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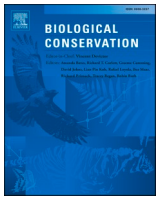

The importance of negative density dependence for rare species persistence

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ABSTRACT

Determining the predictors of extinction risk is a major goal of conservation biology. Theory suggests that population characteristics such as low abundance and declining trends should equate to high extinction risk. However, rare species persist and account for nearly half of all species across global communities. Here we employ the Chicago Botanic Garden's long-term, rare species monitoring dataset to investigate population dynamics and hypothesized predictors of extinction risk of 73 populations of 43 rare species. Specifically, we ask how important negative density dependence is for rare species persistence and how well population size, population trends, life cycle duration, and clonality predict estimates of extinction risk in rare species. Extinction risk was estimated using density-dependent and density-independent population viability analyses. Based on our simulations, we found that only 33 of our populations had concerning extinction risks (>20 %). The key to these relatively low extinction risks for so many rare, listed species was negative density dependence. Population size, population trends, life cycle duration, and clonality were not good predictors of extinction risk based on our modeling efforts, though their relationships to extinction risk did agree with theoretical expectations. Our results highlight the potential importance of negative density dependence for rare species persistence and the importance of incorporating density dependence in population projection models for extinction risk assessment.

1. Introduction

A major challenge in conservation biology is to understand the determinants of extinction risk for species and individual populations, because this allows one to focus limited conservation resources on those species which need it most. Undoubtedly, a major driver of extinction at both the level of individual populations and species is anthropogenic activity, resulting directly or indirectly in habitat loss and degradation, species invasions, and overexploitation (Diamond, 1984; Nic Lughadha et al., 2020). Beyond these threats, there is support for additional non-random, population-level predictors of extinction risk in organisms (reviewed in Chichorro et al., 2019). For example, the probability of extinction might be higher for numerically small or geographically small populations (Wilson and MacArthur, 1967; Pimm et al., 1988; Gaston et al., 2000), declining populations (Işik, 2011), and populations of organisms with slow life histories (Purvis et al., 2000).

Of the above-mentioned predictors, species' population sizes and geographic extents are often the most readily available characteristics for organisms, especially plant species. Consequently, they are commonly employed by various conservation organizations (e.g., IUCN, 2019) in defining rarity and assessing extinction risk. However, some species are habitat specialists and are thus inherently rare based on population size and geographic extent but are not necessarily threatened by extinction (Rabinowitz, 1981). To distinguish between rare species with high extinction risks and rare species with low extinction risks, additional research exploring population dynamics of rare species is needed. Specifically, how informative of extinction risk are population size and population trends? What other population-level properties or species traits affect extinction risk? These questions are outstanding, especially among rare plants, as there are very few long-term rare plant datasets and consequently very little research investigating plants and their predictors of extinction risk (Chichorro et al., 2019).

One population-level property that could be important in assessing extinction risk is negative density dependence (Dibner et al., 2019). In this case the growth rate of a population will increase as its density decreases. This provides a mechanism for rare species to recover from low abundance. If a species exhibits strong density dependence it might be able to persist despite being rare, because when any of its populations fall below average size, their growth rates become higher than average, allowing them to recover from low density (Herrando-Pérez et al.,

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2012).

Species with slow life histories are associated with higher extinction risks due to their inability to compensate for increasing mortality with increased fecundity (Wilson and MacArthur, 1967; Purvis et al., 2000). Perennial plants, relative to annual plants, tend to have lower population growth rates and thus could face higher extinction risks (Pimm et al., 1988). However, perennial plants can buffer population declines in unfavorable environmental conditions by waiting for optimal conditions before reproducing, which could result in a lower extinction risk as compared to annual species (Stefanaki et al., 2015). Additionally, the ability to reproduce clonally allows plant species to form large individuals to buffer against environmental perturbation, and thus extinction (but see Honnay et al., 2005).

We used density dependent and density independent population viability analyses (PVAs) to estimate extinction risks and explore the population dynamics and hypothesized predictors of these risks for locally rare plant species. PVAs are a suite of frequently used projection models apt for this task (Menges, 2000). PVAs offer a suite of models varying in complexity to relatively easily explore population dynamics and compute the probability that a population will drop below an extinction threshold sometime in the future (Morris and Doak, 2002). In addition, model outputs provide clear information about a population's extinction risk, which allow for prioritizing conservation resources (Morris et al., 2002).

As models, PVAs are not always accurate (e.g. Crone et al., 2013), but in the absence of a 30+ year dataset featuring annual population surveys of multiple populations of multiple rare plant species, they can be an excellent approach. By only building models for select populations with at least ten years of survey data, in addition to incorporating density dependent and independent processes, more complicated PVAs can be relatively fruitful. Still, a large demographic dataset is required to fit these more complicated PVAs.

Demographic data are difficult to collect for any species. In addition, rare species are, owing to their nature, difficult to locate. Thus, collecting demographic data for multiple rare species requires significant manpower and a central organizing body. As a result, the collection of such data requires large programs, capable of organizing hundreds of people to repeatedly conduct annual population surveys over long time periods. Botanical gardens are one type of organization exceptionally suited to accomplish a project of this magnitude (Havens et al., 2006; Donaldson, 2009; Havens et al., 2014). The Plants of Concern (POC) program was launched in 2001 and has acquired population count data on hundreds of species across thousands of populations, providing a unique opportunity to explore rare species population dynamics (Vitt et al., 2009; Havens et al., 2012; Bernardo et al., 2018, 2020).

Here we use the comprehensive POC dataset to first assess the prevalence of density dependence and second conduct PVAs to estimate the population dynamic consequences of 73 distinct populations of 43 locally rare plant species. We then compare the PVA model estimates of rare plant extinction risks to population-level predictors of extinction risk. Specifically, we address four questions, (1) how prevalent is density dependence among rare plant species? (2) Does the inclusion of density dependence (density-dependent versus density-independent models) affect extinction risk estimates? (3) Does population size predict population extinction risk within or across rare plant species? (4) Do trends in population size over time, life cycle duration or clonality influence extinction risk?

2. Methods

2.1. Plants of Concern program

Plants of Concern is a rare plant monitoring program from the Chicago Botanic Garden driven by community scientists (Havens et al., 2012). Founded in 2001, the program comprises two decades of survey (count) data in and around Chicago, Illinois, USA. As of January 2020, the POC dataset comprises information about 247 taxa across 2323 populations. The POC dataset is relatively localized, with most populations surveyed occurring in and around Chicago. However, some populations in southern Wisconsin and western Indiana are also included. POC taxa selection is largely based on plants listed by the Illinois Endangered Species Protection Board (IESPB, 2020), though regionally rare taxa are also included. Given the diverse nature of the POC dataset, we used the designations of rarity supplied by POC and thus indirectly by the Illinois ESPB which rely largely on population sizes but also sometimes on geographic extent (IESPB, 2020). In addition, because these listings are specific to Illinois, some of our species are only locally rare. We did not endeavor to devise a uniform definition of rarity across the studied taxa.

2.2. Plants of Concern data collection and supplementation

Once a taxon was selected, it was located using element occurrence records from the Illinois Natural Heritage Database (INHD, 2020), land manager records and sightings by POC staff and volunteers. Populations are then monitored annually. In the case of large populations that have remained stable for years, surveys are conducted every couple of years. A primary goal of monitoring populations is to collect information on population size in terms of the number of individuals present. Population sizes are assessed by counting plants as number of stems, clumps, or rosettes, depending on the growth form of the taxa. In cases where populations are too large to count all individuals (usually populations >200 individuals), individuals are counted in a subset of the population, and population size is estimated based on total area occupied.

We supplemented the original POC dataset with information on habitat types extracted from the land cover classification dataset from the Illinois Gap Analysis Program (IGAP, 2000) using the *raster* package in R (Hijmans et al., 2013). One land cover class was assigned to every population in the POC dataset. Eight broad vegetation classes were used: forest, prairie, savanna, dune, wetland, agriculture, urban, or other. However, most populations occurred in either forest, prairie, or savanna habitats, and these are the only habitats we report in this study. We visually verified and corrected habitat assignments for each plant population using Google Earth. Habitat assignments remained consistent across all years of monitoring data. We also supplemented the POC data with information on life cycle duration and clonality based on a literature search in Google Scholar for all POC taxa using their scientific name (Appendix Table 1).

2.3. Listing status of species

All listing statuses presented in this paper were based on Illinois state listings as determined and published by the Illinois Endangered Species Protection Board (IESPB, 2020). In some cases, species names in the POC dataset were matched to names in the IESPB list using synonyms acquired through a Taxonomic Name Resolution Service (TNRS; Boyle et al., 2013) search.

The International Union for the Conservation of Nature (IUCN) Red List of Threatened Species is the most widely employed tool for assessing species extinction risks (Mace et al., 2008). We employ their thresholds to categorize our population viability extinction risk results into endangered (>20 % probability of extinction in 20 yrs.) and critically endangered (>50 % probability of extinction in 10 yrs.; IUCN, 2019). However, we employ these categories loosely and largely for organizational purposes, as all of our population viability analyses were projected 20 years into the future.

2.4. Count based population viability analysis

Populations were selected for population-level projection modeling if they included at least ten survey years and never dropped below 11 individuals in any year, as these thresholds serve as a minimum for

reliable modeling results (Gerber et al., 1999; Meir and Fagan, 2000; Morris and Doak, 2002). This resulted in a dataset of 43 species and a total of 73 populations. Of the 43 species we modeled, 29 had only a single population in our dataset with sufficient data for projection modeling. The remaining 14 species had multiple populations in our dataset with sufficient data for projection modeling.

For each population, we first calculated a log response ratio (LRR) to quantify the change in population size from one growing season (N_t) to the next (N_{t+1}) as in Bernardo et al. (their eq. 1; 2018):

$$LRR_{t\to t+1} = ln(N_{t+1}) - ln(N_t) \quad (1)$$

When population growth is density independent, LRR is equivalent to the intrinsic rate of increase (r), where negative values indicate a declining population and positive values an increasing population. We used these LRR values to test for density dependence by regressing LRR on log-transformed population size using linear regression. Next, using the LRR values, we fit density-independent and density-dependent models to the data using nonlinear least squares regression of *LRR* against N_t for each of our 73 populations (Morris and Doak, 2002). The two underlying models we used were (Morris and Doak, 2002):

$$Density\ independent\ model: LRR = r \quad (2)$$

$$Ricker\ model: LRR = r^*\left(1 - \left(\frac{Nt}{K}\right)\right) \quad (3)$$

where in the density-independent model, the growth rate (r) is unaffected by population size. In contrast, in the density-dependent Ricker model the log population growth rate (r) can be influenced by the population size (Nt) and carrying capacity (K). We initially included the Theta logistic model as well (Morris and Doak, 2002), but it was not possible to achieve convergence for this more complicated model given the available data. We used non-linear regression to fit the density-independent and density-dependent models as described in Morris and Doak (2002). These analyses were programmed in R using the "nls" function (R Core Team, 2022). Density independent model fitting resulted in an estimate of the growth rate (r) and residual variance (V_r). Ricker model fitting resulted in estimates of the carrying capacity (K), growth rate (r) and an estimate of the residual variance (V_r). We used the Akaike information criterion (AIC) to evaluate the density independent and Ricker model's ability to explain the growth rate (LRR) dynamics of each of our 73 populations.

The model determined to be most suitable to represent each population based on AIC was then used to project the associated population 20 years into the future. In cases where the density-independent model resulted in the best fit, we first calculated a normal distribution of growth rates for each population based on the mean and standard deviation of its growth rates (LRR). We then stochastically projected population size 20 years into the future by running 20 iterations of the following equation and randomly drawing an LRR value for each iteration as in Bernardo et al. (their eq. 2; 2018):

$$N_{t+1} = N_t^* exp(LRR) \quad (4)$$

Each simulation was started with a population size (N_t) equivalent to the most-recent recorded population size in our data set and was replicated 50,000 times. We set a quasi-extinction threshold of ten individuals following Bernardo et al. (their eq. 1; 2018). This number represents the critical population size below which a population is in serious peril and difficult-to-evaluate population processes take effect (Ginzburg et al., 1982; Morris and Doak, 2002). The extinction probability was calculated as the number of replicate projections that dropped below ten individuals at any point during or at the end of the 20 iterations, divided by 50,000 replicates.

In cases where the Ricker model was determined to be the most suitable model for a population, we used the following equation from Morris and Doak (their eq. 4.2; 2002) with the theta parameter set to 1, and thus removed, as required for the Ricker model:

$$N_{t+1} = N_t^* exp\left(r\left[1 - \frac{N_t}{K}\right] + \epsilon_t\right) \quad (5)$$

Here, N_t was equivalent to the most-recent recorded population size in our data set and the r and K represented the parameter estimates of the growth rate and carrying capacity, respectively, from the Ricker model-fitting step (Eq. (3)). The environmental variation (ϵ_t) introduced into the population growth process was based on the residual variance (V_r) estimated during the model-fitting step. However, the residual variance alone gives a biased estimate of environmental variance (Dennis et al., 1991). To calculate an unbiased estimate of the environmental variance (σ^2) we used the following equation following Morris and Doak (their eq. 4.10; 2002):

$$\sigma^2 = \frac{qV_r}{q-1} \quad (6)$$

In this equation, V_r was the residual variance as estimated from the Ricker model fitting regression (Eq. (3)) and q was the number of data points available for the population (Dennis, 1989; Dennis et al., 1991; Dennis and Taper, 1994; Morris and Doak, 2002). We then stochastically projected population size 20 years into the future by running 20 iterations of equation five, generating a random value for the environmental variation (ϵ_t) during each iteration from a normal distribution with a mean of zero and a variance of σ^2. Identical to the density independent model, each simulation was replicated 50,000 times with a quasi-extinction threshold of ten individuals. We only projected our populations 20 years into the future because of the limited census data available for our populations (10–20 yrs.; Fieberg and Ellner, 2000).

It is important to note that our analyses report extinction probabilities for populations and thus extirpation or local extinction risks for species. We initially tried to model the extinction risk of species by incorporating all their populations into multi-site PVAs. However, we were unable to do this for two reasons. First, most of our species only had enough demographic data for one or a few populations. Second, multi-site PVAs require assessing the extent of correlation in vital rates between populations across space to understand how coupled they are. This in turn requires that each rare species population was surveyed in the same year for several years at least and ideally upwards of ten years (Morris and Doak, 2002). Yet, POC populations are not always surveyed annually or synchronously within species. Thus, while we had sufficient data for population modeling, we did not have sufficient overlapping or synchronous data for species-wide modeling (within our sampling area).

2.5. Statistical analyses

Next, we explored how extinction risk, the dependent variable, was predicted by the independent variables of geometric average population size, the count value at which each modeling iteration started, trends in log population size over time, significant trends in log population size over time, plant life cycle duration, clonality, and the listing status of the species. The trends in log population size over time were calculated as the slope of the linear regression of the log-transformed population count versus time for each of our 73 populations. The 'significant trends in log population size over time' represent a subset of the trend in log population size over time based on a linear model p-value < 0.05.

We evaluated associations between our response variable, extinction probability, and predictor variables, with binomial mixed-effects models. Specifically, we used the binomial distribution to model the probability of extinction based on the 50,000 replicate projections as a function of a given predictor variable using the *glmer* function from the *lme4* package in R (Bates et al., 2014). In each model, we used extinction probabilities of populations across all species as a response variable and set species as a random intercept term to control for the non-independence of populations of each species (Harrison et al., 2018). Each model was summarized by the fixed effects estimates and their 95

% confidence intervals, and a marginal and conditional pseudo R^2 after Nakagawa and Schielzeth (2013) to represent the explanatory power of each predictor variable and the model as whole, respectively. These summary statistics are reported for each model except for the mixed-effects model examining whether extinction probabilities were significantly higher among federally or state listed species as compared to unlisted species. For this ANOVA mixed-effects model we only report the chi-squared (χ^2), degrees of freedom (df) and *p*-value (P) from a Type II Wald χ^2 test for models without interactions.

Within each of the four species that had at least 4 populations modeled, *Agalinis auriculata*, *Cypripedium candidum*, *Eurybia furcata*, and *Viola conspersa*, we regressed the population extinction probabilities against the trend in log population size over time, the geometric average population size, the count value at which each modeling iteration started, and the minimum geographic distance to other populations of the same species. These regressions were performed separately for each species. Because the random effect of species no longer applied, we used generalized linear models and the binomial distribution for these analyses, executed with the *glm* function from the *stats* package in R (R Core Team, 2022). Each model was summarized by the estimates of the slope and intercept and their 95 % confidence intervals. We also calculated McFadden's pseudo R^2 (McFadden, 1973).

For these analyses, geographic distances were calculated between the centers of populations using the *pointDistance* function from the *raster* package in R (Hijmans et al., 2013) on a World Geodetic System (1984) reference ellipsoid.

Finally, we evaluated the difference between extinction risks resulting from the density independent and density dependent models using a binomial mixed-effects *t*-test model. Specifically, we used the binomial distribution to model the probability of extinction based on the 50,000 replicate projections as a function of model type using the *glmer* function from the *lme4* package in R (Bates et al., 2014). We used species as a random factor. For this test we employed all 73 extinction risks produced by the density independent model and all 66 extinction risks (7 failed to converge) produced by the density dependent model.

Table 1
PVA modeling results for species which had only sufficient data for one POC population to be modeled. Results for both the density dependent (DD) and density independent (DI) models are reported. Boxes highlighted in grey denote the AIC selected, best-fit model between the DD and DI models. The full version of this table includes the PVA model AIC scores, habitat, and listing status for each row and can be found in the appendix as Table A2.

Species	Successive transitions	Most recent pop. size	Geometric average pop. size	Trend in log(N)	DD P. of ext. over 20 yrs.	DI P of ext. over 20 yrs.	Density dependence		Distance to closest congener pop (km)
							sign	R^2	
Artemisia serrata	11	3098	1491	-0.01	0.04	0.28	neg*	0.92	
Asclepias exaltata	10	32	34	0.06	0.06	0.47	neg*	0.45	3.4
Beckmannia syzigachne	9	12	52	-0.21	0.72	0.49	neg	0.25	3.4
Botrychium campestre	10	189	255	0.01	0.20	0.38	neg*	0.61	-
Carex aurea	11	425	148	0.09	< 0.01	0.40	neg	0.14	4.4
Carex tuckermanii	9	13860	42	0.39	0.13	0.48	neg*	0.45	16.6
Carex woodii	10	55	55	0.12	0.13	0.41	neg*	0.45	3.6
Collinsia verna	11	21872	1393	0.15	0.27	0.34	neg	0.12	-
Cypripedium parviflorum var. makasin	11	247	391	-0.08	< 0.01	0.35	neg	0.19	14.5
Dalea foliosa	9	3444	1841	0.15	< 0.01	0.27	neg	0.33	16.7
Filipendula rubra	9	26	23	0.06	NA	0.40	neg	0.05	44.7
Gratiola quartermaniae	12	156	1015	-0.07	0.93	0.51	neg*	0.37	2.0
Hybanthus concolor	11	20340	28674	-0.06	< 0.01	0.32	neg*	0.90	42.8
Hydrastis canadensis	9	3794	3750	0.09	0.01	0.27	neg	0.29	15.3
Isoetes butleri	15	48	147	-0.13	0.10	0.51	neg	0.19	2.5
Lathyrus ochroleucus	9	594	259	0.19	< 0.01	0.24	neg*	0.67	6.0
Malvastrum hispidum	12	4697	7918	0.16	0.11	0.44	neg	0.31	-
Menyanthes trifoliata	9	1126	756	0.02	< 0.01	0.40	neg	0.22	13.5
Mononeuria patula	15	3867	5925	0.08	0.23	0.42	neg*	0.31	21.2
Platanthera flava var. herbiola	14	387	136	0.07	< 0.01	0.24	neg	0.05	2.5
Ranunculus rhomboideus	14	24	32	-0.07	0.04	0.48	neg*	0.32	4.9
Scirpus hattorianus	12	17	19	0.06	NA	0.50	neg	0.26	5.7
Silene regia	16	111	82	0.08	0.58	0.45	neg*	0.55	51.2
Spiranthes lucida	18	29	25	-0.06	0.32	0.48	neg*	0.28	5.3
Synthyris bullii	12	42	86	-0.03	0.07	0.52	neg*	0.46	52.4
Tetraneuris herbacea	10	44	31	0.07	0.02	0.41	neg*	0.51	11.2
Trientalis borealis	9	261	221	0.21	0.01	0.27	neg	0.14	6.0
Triglochin maritima	10	120	48	0.10	0.01	0.34	neg	0.32	10.6
Valeriana uliginosa	13	471	223	0.00	0.07	0.49	neg*	0.60	8.6

Successive transitions: Number of successive annual population surveys for which LRR was calculated.
Most recent pop. size: Last known population size
Geometric average pop. size: geometric average of population sizes through time
Trend in log(N): slope of the logarithmic population size trend through time.
DD/DI P. of ext. over 20 yrs.: the probability of extinction over the next 20 years based on the density dependent (DD, Ricker) and density independent (DI) model (grey highlighting indicates the best model).
Density dependence sign: sign of slope of relationship between growth rate and population size (N) (asterisks indicate statistically significant ($p < 0.05$) relationships).
Density dependence R^2: the proportion of variation in growth rate explained by population size (N).
Distance to closest congener pop (km): the geographic distance in meters to the closest POC population of the same species.

3. Results

3.1. Negative density dependence in modeled populations

We simulated population trajectories and calculated extinction probabilities for 73 populations of 43 species. Of the 43 species we modeled, 29 had only a single population in our dataset with sufficient data for projection modeling, and the remaining 14 species had multiple populations. All 73 populations exhibited negative density dependence, although not always significantly so. This negative density-dependent trend was significant for 50 % (37) of our populations. Among the populations with significant density dependence, log-transformed population sizes explained, on average, 51 % of the variance in growth rates (R^2 min = 0.27, R^2 max = 0.92; Tables 1 and 2). Consequently, 75 % (55) of our populations were best represented by the Ricker, density-dependent model (Tables 1 and 2), which resulted in significantly lower predictions of extinction probabilities than the density-independent models (mixed-effects *t*-test: $\chi^2 = 98{,}796$, df = 1, $p < 0.001$).

3.2. Predictors of extinction risk

Our models suggest relatively low extinction risks for most of our populations, and these extinction risks were not predicted by listing status (Fig. 1). Among the 73 populations we modeled, less than half (33) had a >20 % chance of extinction in the next 20 years (Endangered threshold; IUCN, 2019). Of these 33 populations, only ten had a >50 % chance of extinction (Critically endangered threshold; IUCN, 2019). Of the 43 species whose populations we modeled, 40 % (29 species) were listed as threatened or endangered. However, we did not find any significant difference among the extinction probabilities of the 73 populations and their species' listing status (mixed-effects ANOVA: $\chi^2 = 1.36$, df = 2, $p = 0.51$; Fig. 2).

The log population size (N) trends over time of our 73 populations

Table 2
PVA modeling results for species which had sufficient data for multiple POC populations to be modeled. Each line of data represents a different population. Results for both the density dependent (DD) and density independent (DI) models are reported. Boxes highlighted in grey denote the AIC selected, best-fit model between the DD and DI models. For complete header descriptions, see the bottom of Table 1. The full version of this table includes the PVA model AIC scores, habitat, and listing status for each row and can be found in the supplemental information found in the appendix as Table A3.

Species	Successive transitions	Most recent pop. size	Geometric average pop. size	Trend in log(N)	DD P. of ext. over 20 yrs.	DI P of ext. over 20 yrs.	Density dependence		Distance to closest congener pop (km)
							sign	R^2	
Agalinis auriculata	11	81	142	0.29	0.02	0.29	neg	0.12	1.1
Agalinis auriculata	15	94	86	0.09	0.22	0.39	neg*	0.29	11.6
Agalinis auriculata	15	208	1906	0.10	0.44	0.53	neg	0.09	6.0
Agalinis auriculata	17	54	312	-0.03	0.46	0.47	neg	0.22	6.0
Agalinis auriculata	14	85	105	0.07	0.82	0.48	neg*	0.43	0.7
Asclepias lanuginosa	10	94	71	0.09	< 0.01	0.39	neg	0.37	13.4
Asclepias lanuginosa	12	66	100	-0.05	< 0.01	0.50	neg	0.28	5.0
Carex crawei	9	15420	3891	0.02	0.41	0.43	neg*	0.45	4.8
Carex crawei	12	734	564	0.17	NA	0.51	neg	0.14	21.7
Cirsium hillii	9	27	29	-0.01	< 0.01	0.57	neg	0.31	16.6
Cirsium hillii	12	22	23	-0.01	< 0.01	0.34	neg	0.28	15.2
Cypripedium candidum	18	202	148	0.00	< 0.01	0.37	neg*	0.66	8.3
Cypripedium candidum	11	931	546	0.07	< 0.01	0.32	neg*	0.60	11.6
Cypripedium candidum	11	110	226	0.08	0.61	0.39	neg*	0.53	6.4
Cypripedium candidum	20	55	60	0.00	< 0.01	0.15	neg*	0.51	14.0
Cypripedium candidum	13	326	194	0.12	< 0.01	0.31	neg	0.30	8.2
Cypripedium candidum	14	812	450	0.12	0.07	0.40	neg*	0.34	38.1
Cypripedium candidum	16	90	28	0.16	< 0.01	0.17	neg	0.01	16.3
Cypripedium candidum	13	211	309	-0.03	0.20	0.48	neg*	0.62	6.8
Cypripedium candidum	9	42	20	0.16	NA	0.31	neg	0.19	1.4
Cypripedium candidum	9	20	76	-0.06	0.60	0.51	neg	0.37	5.0
Eurybia furcata	11	481	143	0.04	0.05	0.35	neg	0.35	7.7
Eurybia furcata	16	1061	246	0.06	0.05	0.36	neg*	0.27	1.6
Eurybia furcata	14	843	93	0.16	NA	0.27	neg	0.00	1.6
Eurybia furcata	16	54578	910	0.23	0.04	0.32	neg	0.01	3.5
Liatris scariosa var. nieuwlandii	11	245	136	0.19	0.01	0.33	neg	0.21	40.8
Liatris scariosa var. nieuwlandii	11	25	36	-0.14	0.34	0.53	neg*	0.41	16.2
Oenothera perennis	13	320	411	0.07	< 0.01	0.35	neg*	0.34	0.9
Oenothera perennis	12	83	150	-0.04	< 0.01	0.45	neg	0.21	22.2
Oenothera perennis	17	48	92	0.02	0.67	0.44	neg*	0.66	1.4
Rubus odoratus	9	317	209	0.09	< 0.01	0.30	neg	0.30	12.7
Rubus odoratus	13	89	25	0.02	NA	0.24	neg	0.08	12.7
Rubus pubescens	10	3127	711	0.08	0.01	0.37	neg*	0.51	0.6
Rubus pubescens	11	9773	9504	-0.03	0.50	0.36	neg*	0.63	6.6
Triantha glutinosa	12	497	344	-0.01	0.02	0.38	neg*	0.55	3.8
Triantha glutinosa	14	40	48	-0.03	NA	0.50	neg	0.27	20.3
Triglochin palustris	9	430	607	0.01	< 0.01	0.41	neg*	0.49	8.2
Triglochin palustris	16	31	54	0.04	0.60	0.49	neg*	0.48	6.7
Veronica scutellata	11	62	595	-0.48	0.75	0.57	neg	0.19	0.7
Veronica scutellata	9	570	880	0.04	0.02	0.38	neg*	0.58	19.7
Viola conspersa	9	599	702	-0.02	< 0.01	0.42	neg*	0.64	1.0
Viola conspersa	13	200	338	-0.07	0.05	0.45	neg*	0.55	21.7
Viola conspersa	11	81	422	0.14	0.07	0.41	neg	0.33	3.8
Viola conspersa	15	76	476	-0.04	0.28	0.45	neg*	0.47	2.9

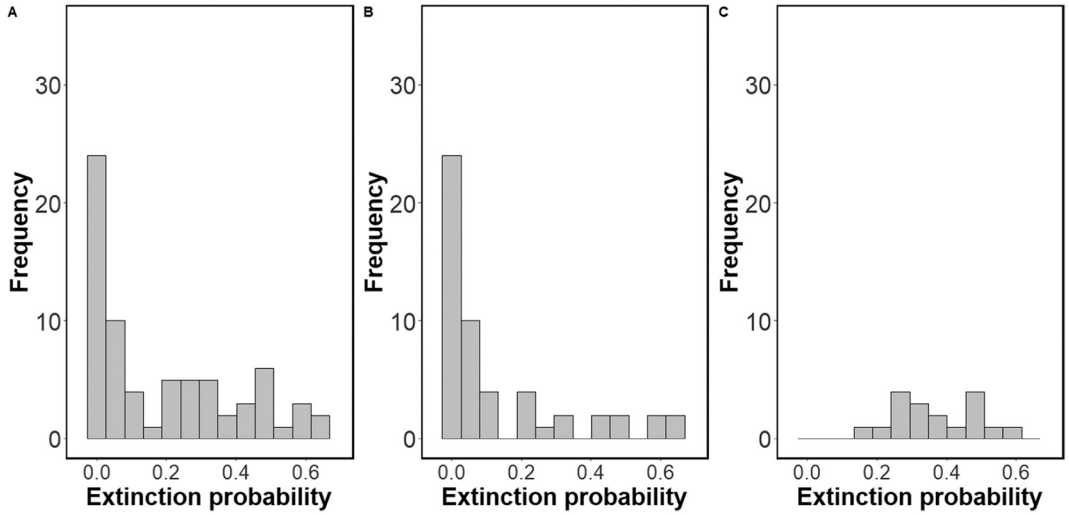

Fig. 1. Frequency distribution of extinction probabilities for A) all 73 populations modeled with PVAs, B) the 55 populations for which the Ricker model was the best model, and C) the 18 populations for which the density independent model was the best model.

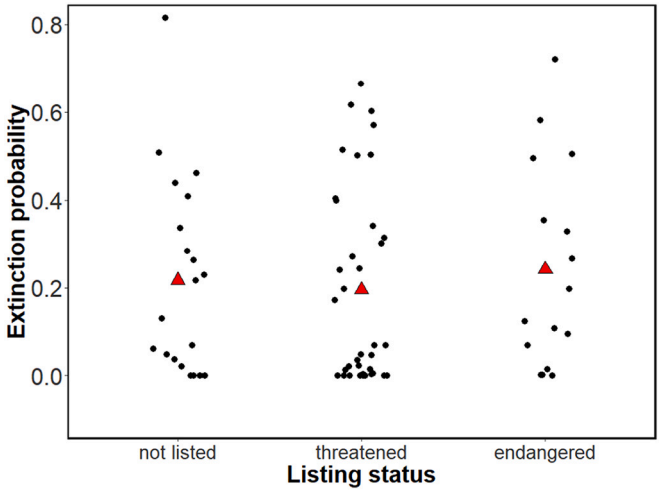

Fig. 2. Distribution of extinction probabilities across all three listing categories with means shown by red triangles. Each black point represents one of our 73 modeled populations from tables one and two. Endangered, threatened, and unlisted species had, on average, similar extinction probabilities and this was confirmed by a binomial mixed-effects model with extinction probability as the response variable and listing status as the predictor variable ($\chi^2 = 1.36$, df = 2, $p = 0.51$). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

had negligible effect sizes with respect to their predictive power of extinction risk both across and within species, regardless of whether all trends or only significant trends were used as a predictor. Of our 73 modeled populations, 24 showed a negative slope in their log population size (N) over time, or decreasing tendency, but only five of these 24 were significant trends (Fig. 3). Most of the 73 modeled populations (49) exhibited an increasing trend in log population size (N) over time, and this trend was significant in 24 of these 49 populations (Fig. 3). The slopes of log population size trends over time exhibited a negative relationship to the estimated probability of extinction over 20 years, but the fixed effects contributed very little explanatory power ($R^2_m = 0.03$, $R^2_c = 0.73$). When examining this relationship within species for the four species that had sufficient data (species with at least 4 modeled populations), we found a similar negative relationship among three of them (R^2 ranged from 0.02 to 0.43) and the opposite pattern amidst the fourth (*E. furcata* $R^2 = 0.89$, Table 4). When only considering the slopes of the significant log population trends over time and for all populations of all species, decreasing slopes (declining populations) predicted higher estimated extinction probabilities but with negligible effect sizes ($R^2_m < 0.01$, $R^2_c = 0.69$; Table 3).

The geometric average and most recent population size of modeled populations ranged from 19 to 28,674 and 12 to 54,578 individuals, respectively, and only most recent population size offered some predictive power of extinction risk. We detected a negative relationship between the probability of extinction of a population and its geometric average log population size, but the fixed effect size was very low ($R^2_m = 0.02$, $R^2_c = 0.73$; Table 3). Increasing most-recent recorded population size resulted in a decrease in extinction risk ($R^2m = 0.09$, $R^2_c = 0.76$, Table 3). Within species, the results were equally mixed (Table 4).

With respect to life cycle duration (Table A1), we found that perennial species tend to exhibit higher extinction risks than annual species, albeit with low explanatory power attributed to the fixed effects ($R^2_m = 0.05$, $R^2_c = 0.72$, Table 3). Species that are capable of clonal growth (Table A1) were predicted to have lower extinction probabilities than species not capable of clonal growth, but again, the fixed effects of this model explained very little of this pattern ($R^2_m = 0.01$, $R^2_c = 0.72$, Table 3).

We only analyzed geographic distance between populations of the same species as a predictor of extinction risk within species. We found that increased distances between POC populations predicted lower extinction risks for all four species (R^2 ranged from 0.06 to 0.21, Table 4).

4. Discussion

In this study we evaluated the population dynamics of and estimated the extinction risks for 73 populations of 43 locally rare plant species growing in prairie, savanna, and forest habitats from the uniquely extensive Chicago Botanic Garden's POC rare plant dataset. We found two major results. First, a negative density dependent trend was detected in every population. This trend was significant for half of our populations, for which average population size explained half of the variation in growth rate. Consequently, PVA models incorporating density dependence were largely favored by AIC, and significantly reduced extinction probabilities as compared to the density-independent models. Second, our predictors of trends in log-transformed population size (N) over time, most recent and geometric average population size, life cycle duration, clonality, and distance to closest population of the same species were not very effective in predicting estimated extinction

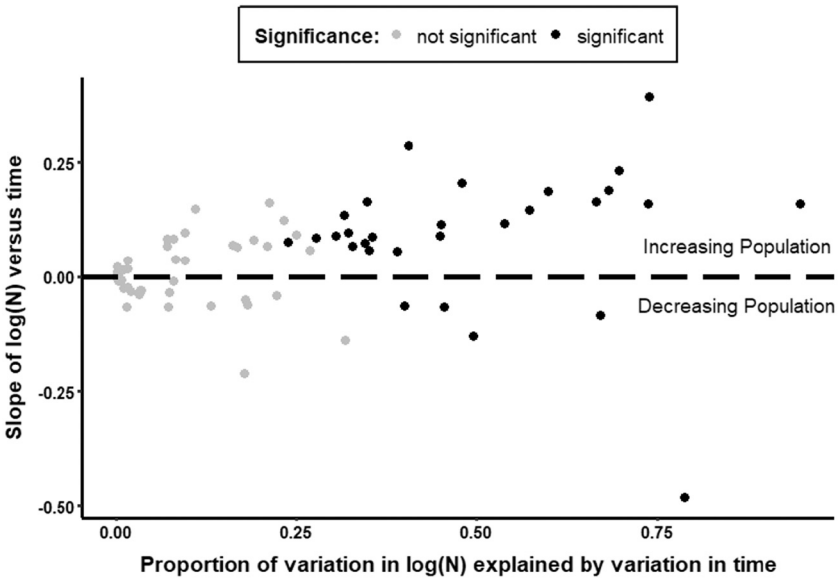

Fig. 3. Slope versus r-squared of the trend in log population size over time for all 73 modeled populations. Each point represents one population. Dashed line shows cutoff between populations that showed increasing (above dashed line) and decreasing (below dashed line) trends. Significant trends ($p < 0.05$) in log population change over time are designated by solid black points and insignificant ones by solid grey points. Overall, most of our populations showed increasing trends over time.

Table 3
Statistical summary table for the binomial mixed-effects models used to evaluate associations between our response variable (extinction probability) and predictor variables. For each model we included the extinction probability of the number of populations displayed in the *Populations included* column as a response variable and set species as a random effect. The table presents the fixed effects estimates of the intercept and the slope and their 95 % confidence intervals, and a marginal (R^2m) and conditional (R^2c) pseudo R^2 after Nakagawa and Schielzeth (2013) to represent the explanatory power of each predictor variable and the whole model, respectively.

Predictor variable	Populations included	Intercept			Slope			R^2m	R^2c
		Estimate	Upper CI	Lower CI	Estimate	Upper CI	Lower CI		
All trends in log population size (N) over time	73	−2.28	−1.45	−3.14	−4.89	−4.83	−4.95	0.03	0.73
Significant trends in log population size (N) over time	29	−2.78	−1.33	−3.66	−0.39	−0.11	−0.73	0.00	0.69
Geometric average population size	73	−0.84	0.07	−1.80	−0.30	−0.29	−0.31	0.02	0.73
Most recent population size	73	0.62	1.49	−0.31	−0.55	−0.55	−0.56	0.09	0.76
Duration	73	−0.45	2.14	−2.57	−2.27	−0.01	−4.88	0.05	0.72
Clonality	73	−2.22	−1.14	−3.39	−0.52	1.09	−2.45	0.01	0.72

Table 4
Statistical summary table for the binomial generalized linear models used to evaluate associations between our response variable (extinction probability) and four predictor variables within species. For each model we included extinction probabilities of the number of populations displayed in the *Populations included* column. The table presents estimates of the intercept and the slope and their 95 % confidence intervals and an R^2 value to represent the explanatory power of each predictor variable.

Species	Predictor variable	Populations included	Intercept			Slope			R^2
			Estimate	Upper CI	Lower CI	Estimate	Upper CI	Lower CI	
Eurybia furcata	Trends in population size (N) over time	4	−3.27	−3.24	−3.30	11.57	11.74	11.40	0.89
Viola conspersa		4	−2.20	−2.18	−2.21	−2.71	−2.51	−2.92	0.03
Agalinis auriculata		5	0.38	0.39	0.37	−9.26	−9.15	−9.37	0.43
Cypripedium candidum		10	−1.35	−1.34	−1.36	−2.02	−1.93	−2.11	0.01
Eurybia furcata	Geometric average population size	4	−3.58	−3.50	−3.65	0.36	0.37	0.35	0.12
Viola conspersa		4	2.09	2.44	1.74	−0.70	−0.64	−0.76	0.02
Agalinis auriculata		5	−0.94	−0.90	−0.98	0.09	0.10	0.08	0.01
Cypripedium candidum		10	−0.17	−0.14	−0.20	−0.27	−0.27	−0.28	0.04
Eurybia furcata	Most recent population size	4	−3.87	−3.82	−3.92	0.29	0.29	0.28	0.40
Viola conspersa		4	6.89	7.08	6.71	−1.92	−1.88	−1.97	0.71
Agalinis auriculata		5	−0.66	−0.58	−0.75	0.05	0.07	0.03	0.00
Cypripedium candidum		10	2.27	2.30	2.24	−0.80	−0.79	−0.81	0.34
Eurybia furcata	Distance to closest POC population of same species	4	1.22	1.37	1.07	−0.35	−0.34	−0.37	0.06
Viola conspersa		4	−2.00	−1.88	−2.11	−0.02	−0.01	−0.04	0.00
Agalinis auriculata		5	1.77	1.83	1.71	−0.28	−0.27	−0.28	0.06
Cypripedium candidum		10	5.86	5.94	5.78	−0.82	−0.81	−0.83	0.21

risks of populations within or across species. Collectively, our results highlight the potentially important role of negative density dependence for rare species persistence and suggest that more simplistic quantitative or qualitative predictors of extinction risk such as population size and trend may be misleading.

4.1. Negative density dependence in modeled populations

Throughout our modeling efforts the density-dependent model resulted in significantly lower extinction probabilities than the density-independent model, as expected based on the prevalence of negative density dependence in our dataset (McElderry et al., 2015). The observed negative density-dependent tendencies among all species and significant density dependence observed for 50 % of them could explain the discrepancy between theoretical extinction concerns for plant species at low abundance and the contrasting observation that many rare plant species remain extant (Dibner et al., 2019). In theory, smaller populations should have higher extinction risks than larger populations (Wilson and MacArthur, 1967), and empirical evidence agrees with this theoretical statement (e.g. Matthies et al., 2004). However, a species with smaller populations but strong negative density dependence should be able to avoid extinction more effectively than another species with bigger populations but no density dependence. In fact, the density dependence in this case would also be responsible for the low population size of the first species. One hypothesis is that rare species exhibit stronger negative frequency dependence than abundant species (e.g., Comita et al., 2010; Mangan et al., 2010; Yenni et al., 2017; Rovere and Fox, 2019). Strong negative density dependence may allow a rare species to recover from low density but may also prevent a species from becoming abundant or escaping rarity. Testing this hypothesis in our system would require population abundance data for entire communities, but our results are consistent with the idea that rare species are able to maintain populations at least in part due to negative density dependence.

On the other hand, our observed density dependence may not be indicative of classical density dependence. Crone et al. (2013) suggest that changing habitat conditions could be the cause of observed density dependence. For example, invasive species encroachment could reduce habitat availability and result in apparent density dependence for native species. However, the strong presence of density dependence among all of our populations across many different sites and habitat types suggests that this is unlikely to be the case for every species.

4.2. Predictors of estimated extinction risk

On average our populations showed weak trends in log population change over time, and the predictive power of population trends for extinction risk estimates was negligible. In contrast, at least one other study shows a strong association between declining trends and extinction risk in rare species (Nantel et al., 2018). This negative relationship between population trends and extinction risk is likely temporally dependent, with declines over longer time periods being more predictive of extinction risk. In fact, the study by Nantel et al. (2018) included populations with an average census length of 15 years and a range of 4–35 years as compared to the average of 12 years and range of 9–20 years in this study. In addition, all 36 populations studied by Nantel et al. (2018) were of the same species. We did not detect meaningful trends in our within-species analyses, but this may be attributable to a lack of data; our most abundant species, *C. candidum*, only had 10 modeled populations. However, for three of the four species for which we examined the predictive power of population trends for extinction risk, the trends were negative as in Nantel et al. (2018). Overall, then, declining trends alone, over relatively short time periods (<10 years) may not be representative of population extinction risk (Dibner et al., 2019). In addition, species-specific responses likely play a role. For example, species may not produce aboveground structures during unfavorable conditions, and consequently apparent count-based population trends may not be trends at all, but instead reflect environmental variation instead of population bottlenecks (Bell et al., 2021). Moreover, it is still challenging to incorporate the demographic effect of seed banks, which can decrease extinction risks in PVAs (Doak et al., 2002).

Larger populations had lower estimated extinction risks than theoretically predicted and observed in other studies of rare plants (e.g., Nantel et al., 2018). However, the explanatory power of both most recent (simulation-starting) population size and geometric average population size was surprisingly weak. Using a dataset of 359 populations of eight rare plant species, Matthies et al. (2004) found that the relationship between population size and extinction probability varied widely across species, though for most species, larger populations showed lower extinction risks. While the former is likely to be the case in our dataset, POC does not yet encompass enough data to thoroughly examine relationships between population sizes and extinction risk across species. This lack of data may explain the unexpected positive relationship between population size and extinction risk as observed in our within-species analyses for two species. In contrast, *Cypripedium candidum,* with at least twice as many populations as either of our other three species, showed the predicted negative relationship with higher most recent population sizes and higher geometric average population sizes both strongly predicting lower extinction risks. Among *C. candidum* populations, the predictive power of most recent population size for estimated extinction risk was much stronger than that of geometric average population size. This was expected because the most recent population sizes were directly included in the population projection modeling.

Contrary to our findings, we expected listed species to show higher projected extinction risks than unlisted species based on the assumption that listing efforts were representative of extinction risk (IESPB, 2020). In part this result is likely attributable to the nature of the POC dataset that focuses on rare and threatened species, many of which may be deserving of listing but were not yet listed. This result may also reflect the positive influence of targeted management and recovery efforts of listed species (Hoekstra et al., 2002) as well as the political nature of species listings (e.g., Ando, 1999; Harllee et al., 2009).

Life history traits such as life-cycle duration and traits related to it can play an important role in extinction risk assessment, but neither life-cycle duration nor clonality predicted an appreciable amount of variation in our estimated extinction risks. The effect of life-history traits on extinction risk are often a minefield to dissect because many of them are context dependent (Blackburn and Gaston, 2003). Extinction risk and maximum growth rate (LRR) are inversely related (Blackburn and Gaston, 2003). Since short-lived organisms tend to have higher growth rates, they should in theory have lower extinction risks. However, Hernández-Yáñez et al. (2022) found species with early maturation and high juvenile survival to be more vulnerable to extinction. In addition, species with longer generation times (e.g. perennial and clonal species) are able to buffer extinction risk through time and can persist for long periods with negative growth rates (Eriksson, 1994; de Witte and Stöcklin, 2010). Dissecting these patterns likely requires more fine-scale data than is available for our POC species. For example, it could be important to have more accurate estimates of each species life-cycle duration or even generation time in place of very broad categories such as annual and perennial (Staerk et al., 2019).

For the four species we examined, we found negative relationships between estimated extinction probabilities and the distance to the nearest conspecific population, suggesting spatial coupling of extinction risks. From a conservation perspective, spatially coupled extinction risk decreases the effective number of distinct populations. This in turn reduces the buffering capacity of the species because the extinction of any one population may be closely mirrored in other populations (Morris and Doak, 2002). Thus, a lack of a pattern in the relationship between distance between populations of the same species and the extinction risks of those populations should lower the species-wide extinction risk.

However, because we only examined the relationship between the nearest neighbor extinction risk and distance, as opposed to all neighbors (correlation matrix), our results must be interpreted cautiously. In the future, correlation matrix analyses and the inclusion of geographic factors such as urbanization will be important to definitively determine the extent of spatial coupling in extinction risks. Also, it is difficult to determine how complete the POC dataset is. In particular, the proportion of the total populations of a particular species surveyed by POC is unknown.

4.3. Conclusion

Our study shows that given sufficient data it is possible to detect significant and strong negative density dependence in rare plants, which in turn may explain the empirically observed persistence of rare plants. When using density-dependent models, predictions of rare plant species population persistence may align more closely with empirical observations (Dibner et al., 2019; Enquist et al., 2019). In fact, for all the AIC selected population-level extinction probabilities calculated by the density independent model, the average was 40 % compared to the density-dependent model's average of 17 %. However, these are all estimates, and while the value of PVA models is well established (e.g. Brook et al., 2000; Morris and Doak, 2002), concerns exist about their accuracy (Crone et al., 2013). For this reason, we used relatively rigorous data standards, avoided simpler models based on diffusion approximation and only projected populations 20 years into the future. For example, we chose not to model POC species lacking continuous data collection using diffusion approximation, as this is known to result in unreliable extinction estimates (Kendall, 2009). In addition, our goal was not to set precise forecasts for individual species or populations but to gain a broad picture of rare plant population dynamics and predictors of extinction risk. Therefore, our results should be relatively robust even if projections for individual populations are not very precise. As the POC program continues to grow and more data become available, including extinction data, we expect to be able to evaluate the performance of our PVA models by determining how accurate extinction risk predictions were. This will help us gain a more robust understanding grounded in empirical evidence and directly address concerns about the accuracy of PVA predictions. With increased POC data collection we also expect to detect more significant negative density-dependent trends across populations, resulting in increased preference for the density-dependent model over the density-independent model (Ginzburg et al., 1990; Brook and Bradshaw, 2006). Nevertheless, our analysis of a unique multispecies rare plant dataset emphasizes the importance of negative density dependence for the persistence of rare plant species.

Open research statement

Data are not publicly available due to the threat of poaching rare species using location data. Data can be requested after signing a data confidentiality form by contacting Amy Iler at ailer@chicagobotanic.org.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109729.

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