for data on maximum plant heights (Kattge et al.,  
153 2011). More details on these data sets can be found below and in Table 1.

### 154 2.2.1 Maximum plant height (H)

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

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

### 161 2.2.2 Intrinsic population growth rate ( $r_m$ )

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

### 180 2.2.3 Variance in population growth rate ( $\sigma_r^2$ )

181 Assuming that demographic stochasticity in large-enough populations is negligible  
182 compared to environmental stochasticity (Mace et al., 2008), the variance in the  
183 population growth rate ( $\sigma_r^2$ ) due to environmental stochasticity can be estimated  
184 using time series of population growth rates (Ginzburg et al., 1982; Brook et al.,  
185 2006). Growth rates were calculated from population matrices from the COMPADRE  
186 Plant Matrix Database (version 4.0.1). We selected all time series of at least 9  
187 consecutive years from the same population (Brook et al., 2006). As with the intrinsic  
188 population growth rate, we included only population matrices with an annual  
189 periodicity equal to one. In addition, we excluded time series from managed  
190 populations to ensure that the calculated variance in population growth rate is indeed  
191 mainly due to environmental stochasticity. For each selected population time series,  
192 we calculated the variance in population growth rate ( $\sigma_r^2$ ) from the annual population  
193 growth rates. This led to a total of 51 time series from populations of 23 species with  
194 a maximum height range of 0.25 – 4 m. These populations consisted of an average  
195 of 822 (100 – 3487) individuals (estimated population sizes were only available for 24  
196 time series) which should be enough to make the effect of demographic stochasticity  
197 on population growth rates negligible (Mace et al., 2008). The vast majority of these  
198 time-series were recorded in Europe and North America. Because the selected data  
199 showed a nested structure of multiple populations of each species and because we  
200 expected populations from the same species to be more similar than populations  
201 from different species, we used mixed-effects models with species identity included  
202 as a random intercept effect (Zuur, 2009).

### 203 2.2.4 Carrying capacity (K)

204 Scaling relationships for the carrying capacity of plant species have, to our  
205 knowledge, not been investigated before. However, scaling relationships between  
206 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  $\mu g$  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 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



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

## 258 2.3 Regression models

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

$$262 \log(D) = \log(\gamma) + \beta * \log(H) \quad \text{eqn 3}$$

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

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

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

## 287 2.4 Uncertainty analysis

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

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

304 All analyses were performed using the statistical software environment R, version  
305 3.3.1 (R Core Team, 2016).

## 306 3 Results

### 307 3.1 Allometric regressions

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

315 Variance in population growth rate was calculated from 51 selected time series from  
316 23 different species. These included only shrubs and herbaceous perennials  
317 because time series matching our selection criteria were not available for plants with  
318 other growth forms. Including growth form in the fixed effects part of the regression  
319 model did not improve the regression models (Appendix B Table 2). The fixed effects  
320 part of the selected model shows that variance in population growth rate ( $\sigma_r^2$ ) is  
321 negatively related to maximum plant height with a scaling exponent of -1.24 (95% CI:  
322 -2.16: -0.32,  $p < 0.01$ ,  $r^2_{\text{marginal}} = 0.17$ ,  $r^2_{\text{conditional}} = 0.78$ ) (Fig. 1b). The random effects  
323 part of the model shows a within-species covariance ( $T_{00}$ ) of 0.34 and a within-  
324 species variance ( $\sigma^2$ ) of 0.13 leading to an intraclass correlation coefficient (ICC =  
325  $T_{00}/(T_{00} + \sigma^2)$ ) of 0.72.

### 326 3.2 Extinction vulnerability

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

332 To estimate the effect of the uncertainty in the regression parameters on the  
333 extinction indicators we calculated the Spearman rank correlation coefficient between  
334 the parameters and the extinction indicators at various plant heights. The PE at  
335 intermediate maximum plant heights was most correlated to uncertainties in the  
336 critical population size ( $N_c$ ), with a Spearman rank correlation coefficient of 0.78 (Fig.  
337 3a). The MTE was most strongly correlated to the variation in the population growth  
338 rate due to environmental stochasticity ( $\sigma_r^2$ ) with a Spearman rank correlation  
339 coefficient of -0.92 (Fig. 3b). For the PE, a strong correlation with  $\sigma_r^2$  was also  
340 present ( $\rho = 0.55$ ). Both the PE and MTE were only moderately correlated to the  
341 intrinsic population growth rate ( $r_m$ ) at intermediate maximum plant heights ( $\rho = -0.12$   
342 and  $\rho = 0.29$  respectively). At a maximum plant height of 0.1 m, the correlation  
343 between  $r_m$  and both the MTE and PE disappears. Furthermore, higher correlation  
344 coefficients are found for  $\sigma_r^2$  at both ends of the height scale while for the PE the  
345 correlation with  $N_c$  is highest at intermediate maximum plant heights.

## 346 4 Discussion

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

### 353 4.1 Allometric regressions

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

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

374 Variation in population growth rate ( $\sigma_r^2$ ) due to environmental stochasticity gives an  
375 indication of the susceptibility of a species to environmental fluctuations. Species  
376 with a high susceptibility are expected to be more affected by environmental change  
377 and will have a higher intrinsic extinction vulnerability than less susceptible species  
378 (Ginzburg et al., 1982; Lande, 1993). We found a strong negative relationship  
379 between maximum plant height and the susceptibility to environmental fluctuations.  
380 High sensitivity to environmental fluctuations has been associated with short-living  
381 species for both plants and mammals (Morris et al., 2008). Life span, in turn, has a  
382 positive relationship with maximum plant height (Enquist et al., 1999; Marbà et al.,  
383 2007). This would imply that larger plants should be less sensitive to environmental  
384 fluctuations than their smaller counterparts which is consistent with the results of our  
385 study. Similar to the intrinsic population growth rate, we found no improvements of  
386 the  $\sigma_r^2$  model performance by including growth form. However, for this parameter, we  
387 were only able to include herbaceous plants and a very limited ( $n=3$ ) number of  
388 shrubs.

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

394 than between-species variability. Unexplained variability between species may be  
395 reduced by adding additional functional traits. For example, wood density may be a  
396 good indicator of the structural strength and mortality rates of plants (Visser et al.,  
397 2016).

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

#### 409 4.2 Extinction vulnerability

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

424 Our results are contradictory to those found for mammals and birds by Hilbers et al.  
425 (2016). They found that larger animals were more vulnerable to extinction than their  
426 smaller counterparts mainly due to their lower intrinsic population growth rates ( $r_m$ )  
427 and lower carrying capacities. In mammals and birds,  $\sigma_r^2$  is thought to be related to  
428 size with the same scaling exponent as  $r_m$  (Sinclair, 2003; Hilbers et al., 2016). This  
429 suggests that small species are able to sustain in changing environments due to high  
430 reproduction rates while large species are able to sustain to due to their high  
431 survivorship in such a way that the coefficient of variation in population size is  
432 independent of body size. However, our results show a higher scaling exponent for  $r_m$   
433 than for  $\sigma_r^2$  so that for plants scaling  $\sigma_r^2$  does not fully offset scaling of  $r_m$  as in  
434 mammals and birds. We hypothesize that this difference may be due to the fact that  
435 larger plant species generally have a larger number of seeds per reproductive event  
436 than their smaller counterparts while maintaining a high survivorship. For mammals,  
437 no relationship, or the opposite, is generally observed (Hendriks and Mulder, 2008).  
438 This can offset the relationship between size and intrinsic population growth rate in  
439 favour of larger species as we found in our results where the scaling exponent of -  
440 0.32 for  $r_m$  is higher than the expected scaling exponent of -1 based on allometric  
441 theory (Enquist et al., 1999; Niklas and Enquist, 2001).

442 The extinction vulnerabilities estimated in our approach should be used with caution.  
443 First of all, maximum plant height is not the only trait that matters; other functional  
444 traits, such as wood density or seed mass, are critical to the survival and  
445 reproduction of plants and may be related to extinction risks as well (Díaz et al.,  
446 2016; Visser et al., 2016). Furthermore, the extinction vulnerabilities calculated in this  
447 study are based on populations with an initial population size of 10,000 individuals,  
448 while the relationship with height is not influenced by this choice, absolute values of  
449 the MTE and PE are (see appendix C for a calculation of the MTE using an initial  
450 population size of 100 individuals). Lastly, estimations of extinction vulnerability may  
451 be improved by including other life history parameters such as life span and age of  
452 maturity and number of offspring. However, many of these life history parameters are  
453 in turn also expected to be related to organism size. For example, a strong  
454 relationship between generation time and size has been reported for plants and  
455 animals (Hendriks, 2007).

### 456 4.3 Relevance

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

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

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

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

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

512 In the absence of more detailed demographic information, the results of our study  
513 can help conservation managers to prioritize conservation efforts among populations  
514 of different species under equal external pressures. Additionally, the relationships  
515 presented in this study, with additional traits, may be combined with environmental  
516 indicators such as habitat size and connectivity. For example, combining the  
517 framework with species distribution models (SDMs) may give insights in the changes  
518 of extinction vulnerabilities under climate change or landscape fragmentation (Keith  
519 et al., 2008; Tian et al., 2014; Evans et al., 2016; Zurell et al., 2016). Lastly,  
520 combining demographic rates with global species occurrence maps can help obtain  
521 estimates of the vulnerability of a species to global extinction (Hilbers et al.,  
522 2016). This may be used to obtain first estimates of the extinction vulnerability of data  
523 deficient species. Given the large percentage of data-deficient species for vascular  
524 plants as compared to mammals and birds (IUCN 2016), this would be an important  
525 methodological advance.

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## 539 6 Supporting information

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

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

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

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

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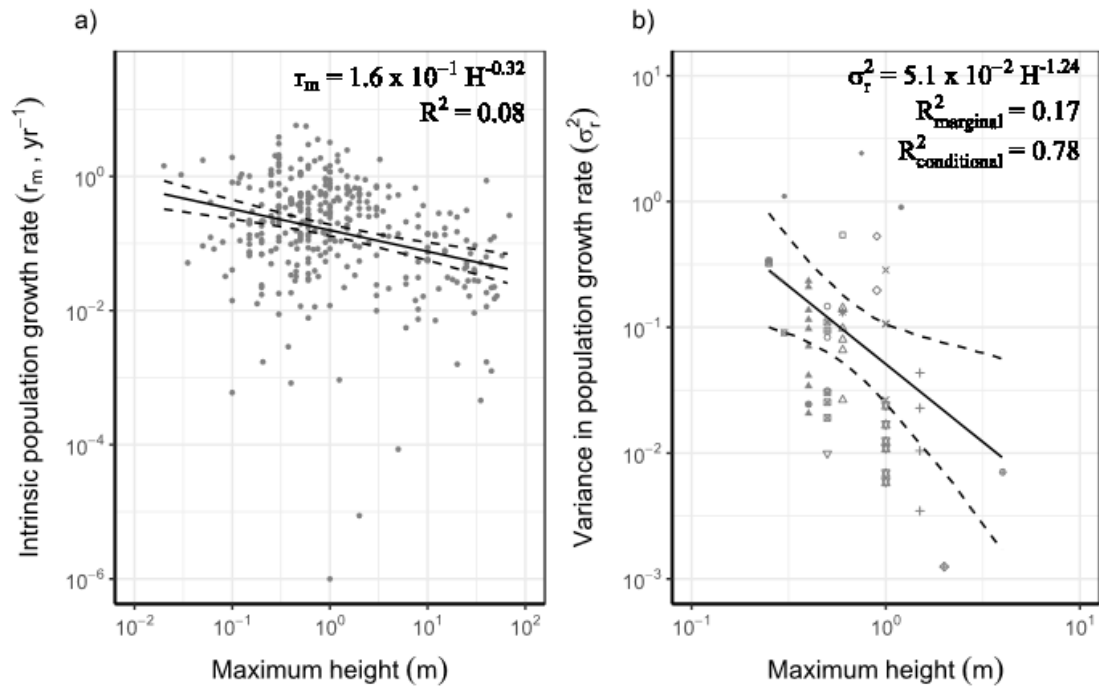
712

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 <sup>-1</sup> )	$\log(r_m) = \gamma_r + \beta_r * \log(H)$ $\gamma_r = -0.80 (-0.89, -0.72)$ *** $\beta_r = -0.32 (-0.43, -0.20)$ *** $r^2 = 0.08$ $N = 339$	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 ( $\sigma_r^2$ , yr <sup>-1</sup> )	$\log(\sigma_r^2) = \gamma_\sigma + \beta_\sigma * \log(H) + 1/Species$ $\gamma_\sigma = -1.29 (-1.62, -0.97)$ *** $\beta_\sigma = -1.24 (-2.16, -0.32)$ **  <i>Random effects</i> $T_{00} = 0.34$ $\sigma^2 = 0.13$  $r^2_{\text{marginal}} = 0.17$ $r^2_{\text{conditional}} = 0.78$ $N = 51$ $\#Species = 23$	COMPADRE Plant Matrix Database Version 4.0.1	
Maximum monospecific plant density ( $N_{max}$ , ind m <sup>-2</sup> )	$\log(N_{max}) = \gamma_r + \beta_r * \log(M)$ $\gamma_r = -0.61 (-0.68, -0.54)$ *** $\beta_r = -0.72 (-0.74, -0.70)$ ***  $r^2 = 0.96$ $N = 230$	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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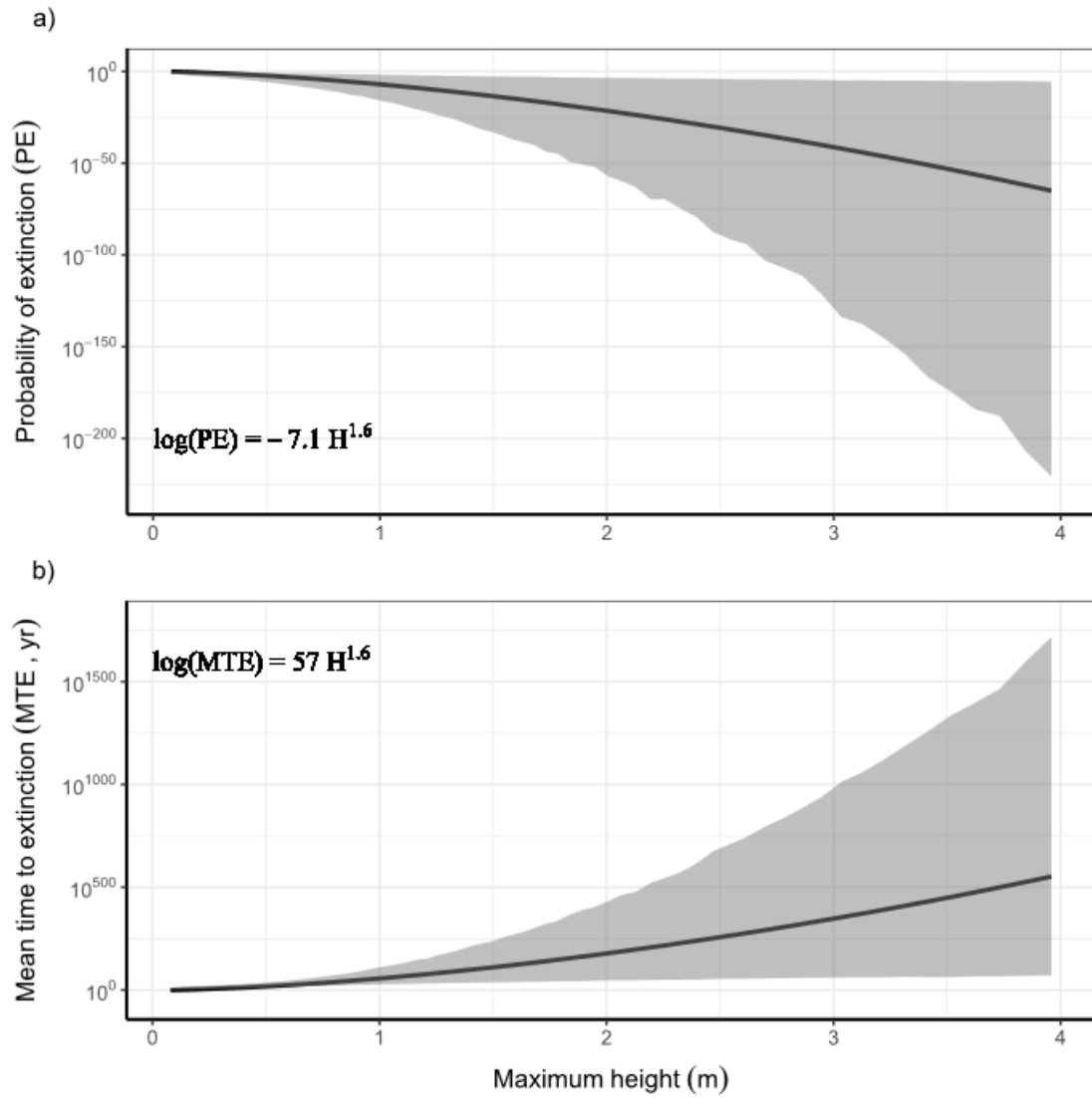
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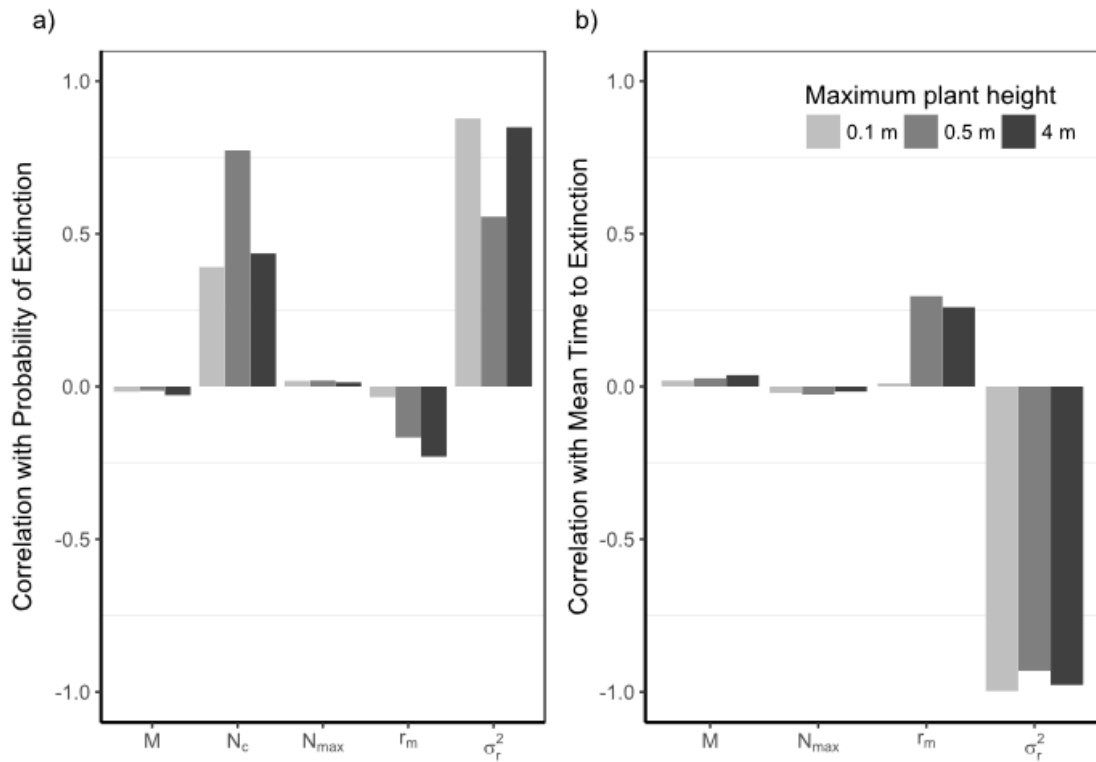
719 Fig. 1: (a) Allometric relationships between plant height and intrinsic population growth rate ( $r_m$ ) and (b)  
 720 variance in population growth rate ( $\sigma_r^2$ ) derived in this study. A total of 339 species (individual data  
 721 points) were used in the regression of model of  $r_m$ . A total of 23 species and 51 observations, multiple  
 722 data points per species (indicated by symbols), were used for  $\sigma_r^2$ . Dashed lines represent the 95%  
 723 confidence interval of the regressions.

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725

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



730

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

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