Sustainable seed harvesting in wild plant populations

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Abstract

Seed harvesting from wild plant populations is key for ecological restoration, but may threaten the persistence of source populations. Consequently, several countries have set guidelines limiting the proportions of harvestable seeds. Here, we use high-resolution data from 298 plant species to model the demographic consequences of seed harvesting. We find that the current guidelines only protect some species, but are insufficient or overly restrictive for others. We show that the maximum possible fraction of seed harvesting is strongly associated with harvesting frequency and generation time of the target species, ranging from 100% in long-lived species to <1% in the most annuals. Our results provide quantitative basis to guide seed harvesting legislation based on species' generation time and harvesting regime.

The restoration of degraded ecosystems is a major goal of global nature conservation (*1*). We have recently entered the 'UN Decade on Ecosystem Restoration' (*2*), working towards reversing the destruction and degradation of billions of hectares of ecosystems. However, ecological restoration at such scales requires high volumes of plant seeds for the re-establishment of native vegetation (*3*). Although there is a growing industry for the production of wild plant seeds in specialised seed orchards (*4*, *5*), large-scale harvesting of seeds from wild populations is still common in ecological restoration, and will continue to be in the future (*6*). This is particularly true for plant species that are long-lived or difficult to cultivate (*7*–*9*).

With increasing demands for wild plant seeds, there is a growing risk of driving source populations to local extinction (*10*, *11*). This risk may be critical because the donor populations are often remnants of habitats with high conservation value (*10*, *12*). Because of this risk, some regions, in particular the US (*13*), Australia (*14*), and Europe (*15*, *16*), have begun to set limits for the maximum fraction of seeds that can be harvested annually from wild plant populations without causing significant negative effects on their long-term viability ('*safe seed fraction*', hereafter). Safe fraction guidelines are inconsistent across countries, with *e.g.* 20% harvest allowed in the US (*17*), 10% in Australia (*14*), but only 2-10% in Germany, depending on plant growth type (*15*). Crucially, these guidelines lack a solid quantitative basis. To do so, one needs to explicitly link seed harvesting rates to population performance across plants and ecosystems (*11*, *18*, *19*).

To quantify the effects of large-scale seed harvesting on the performance of donor populations, and to assess how well current guidelines safeguard long-term population

persistence, we developed a statistical model to test impacts of simulated seed harvesting on wild populations of 298 plant species from the COMPADRE Plant Matrix Database (*20*, *21*). We used matrix population models to calculate 30-year projections of population sizes and simulated seed harvesting as a reduction of the sexually produced new recruits. To allow comparison across species, we expressed effects of seed harvesting as relative population sizes, where *e.g.* 0.8 represents a 20% reduction of population size and 0.5 a 50% reduction over 30 years, in comparison to the population size that would be reached without seed harvesting (SM, section 4). As the safe seed fraction was independent of the biogeographic origins of the examined species (Table S1), we used all species in our dataset to test the guidelines of specific countries.

We found that existing safe seed fraction guidelines protect only some but not all of the examined species (Figure 1). For instance, the current US guidelines (20% seed harvesting allowed) protect long-lived palms, with relative population sizes of 0.6 to 1 after 30 years, but would drive all 10 annual plants in our data to extinction (Fig. 1). With the more restrictive German seed harvesting guidelines (2% seed harvesting allowed), annual plants are projected to persist, with relative population sizes of 0.54 to 0.63 after 30 years. For all other plant growth types, safe seed fractions are much more variable. For example, with the 20% seed harvesting currently allowed in the US, the predicted relative population sizes of herbaceous perennials would range from 1 (no effect) to 0 (local extinction) after 30 years, while that of shrubs would range from 0.99 to 0.12, of succulents from 0.99 to 0.27, and of trees from 0.99 to 0.18 (Fig. 1).

The large variation safe seed fraction within plant growth types showed that the latter is a poor predictor of population vulnerability. Therefore, we next examined whether and which life history traits are better predictors of seed harvesting impacts (Figure 2). To enable practitioners to apply our findings, we restricted our analyses to five key life history traits readily available from public databases (*e.g.,* (*20–22*)) or easy to estimate in the field: generation time, mean age at sexual maturity, the degree of iteroparity (frequency of reproduction) and clonality, and seed bank persistence (Figure 2, SM section 5). We then related these traits to the vulnerability of our 298 species to seed harvesting, defined as the slope of the relative decrease in population size with increasing seed harvesting (SM section 3 and 6, Table S3).

Generation time is the strongest predictor of population vulnerability to seed harvesting. This life history trait alone explains 52.3% of the variation in harvesting vulnerability, with all five examined traits together explaining 62.3% (Fig. 2A). Population vulnerability to seed harvesting decreases with increasing generation time (Fig. 2B). This finding is in line with previous research, showing that the population dynamics of longer-lived species are more strongly determined by impacts on than on reproduction survival (*23*, *24*). The other four life history traits are also significantly related to seed harvesting vulnerability (Fig. 2B) – species that reproduce more frequently and/or postpone their first reproductive event are more vulnerable to seed harvesting, while species with clonal reproduction and/or persistent seed banks are less vulnerable – but the predictive power of these traits is low (Fig. 2A, Table S3). Population vulnerability also differs significantly among plant growth types, but with rather minor effects. Annual plant

species and trees display greater vulnerability to seed harvesting than other growth types, while succulents are least sensitive (Fig. 2C, Table S3).

Having identified generation time as a key determinant of population vulnerability to seed harvesting, we next estimated the safe seed fraction across generation times and harvesting frequencies (SM section 7). Population viability was defined as a <50% decrease of population size during 30 years of seed harvesting, compared to the same population without seed harvesting. A 50% decrease over 30 years corresponds to an annual decrease of about 2%. Such slow declines may be acceptable in population management because they can be monitored, and harvesting practices adjusted in time if necessary. Slow population changes may also be naturally buffered against environmental stochasticity (*25*), such as temporary seed overproduction or enhanced seedling recruitment after disturbances (*26*, *27*), or by density-dependent processes where populations are not seed-limited (*28*). Importantly, this threshold ensured a >95 % probability of population viability under environmental stochasticity in all analysed species (Figure S5).

The safe seed fraction critically depends on generation time, with substantial residual variation among species. For annual harvesting, the safe seed fraction ranged from close to 0% to 100%, with an average of 2.3% (95% CI: 0.5-4.1%) for annual and biennial plants, 10.1% (6.8-14.2%) for species with a 5-year generation time, and 40.1% (36.4-43.7%) for species with generation times of 20 years (Fig. 3A). These results highlight the need for more specific seed harvesting guidelines, since a fixed quota for all plant species (*13*, *16*) is not sensible.

The estimated safe seed fractions for annual harvesting regimes are close to the current German guidelines for herbaceous plants (2% for annuals, 10% for perennials (*29*)). However, for longer-lived species, we show that larger fractions could be harvested than what is currently recommended in the US or Australia, which use a 20% or 10% maximum, respectively, for all species regardless of generation time (*14*, *17*). For short-lived species, the safe seed fraction is low; the question remains whether such low yields are worth the effort of annual seed harvesting (*30*). A solution could be to harvest less frequently. When harvesting only every two years, the safe seed harvesting fraction for annuals and biennials increases from 2.3% to 5.3 % (2.7-7.9%), and with a 5-year or 10-year harvesting interval they increase to 11.3% (6.5-16.0%) and 30.3% (23.8-36.8%), respectively (Fig 3B-D). For plant species with generation times above two years, a 5-year harvesting cycle resulted in an average safe seed fraction of >30% (Fig. 3C), the amount typically removed from perennial grasslands with combine harvesters (*31*).

In summary, our results indicate that seed harvesting in wild populations is possible, but it must be guided by the critical factors of plant generation time and harvesting frequency. For longer-lived species, harvesting large fractions of seeds is unlikely to harm wild populations, particularly if seeds are not harvested every year. For short-lived species, though, more caution is necessary. A profitable harvesting of 20-30% of the seeds of annual species may only be possible if the harvesting regime takes place every 5-10 years or more.

Our results demonstrate the demographic impact of seed harvesting, and how it depends on plant life histories. Yet, we could have overestimated harvesting impacts for

two reasons. First, our analyses are based on matrix population models of species averaged across years and sites, but temporal or spatial variation in demographic rates could buffer some impacts of seed harvesting (*32*). We explored this possibility by re-analysing the 108 species for which we had at least three spatial or temporal replicate matrix population models, allowing us to estimate relative population sizes based on randomly drawn individual (rather than mean) models (SM section). The resulting relative population sizes were slightly larger and the safe harvesting seed fractions on average 1.8% larger (Fig S3, Fig. S4), confirming that matrix averaging may cause overestimation to a small extent. Second, our approach assumes plant populations to be seed-limited. However, longer-lived plants are often limited by safe sites rather than seeds, whereas seed limitation is more common in short-lived species (*28*). It is thus likely that, in longer-lived species, the effects of seed harvesting are even less severe than our findings suggest, but for annuals and short-lived forbs – the most vulnerable to seed harvesting – our results are more likely to be accurate.

We identify the key plant trait, generation time, that predict population vulnerability to seed harvesting. Together with an explicit consideration about the harvesting regime, our results constitute an important step towards much-needed, evidence-based seed harvesting guidelines. However, ultimately, even with improved guidelines, seed harvesting from wild populations is unlikely to cover the growing worldwide needs of ecological restoration (*33*). The ambitious targets of the UN Decade on Ecosystem Restoration (*2*) may only be reached with professional, large-scale seed production in seed orchards (*34*, *35*).

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Figure 1. Predicted effects of seed harvesting on the relative population sizes of 298 plant species worldwide in relation to current guidelines in countries where such legislation exists: USA, Germany, and Australia. Points represent individual species. These results reflect the simulation of seed harvesting on matrix population models parameterised with data from natural populations.

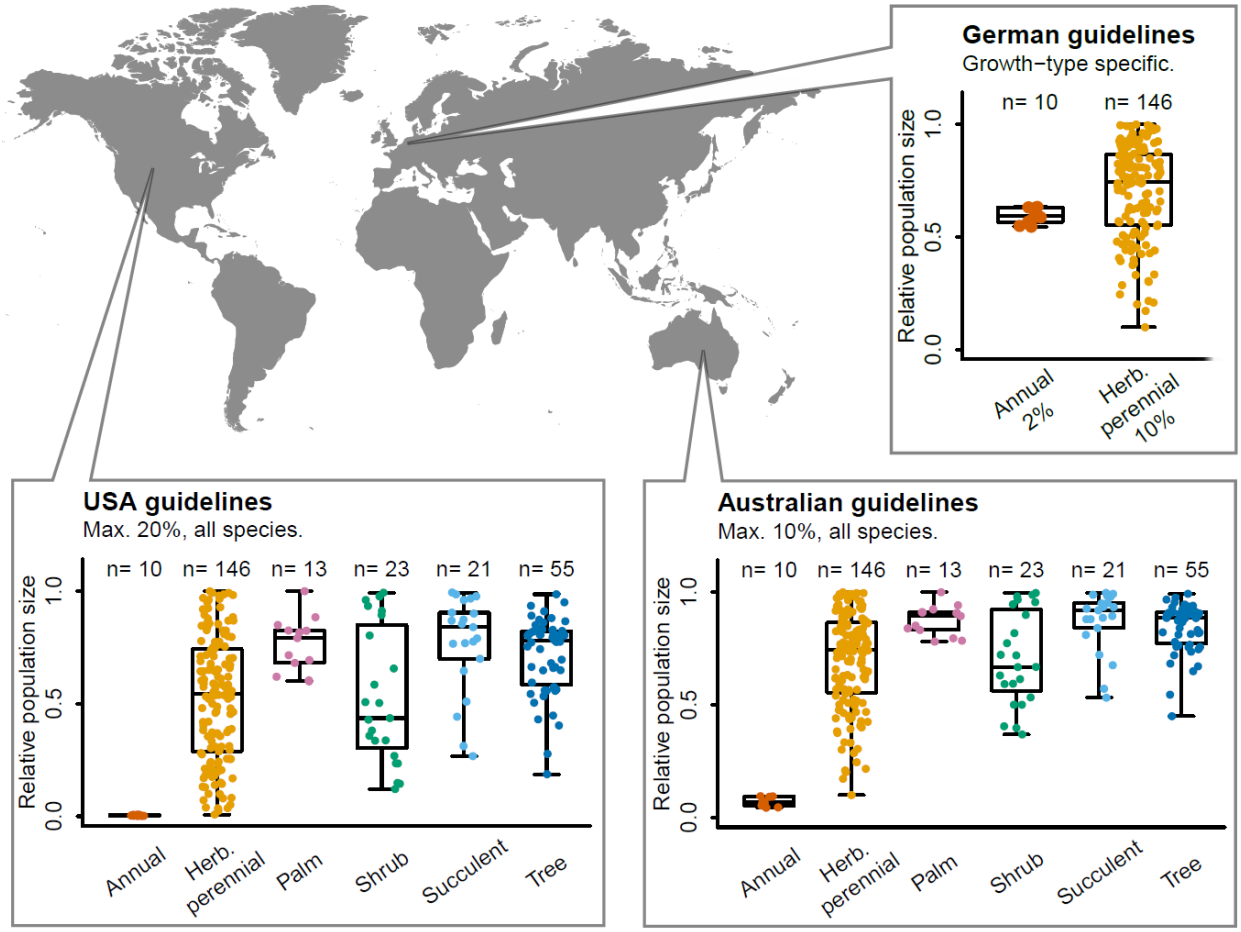
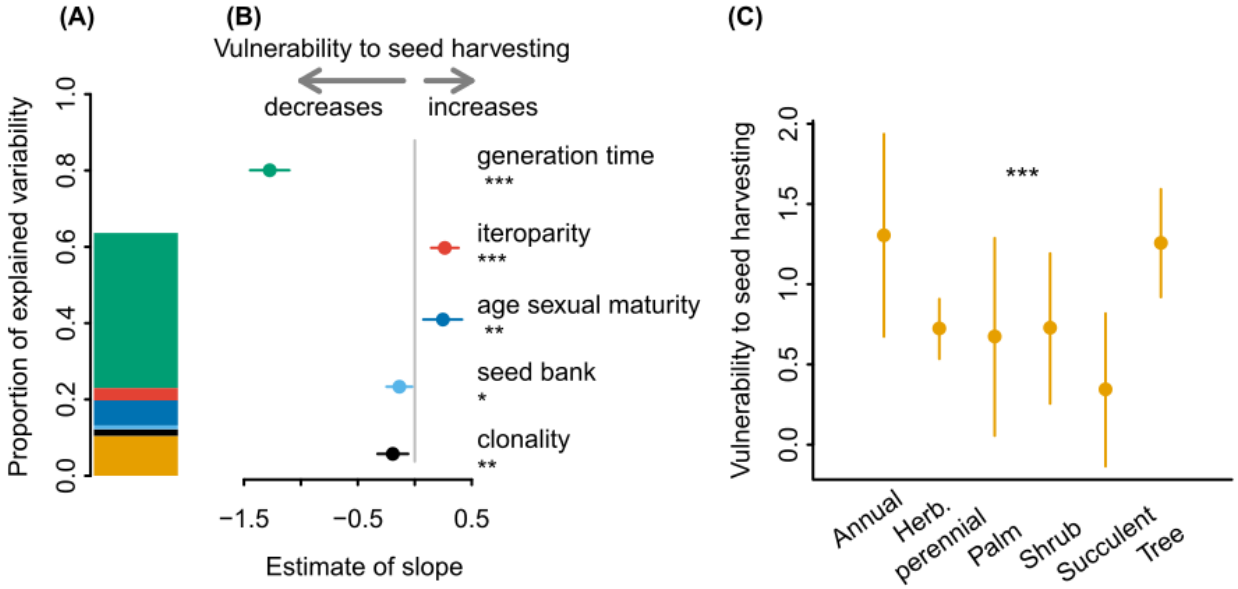


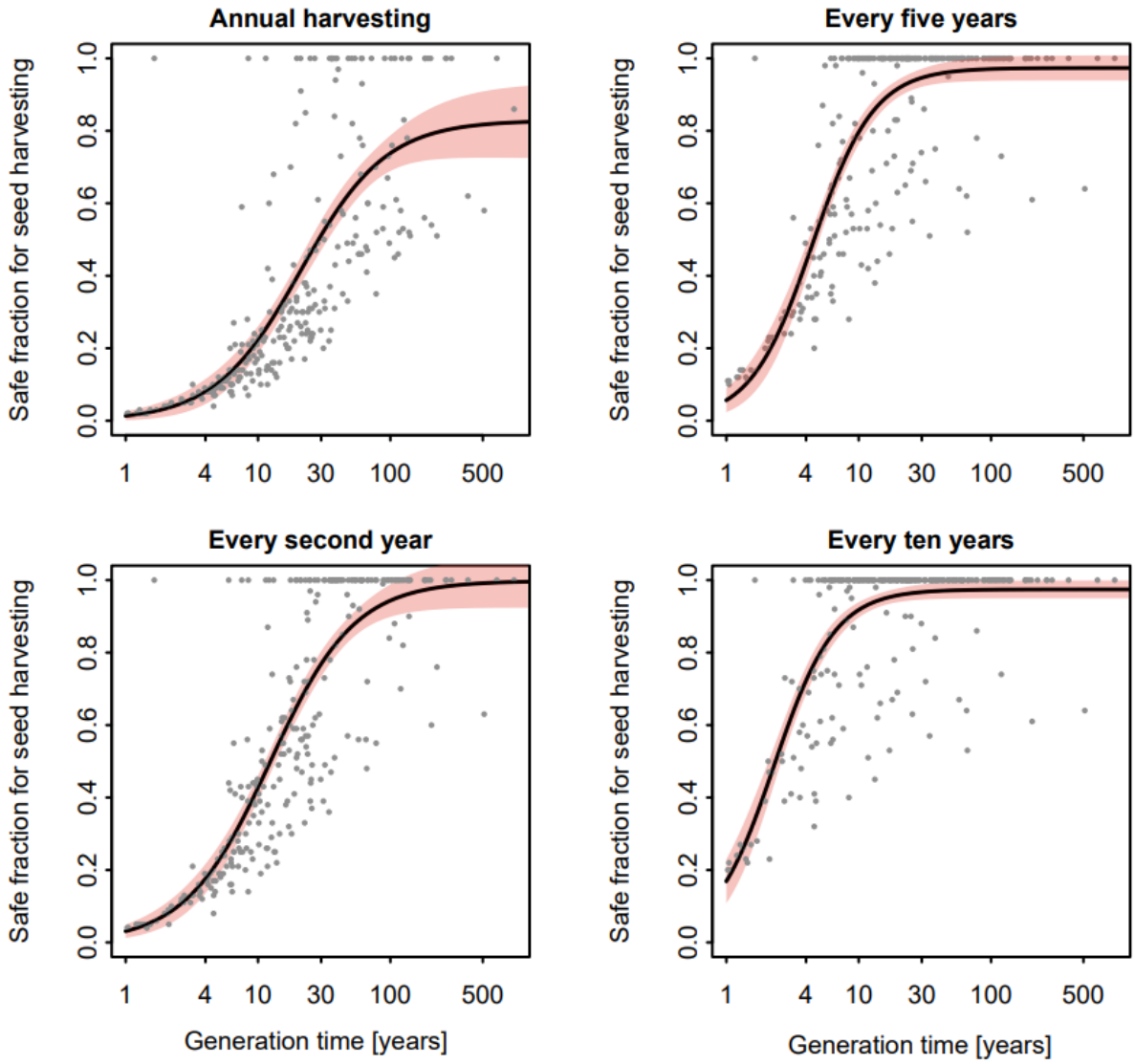
Figure 2. Associations of plant life histories and growth forms with variation in seed harvesting vulnerability, as calculated from matrix population models parameterised with data from natural populations of 298 plant species. (A) Proportion of variability explained by different life history traits, and (B) their effect estimates. (C) The fitted values of vulnerability for different growth types. Estimates in (B) and (C) are presented with their 95% credible intervals. As both vulnerability to seed harvesting and all explanatory variables were standardised prior analysis, the estimates of slope are in arbitrary units. (D) Definitions of the five examined life history traits (for calculation see Table S2).



(D)

Generation time: the mean age of reproductive individuals in a population.
Age at sexual maturity: the average number of years after which individuals in a population become sexually reproductive.
Iteroparity: the frequency of reproduction throughout the lifespan of an individual, with high/low Demetrius' entropy (S) values for highly iteroparous/semelparous populations.
Seed bank: the mean life expectancy of seeds in the seedbank.
Clonality: the per-capita clonal contributions, weighted by the relative frequency of individuals in each stage along the life cycle of the species.

Figure 3. Relationships between the generation times of 298 plant species and their safe fractions for seed harvesting, estimated at different harvesting frequencies. The safe seed fraction is the maximum proportion of annual seed production of a population that can be harvested without reducing the relative population size to below 0.5 in 30 years.



Online supplementary material to

Sustainable seed harvesting in wild plant populations

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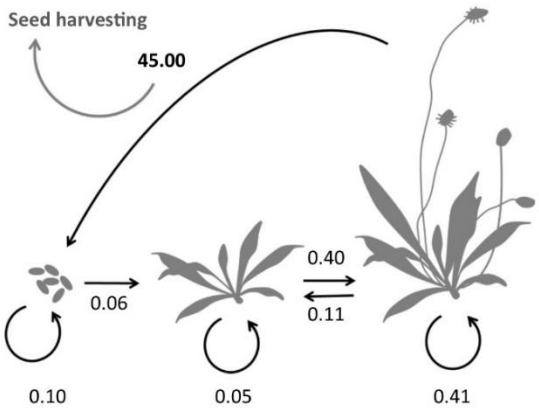
Methods and supplementary results

To quantify the effect of seed harvesting on wild plant populations, we used matrix population models (*1*). We first tested the impacts of seed harvesting by using simulations the regulatory recommendations on seed harvesting in the wild of three regions where such regulations are in place (Australia, Germany and USA). Second, we calculated the population vulnerability to seed harvesting for each of the 298 plant species examined. Third, we related those effects to plant key life history traits (*i.e.* defining characteristics of their life cycles; e.g. generation time, age at maturity). In the fourth step, we used the life history traits that explained most of the vulnerability of natural populations to seed harvesting to formulate biologically-sound management recommendations. The ultimate goal of such recommendations is to impose a threshold to seed harvesting so that (i) the population size does not decline more than by 50% over 30 years of consecutive (*i.e.* annual) seed harvest and (ii) the population may still have a 95% probability of persistence. All calculations and statistics were performed in R(*2*), and the reproducible, commented scripts are found in an online repository (*specify*).

1 Matrix population models

1.1 General introduction

Matrix population models (MPMs, hereafter) are a widely used tool for investigating population dynamics (*1*). Briefly, an MPM describes the life cycle of an organism in terms of age, size and/or developmental stages along its lifecycle and the transitions between stages, usually from one year to the next, as well as the sexual and clonal per-capita contributions to the population by individuals in each of those stages (Figure S1). One of the many applications of MPMs is the ability to project the dynamics of a population through time (*1*), whereby a long-term population growth rate can be estimated (Figure S1). Importantly here, MPMs can also be used to calculate a wide range of population characteristics such as life history traits (*3*), extinction probability (*4*), and the effects of different hypothetical events (such as seed harvesting) on the long-term viability of a population (*5*, *6*).



Population projection matrix

λ = 1.24		YEAR 1		
		Seed	Vegetative	Flowering
YEAR 2	Seed	0.10	0	**45.00**
	Vegetative	0.06	0.05	0.11
	Flowering	0	0.40	0.41

$$\lambda = \frac{N_{(t+1)}}{N_t}$$

Figure S1: Life cycle of a hypothetical plant species with three stages (seedbank, juvenile, and adult) and its corresponding matrix population model (MPM), with *λ* indicating its long-term population growth rate, which is a

347 function of population size (*N*) between two time-points *t* and *t*+1. Seed harvesting in this study was simulated by
348 manipulating the transitions that describe generative reproduction.

349 In this study, we used MPMs to simulate seed harvesting as reduction of the per-capita
350 contribution(s) describing seed production (Figure S1). We did so by simulating the harvesting of
351 newly produced seeds while keeping all other demographic processes unaltered. The resulting
352 MPM thus describes the population dynamics in a year where seed harvesting took place.
353

354 ## 1.2 COMPADRE database

355 We used data stored in THE COMPADRE Plant Matrix Database (version 5.0.0.), last accessed
356 25.8.2019 (*7*). In this version, COMPADRE contains 9121 MPMs from 647 published works
357 describing life cycles of 760 plant species, ranging from algae to trees worldwide. MPMs in the
358 database are accompanied by extensive metadata including the continent where the study was
359 carried out, whether it was carried in captivity or in the wild and standardized information about
360 each life cycle stage in three categories: propagules, individuals photosynthetically active, and
361 individuals in vegetative dormancy. In the vast majority of MPMs in COMPADRE, the full MPM ***A***
362 is divided into three submatrices (*3*): ***U*** includes demographic processes that depend on survival
363 of individuals alive at the beginning of the census (i.e., progressive growth, stasis, retrogressive
364 growth, seedbank persistence, and vegetative dormancy), ***F*** includes sexual reproduction (e.g.
365 production of seeds and juveniles), and ***C*** includes clonal reproduction (*i.e.* vegetative
366 reproduction of ramets), such that

367 $$\boldsymbol{A} = \boldsymbol{U} + \boldsymbol{F} + \boldsymbol{C} \qquad \textit{eq. 1}$$

368

369 ## 1.3 Selection of the MPMs

370 We selected species and MPMs from COMPADRE based on the following criteria to allow for
371 inter-specific comparisons for our specific questions:

372 - Only angiosperms and gymnosperms, since the ultimate goal of this study is to simulate
373 the effect of seed harvesting on seed-producing plants.
374 - MPMs parameterised from field data from wild populations and under unmanipulated
375 conditions, because the aim of this study is to understand the effect of seed harvest on
376 natural, wild populations.
377 - MPMs for which the sexual reproduction component had been quantified explicitly, and
378 separated from other processes in order to allow us to accurately perturb sexual reproduction
379 (seed production; see below).
380 - MPMs that are irreducible, ergodic, and primitive, so the dominant eigenvalue
381 (population growth rate) and other key properties could be calculated (*1*).
382 - When multiple studies per species were available (n = 235 species), we selected the single
383 study per species that:
384 - Documented a seed bank, because inclusion of the transition in MPMs is vital
385 to correct estimation of life history traits (*8*)
386 - Contained a higher number of individual MPMs (*i.e.*, from more populations or
387 more years) to use the most representative demographic information for the
388 target species.

389

390 These selection criteria resulted in 467 MPMs from 467 plant species. Next, we checked the
391 reliability of incorporating a seed bank in them or not. While survival of seeds in the seed bank is
392 well documented in many demographic studies (*9*), between 42.9% and 47.3% of studies using
393 MPMs in plant species unjustifiably exclude seed banks (8), thus assigning seedlings in year *t* to
394 reproductive plants in *t*-1 (e.g. (*10*)). However, this assumption is only correct in species with
395 transient seed bank, i.e. seeds survive in the soil less than one year and thus, do not form a
396 permanent soil seed bank (*8*). For those studies in our list were seed banks were not explicitly
397 considered in their MPMs, we verified whether the species indeed has only transient seed bank
398 or not. We did so by carefully examining the original source of the MPM(s). If the source did not
399 mention seed bank, we further searched in the TRY database (*11*) for its potential existence.
400 Consequently, we excluded 169 species where seedbanks were unjustifiably excluded from their
401 MPMs.

402 This final selection criterion resulted in dataset 298 species (each species having a
403 representative MPM) from 84 taxonomic families. This is the final set of species and data that
404 were used for the simulations described below.

405

406 1.4 Mean MPMs vs individual MPMs

407 For the majority of studies in COMPADRE, MPMs are available for several annual transitions and
408 populations, and so this was also the case in our final dataset. For all calculations, except in the
409 case of stochastic simulations (Section 8), we used a single *mean* MPMs per species across all
410 years and populations of demographic data available for that species. This mean MPM was

411 calculated as the element-by-element arithmetic mean of the aforementioned MPMs, or pooled
412 directly (e.g. weighted mean by sample size) from the individual-level data when provided by the
413 author in the publication or through personal communications with the COMPADRE team.

414 For the stochastic simulations, we used *individual* MPMs, which represent the population
415 dynamics during a given annual transition and at a given population. For this purpose, we used
416 only species that were represented in the database by at least three individual MPMs (Section
417 8), resulting in 1676 individual MPMs from across 114 plant species in our dataset.

418 2 Simulating seed harvesting

419 We used MPMs to simulate the impact of seed harvesting on populations. We used the following
420 approach, where we first used the mean MPM (Section 1.4) for each species, and simulated seed
421 harvesting as a reduction in the values describing reproduction via seed in the sexual
422 reproduction matrix $\boldsymbol{F}$ (see equation 1). Specifically, we created a modified MPM $\boldsymbol{A'}$ with reduced
423 per-capita contributions of seed production in $\boldsymbol{F}$. To carry out our projections, we initiated the
424 population vector $\boldsymbol{n_0}$ as the stable stage distribution of the original MPM $\boldsymbol{A}$. This vector $\boldsymbol{n_0}$ was
425 obtained as the right-eigenvector of $\boldsymbol{A}$ following methods described by Caswell (2001). We then
426 projected $\boldsymbol{n_0}$ 30 years using the modified MPM $\boldsymbol{A'}$ and the chain rule (*1*). We chose this period of
427 time for our projections because it is long enough to observe even minor changes in the overall
428 population size N that are not typically possible to quantify by short-term monitoring (*12*), while
429 it is of sufficient length to fit within the active career of a land manager or conservation
430 practitioner. We benchmarked the resulting population size $N_{30\ \mathrm{harvest}}$ relative to the population

size $N_{30\ no\ harvest}$ that would have been achieved in the absence of seed harvesting as in equation 2:

$$N_{30\ relative} = \frac{N_{30\ harvest}}{N_{30\ no\ harvest}} \qquad eq.2$$

The relative population size $N_{30\ relative}$ thus ranges between 1 (when seed harvesting has no effect on population size; $N_{30\ harvest} = N_{30\ no\text{-}harvest}$) to 0 (when the effect is so drastic it drives N to 0 within 30 years). For example, a value of $N_{30\ relative} = 0.1$ means that the population size achieved with seed harvesting is 10% of the population size that would have been achieved without seed harvesting. The use of this metric as measure of seed harvesting impact allowed us next to implement intra- and inter-specific comparisons, regardless of the variable population growth rates of each species' population. When calculating the population sizes with and without harvest ($N_{30\ harvest}$ and $N_{30\ no\ harvest}$), we included only the active but not dormant (seed bank, dormant vegetative) life stages of the population vectors N_{30} because practitioners and scientist commonly evaluate population size based on counting active, standing individuals.

3 Vulnerability to seed harvesting

We used mean MPMs to calculate species vulnerability to seed harvesting. For each species, we created 101 MPMs that describe population dynamics when harvesting 0-100% of seed production, in 1% steps (Figure S1). As in section 2, we used these virtual MPMs to project population size over 30 years. We then fitted an exponential-decay model to quantify the effects of the varying proportion of harvested seed (p) on the relative population size in the 30 years ($N_{30\ relative}$) as follows:

$$N_{30\,relative} = e^{p(-b)} \qquad \text{eq. 3}$$

where *b* determines how steeply the relative population size ($N_{30\ \text{relative}}$) decreases with increasing proportion of harvest pressure, such that the larger *b*, the steeper this decrease is. We hereby refer to this coefficient as *vulnerability to seed harvesting* (Figure S2).

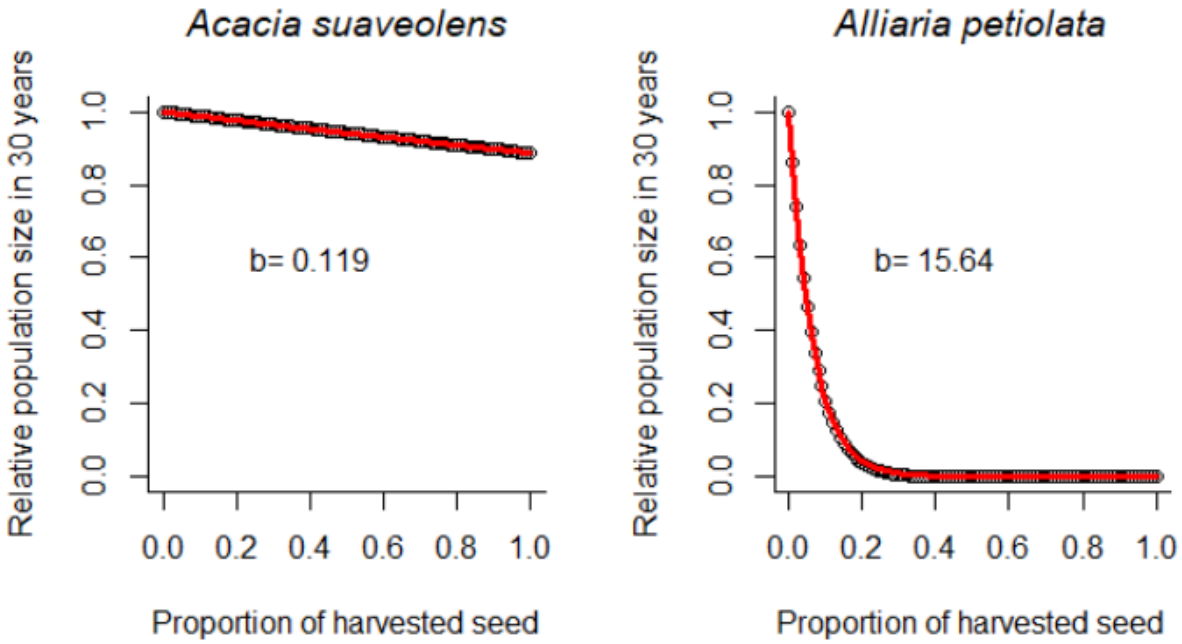


Figure S2. Vulnerability of population dynamics to seed harvesting (*b* in equation S3) in two of our 298 examined plant species. Note how the larger the value of *b*, the more vulnerable the given species is to seed harvesting. Black dots: simulated values; red line: fitted exponential-decay model as per equation 3.

461 # 4 Testing current recommendations

462 We used MPMs to simulate the impact of seed harvesting according the current rules on the
463 relative population size $N_{30\ relative}$. As far as we are aware of, explicit recommendations for the
464 maximal proportion of seeds that can be harvested from natural populations exist only in three
465 countries. In USA and Australia, this value is 20% and 10%, respectively, for common plant species
466 when harvesting seeds for restoration projects (*13*, *14*). German rules are available for
467 herbaceous plants: 2% for annual and 10% for perennial when harvested every year (*15*).

468 As the current recommendations are partly growth-form specific (*15*),we examined the
469 reduction in relative population size as a function of plant growth form. Namely the levels were
470 annual, herbaceous perennial, epiphyte, palm, succulent, shrub, and tree, as indicated in the
471 metadata in COMPADRE. For this analysis, we excluded growth forms represented by less than
472 5 species, that is epiphytes (n=4) and lianas (n=1), as well as plant species whose generation
473 time disagreed with the metadata of the species - specifically, annual species with generation
474 time larger than two years (n=4). As the vulnerability to seed harvesting of individual species
475 (Section 3) depended neither on a continent nor on the interaction between a continent and
476 plant growth form (Table S1), we grouped species only by growth form and used the same set of
477 species to test the recommendations from Australia, USA and Germany (Figure 1 in the main
478 text).

479 **Table S1:** The effects of continent and plant growth form on vulnerability to seed harvesting. Results of
480 linear model with vulnerability to seed harvesting (log-transformed) as a response variable and plant
481 growth form, continent, and their interaction as explanatory variables. We report results of a simple

linear model because generalized least square model with phylogenetic correction failed due to singular fit. Terms are fitted sequentially; significant values are in bold. Adjusted R^2=0.15

	df	resid. df	F	p
Plant growth form	5	242	10.31	**<0.001**
Continent	5	242	1.12	0.349
Plant growth form × Continent	13	242	0.99	0.462

5 Life history traits

We used life history traits to explain species vulnerability to seed harvesting. A life history trait is a key feature that describes the life cycle of the organism (e.g. generation time, age of sexual maturity, iteroparity, clonal propagation, survival of seeds in the seed bank). As our ultimate motivation was to facilitate the translation of our findings to land managers and practitioners, out of the wide range of life history traits that can be derived from MPMs (e.g (*1*, *3*)), we selected the traits that are readily available in trait databases or easy to estimate in the field (Table S2). All life history traits were calculated based on the matrix A of the mean MPM of each of our 298 species.

Table S2: Formulation of the life-history traits used to explain species vulnerability to seed harvesting in the studies 298 vascular plant species. λ is the population growth rate, which corresponds to the dominant eigenvalue of the matrix ***A***; l_x and m_x are stage-specific survival and fertility schedules, ***C*** is the submatrix describing clonal reproduction, m is the dimension of the matrix ***C***, ***w*** is the stable stage distribution of the matrix ***A***, j column entries of the matrix population model.

Life history trait	**Biological meaning**	**Formula**
Generation time *T*	Number of years necessary for the individuals of a population to be fully replaced by new ones	$T = \frac{log(\int_1^{\infty} l_x m_x \, dx)}{log(\lambda)}$
Age at sexual maturity L_α	Number of years that it takes an average individual in the population to become sexually reproductive	L_α as described in Caswell 2001's equation 5.41 (*1*)
Degree of iteroparity *S*	Spread of reproduction throughout the lifespan of the individual as quantified by Demetrius' entropy (S). High/low S values correspond to iteroparous/semelparous populations	$S = -e^{-log\lambda} l_x m_x log(e^{-log\lambda} l_x m_x)$
Clonality K	Per-capita clonal contributions weighted by the stable stage distribution of the MPM	$K = \sum_1^m \bar{C}_j \bar{w}_j$
Seed bank residence	Mean amount of time individuals are expected to stay in the seedbank stage	As described in Caswell 2001's equation 5.36 (*1*) according to the fundamental matrix approach for the life cycle stage(s) that correspond to the seed bank stage(s)

501 # 6 The effect of life history traits on vulnerability to seed harvesting

502 We used linear model to determine which life history traits (generation time, age at sexual
503 maturity degree of iteroparity, clonality, seed bank residence) best explain species' vulnerability
504 to seed harvesting (Section 3). We also added plant growth form as an explanatory variable (as
505 defined in the COMPADRE database (*7*)) to the model to test whether it explains any additional
506 variability. Restricting the model to key life history traits allowed us to keep the full model and
507 avoid model selection, which is known to produce exaggerated effect sizes and spurious effects
508 (*16*). Species vulnerability to seed harvesting was log-transformed prior analysis to achieve
509 normality. Other explanatory variables except plant growth type (factor) were log-transformed
510 and standardised to adhere to the model assumptions of normally distributed errors.

511

512 **Table S3:** The effect of life history traits on vulnerability to seed harvesting, results of the model, significant values
513 (*P*<0.05) are in bold. Adjusted R^2 = 0.62.

	df	resid. df	F	p
Generation time	1	263	210.92	**<0.001**
Degree of iteropartity	1	263	18.80	**<0.001**
Age at sexual maturity	1	263	8.24	**0.004**
Seed bank residence	1	263	5.66	**0.018**
Clonality	1	263	7.98	**0.005**
Plant growth type	5	263	4.64	**<0.001**

514

515 To illustrate the importance of the life history traits for predicting the species vulnerability to
516 seed harvesting (Figure 2 in the main text), we expressed the relative importance of each
517 predictor in the model as the proportion of explained variability assigned to each predictor. As
518 the explained variability can depend on the sequential order of the predictors in the model, we
519 averaged the sequential explained variability for each predictor across all possible ordering of
520 the predictors using the R package *relaimp* (*17*). To visualize effect sizes of the effect of life history
521 traits on the species vulnerability to seed harvesting, as well as uncertainty of these effects, we
522 used 95% credible intervals, a Bayesian analogue of confidence intervals. These were calculated
523 from 10,000 simulations of the mean and variance of each estimate, using the *sim* function in the
524 R package *arm* with non-informative prior (*18*).

525 We also run a model including the phylogenetic relationships among species to test the extent
526 to which the explanatory power of life history traits on species' vulnerability to seed harvesting
527 is in fact driven by the phylogenetic inertia in the quantified plant life-history traits (*19*). We used
528 a phylogenetic generalized least square model to include the phylogeny of our species. We
529 obtained the phylogeny from COMPADRE, following methods detailed elsewhere (*3*). With this
530 model, we estimated Pagel's λ (not to be confused with the population growth rate, also referred
531 to as λ in the demographic literature (*1*)), a measure of phylogenetic signal in the trait structure.
532 Briefly, Pagel's λ=0 indicates no effect of the phylogenetic structure in the dataset in explaining
533 variation in a given trait, while Pagel's λ=1 indicates that the phylogenetic structure perfectly
534 predicts, i.e. is responsible for, the life history trait structure. Negative values suggest that closely
535 related species have more different traits than would be expected by random ((*19*). In our
536 phylogenetic generalized least square mode, the phylogenetic signal was overall weak and

537 negative (Pagel's λ=-0.1). Based on this result, we opted to present in this paper results from the
538 linear model without phylogenetic correction.

539

540 7 Assessing limits of seed collection

541 We used the mean MPM per species to estimate how large a proportion of seed production can
542 one collect from the natural population while only moderately affecting its dynamics. As a
543 moderate effect, we defined a reduction in population size *N* of not less than 0.5 times the size
544 that would have been achieved without seed harvesting during the course of 30 years of a
545 constant annual harvest intensity. While a reduction of population size by 50% over 30 years may
546 seem to be relatively high, it corresponds to an annual decline of <2%. Importantly, this threshold
547 also allows for the persistence of the natural population under environmental stochasticity in
548 >99% of species (see 8.2).

549 For each species' MPM, we simulated the effect of seed harvesting as a reduction of seed
550 production transition by 0-100%, in 1% intervals. We used such reduced, virtual MPMs to
551 simulate population dynamics across 30 years We recorded the final population size and
552 expressed it as relative to population size that would be achieved without seed harvesting (see
553 Section 2, note this calculation is the same as the first step of calculation of vulnerability to seed
554 harvesting, Section 3). Apart of annual harvest, we also modelled the effect of harvesting seeds
555 once in 2, 5 or 10 years because reducing harvesting frequency up to once in 10 years is
556 sometimes recommended to limit negative effects of seed harvest on population dynamics (*20*).

557 In this case, we modelled population dynamics with the original mean MPM and the reduced
558 MPM was used every 2nd, 5th or 10th run. As the safe fraction for seed harvesting, we considered
559 the largest proportion of seed that was possible to harvest without exceeding the 50 % reduction
560 of the relative population size.

561 We related the safe fraction for seed harvesting to the generation time, as the most important
562 predictor of species vulnerability to seed harvesting -this trait alone explained 52.3% of total
563 variability in species vulnerability to seed harvesting. We used non-linear regression in *R* (*nsl*) to
564 describe the sigmoid relationship between the safe fraction of seed harvesting and the
565 generation time, and used function in package *investr* (*21*) to generate confidence intervals of
566 the relationship (Figure 3 in the main text).

567 8 Effect of environmental stochasticity

568 In a portion of our studied species, we simulated the effect of environmental stochasticity on
569 population dynamics to understand how environmental stochasticity affects our prediction for
570 seed harvesting based on the mean MPMs. We used all species in our dataset represented by at
571 least three individual MPMs (Section 1.4), resulting in 1,578 MPMs across 108 plant species. We
572 simulated environmental stochasticity as projecting vector of stable stage distribution by
573 randomly drawn individual MPM in each step. To obtain probability distribution of results under
574 environmental stochasticity, we repeated the process 1,000 times. We expressed the results as
575 $N_{30\ \mathrm{relative}}$ (equation eq. 2). The effect of seed harvesting was simulated as above (Section 4), with
576 the difference that in each of the 30 annual time-steps in each of the 1,000 simulation runs, we
577 randomly draw one individual MPM from the set of individual MPMs available for given species.

578 ## 8.1 The effect of seed harvesting on population size based on environmental
579 stochasticity versus mean MPM

580 To understand how environmental stochasticity affects our results, we estimated the robustness
581 of our results in stochastic environments. As an example, we used the effect of harvest of 20% of
582 seed production, expressed as $N_{30\ \mathrm{relative}}$, and simulated seed harvesting either using mean MPMs
583 or stochastic simulation. Further, we compared the safe fraction for seed harvesting ($N_{30\ \mathrm{relative}}$ >
584 0.5) based on the mean MPMs to the median of seed safe fraction based on the stochastic
585 simulations.

586 The median of relative population sizes $N_{30\ \mathrm{relative}}$ based on 1,000 permutations of stochastic
587 simulations (y axis in the Figure S3) closely correlated with the $N_{30\ \mathrm{relative}}$ based on the mean MPMs.
588 Interestingly, the relative population size $N_{30\ \mathrm{relative}}$ based on stochastic simulation (orange points
589 in the Figure S3) was slightly higher than the $N_{30\ \mathrm{relative}}$ based on mean MPMs (black line in Figure
590 S3), especially in species that are more vulnerable to seed harvesting. Consequently, the safe
591 fraction for seed harvesting based on the median of stochastic simulations was on average 0.017
592 higher that safe fraction based on the mean MPMs (Figure S4). This suggests that environmental
593 stochasticity partly buffers the predicted decrease of population size caused by seed harvesting.

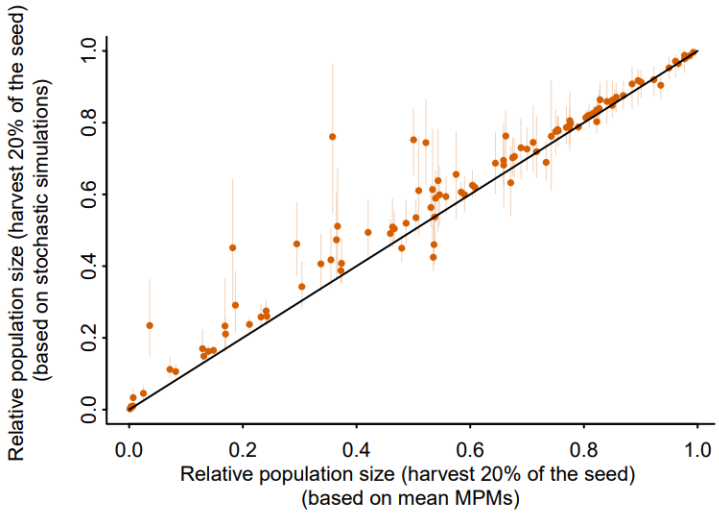


Figure S3: Comparison of relative population size $N_{30\ relative}$ when 20% of seeds was harvested, based on mean MPMs (x axis) with the $N_{30\ relative}$ from calculations with implemented environmental stochasticity (y axis).

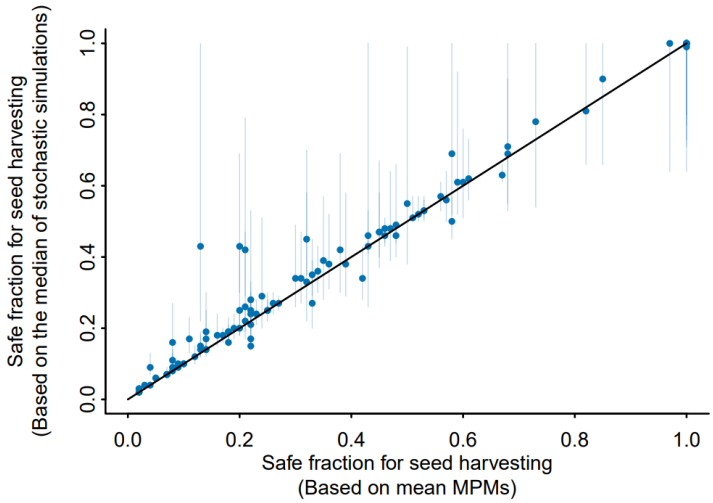


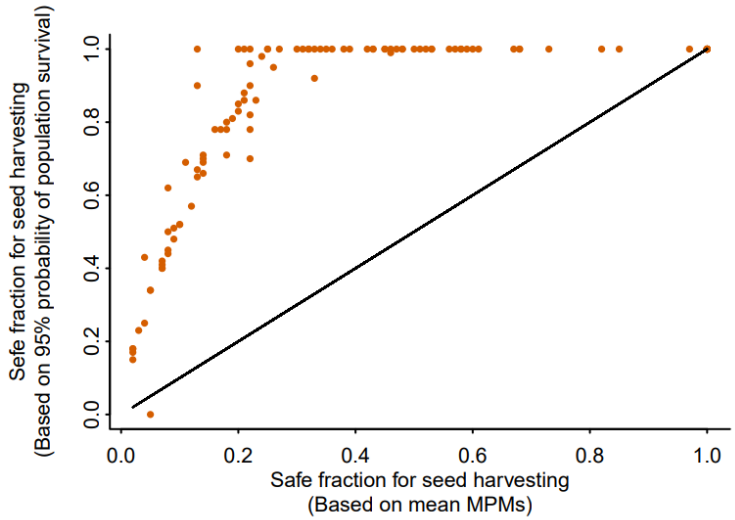
Figure S4: Comparison of the safe fraction for seed harvesting based on $N_{30\ relative} > 0.5$ as calculated from the mean MPM (x-axis and the 1:1 black line), with the median of safe fraction for seed harvesting based on $N_{30\ relative} > 0.5$, as based on stochastic simulations (with 95% CI).

8.2 Threshold for seed harvesting based on mean MPM versus extinction probability

In the models above, we have set a threshold for seed harvesting so that the relative population size $N_{30\ relative}$ decreases to a maximum value of 0.5. In this section, we tested whether this threshold also prevents population from extinctions. For each species, we computed how large a proportion of seeds could be sustainably harvested without causing extinction in at least 95% of permutations of stochastic simulations. Here, we considered a population to go locally extinct when $N_{30\ relative} < 0.01$ (see Section 2 for definition of $N_{30\ relative}$). For each species, we compared the threshold based on the 95% probability of population survival with the threshold based on mean MPM and $N_{30\ relative}$ >maximum decline to 0.5.

612 In the vast majority (<99%) of examined species, the threshold based on $N_{30\ relative} > 0.5$ (as

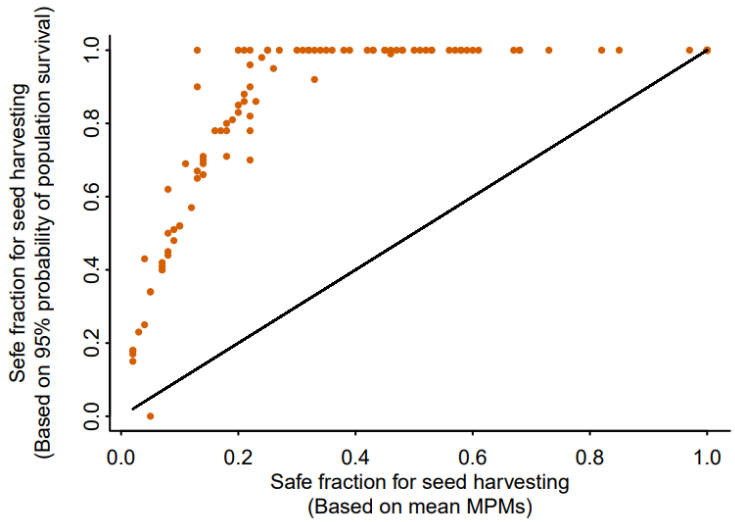
613 calculated using mean MPMs, black line in the



614

615 **Figure S5**) allowed for the collection of a lower proportion of seeds than the threshold based on

616 95% probability population survival when using stochastic simulations (points in the



617

618 **Figure S5**). This pattern suggests that the rules based on $N_{30\ relative} > 0.5$ derived from the mean

619 MPMs prevent populations from going locally extinct.

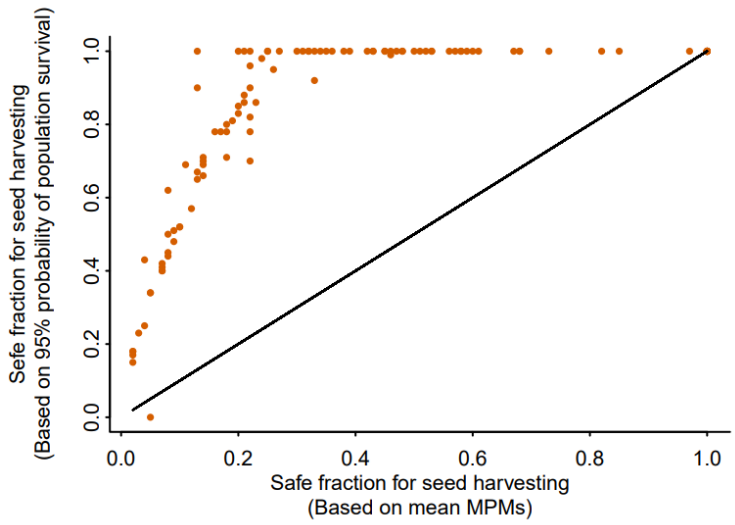


Figure S5: Comparison of the threshold for maximal seed harvest based on $N_{30\ relative} > 0.5$ as calculated from the mean MPM (x-axis and the 1:1 black line), with the maximal seed harvest that allows 95% probability of population survival of each considered species, as based on stochastic simulation.

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