# Synergistic effects of climate change and harvest on extinction risk of American ginseng

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*Abstract.* Over the next century, the conservation of biodiversity will depend not only on our ability to understand the effect of climate change, but also on our capacity to predict how other factors interact with climate change to influence species viability. We used American ginseng (*Panax quinquefolius* L.), the United States' premier wild-harvested medicinal, as a model system to ask whether the effect of harvest on extinction risk depends on changing climatic conditions. We performed stochastic projections of viability response to an increase in maximum growing-season temperature of 1°C over the next 70 years by sampling matrices from long-term demographic studies of 12 populations (representing 75 population-years of data). In simulations that included harvest and climate change, extinction risk at the median population size ($N = 140$) was 65%, far exceeding the additive effects of the two factors (extinction risk = 8% and 6% for harvest and climate change, respectively; quasi-extinction threshold = 20). We performed a life table response experiment (LTRE) to determine underlying causes of the effect of warming and harvest on deterministic λ ($\lambda_d$). Together, these factors decreased $\lambda_d$ values primarily by reducing growth of juvenile and small adult plants to the large-adult stage, as well as decreasing stasis of the juveniles and large adults. The interaction observed in stochastic model results followed from a nonlinear increase in extinction risk as the combined impact of harvest and warming consistently reduced λ values below the demographic tipping point of $\lambda = 1$. While further research is needed to create specific recommendations, these findings indicate that ginseng harvest regulations should be revised to account for changing climate. Given the possibility of nonlinear response like that reported here, pre-emptive adaptation of management strategies may increase efficacy of biodiversity conservation by allowing behavior modification prior to precipitous population decline.

Key words: *climate change; ginseng; harvest; local adaptation;* Panax quinquefolius *L.; stochastic demographic modeling.*

## Introduction

Past and ongoing fossil fuel consumption will result in significant climatic warming even if carbon emissions cease immediately (Solomon et al. 2009, 2010). As a result of elevating levels of atmospheric greenhouse gases, mean global temperature has increased ~0.7°C since the beginning of the 20th century (IPCC 2007). Already, this seemingly small degree of warming has altered species' interactions, distributions, and phenology, and has been linked to decline and extinction at both the population and species level (Hughes 2000, Walther et al. 2002, Parmesan and Yohe 2003, Root et al. 2003, Parmesan 2006, Pounds et al. 2006). Climate change is not occurring in isolation, but against a backdrop of many forms of anthropogenic change and environmental stress. In many cases, climate change

alone is not the proximate driver of decline or extinction (Brook et al. 2008). For instance, the extinction of the Monteverde harlequin frog and the golden toad was caused, not by temperature surpassing physiological tolerances, but rather by the interaction of climate change and the pathogenic Chytrid fungus (Pounds et al. 2006). Understanding synergies among multiple stressors on extinction risk and appropriately modifying human behavior in order to diminish the likelihood of climate change-driven extinction will be critical for biological conservation over the next century (Hannah et al. 2002*a, b*, Travis 2003, Brook et al. 2008, Heller and Zavaleta 2009, Lawler 2009, Dawson 2011, Cahill et al. 2013).

Stochastic demographic models are used routinely to evaluate the effect of anthropogenic change or the consequences of protection strategies on population viability (McLaughlin et al. 2002, Morris and Doak 2002, Maschinski et al. 2006, Jenouvrier et al. 2009, Hunter et al. 2010, Bellard et al. 2012). While model construction differs, stochastic demographic models all incorporate the effect of variation in vital rates on

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extinction risk or population growth, typically through the use of iterative, Monte Carlo simulations (Atkins and Travis 2010, Bellard et al. 2012). In the context of climate change, these models have shown that climate change can negatively affect long-term persistence of narrow-range endemics such as cliff rose (Maschinski et al. 2006) or checkerspot butterfly (McLaughlin et al. 2002), and Arctic or Antarctic species, such as the polar bear (Hunter et al. 2010), or Emperor Penguins (Jenouvrier et al. 2009). While ideal for examining the interplay of climate change with other factors on extinction risk, stochastic demographic models have rarely been used in this way (though see Rivalan et al. 2010), likely because of substantial data requirements to sufficiently parameterize multifactorial models.

A previous study found that demographic response to interannual climate variation suggests that populations of American ginseng (*Panax quinquefolius* L.) are locally adapted to temperature (Souther and McGraw 2011); these findings were further supported by a reciprocal transplant experiment that detected genetic differentiation of populations along a temperature gradient (Souther et al. 2012). Local adaptation allows populations to maximize fitness when conditions are stable, however, directional change away from historic environmental norms comes at a fitness cost (Holt and Gaines 1992, Davis and Shaw 2001). For locally climatically adapted species, the climatic niche at the population level may be narrow even if the species occurs over a wide climate gradient (Atkins and Travis 2010). If future climatic conditions exceed the population-level climatic niche, climate change may drive extinctions of species with seemingly broad climatic niches (Fig. 1; Holt and Gaines 1992, Davis and Shaw 2001, Atkins and Travis 2010). In this way, ginseng and other locally climatically adapted species may be vulnerable to climate change-driven extinction.

Ginseng is a wild-harvested species, primarily exported to China, where the root is highly valued in traditional Chinese medicine (McGraw et al. 2013). In 1975, ginseng was listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) amidst growing concern that unregulated harvest was leading to increased scarcity. Prompted by CITES listing, the U.S. government established a management program for ginseng, overseen by the U.S. Fish and Wildlife Service (USFWS). Prior to export, the USFWS, in collaboration with state ginseng programs, must find that harvest is of "no detriment" to the long-term persistence of the species. As as condition of the CITES export permit, harvest regulations simply state that it is illegal to harvest individuals less than five years of age. Often, individual states enact additional harvest regulations, resulting in a patchwork of laws that vary in degree of protectiveness (Robbins 2000).

Harvest is destructive to the plant, and has been linked to reduction in population growth rates and genetic diversity (Nantel et al. 1996, Cruse-Sanders and Hamrick 2004a, Cruse-Sanders et al. 2005, Van der Voort and McGraw 2006, Farrington et al. 2009). State laws stipulate a harvest season, and many specify a minimum harvest size, as well as require harvesters to plant the seeds of harvested individuals at the site of removal. These regulations encourage harvest of reproductive individuals bearing ripe berries, thus increasing the likelihood that harvested plants are replaced within the population. Harvester behavior impacts population growth rates (Van der Voort and McGraw 2006). Regulation-compliant harvest is still often detrimental to population growth, whereas a stewardship style of harvest, in which the harvester delays harvest to allow berry maturation, removes only seed-bearing plants, and plants berries at the harvest site, maintains population growth rates comparable to populations with no harvest (Van der Voort and McGraw 2006). Illegal harvest, harvest that occurs out of season or that involves the removal of undersized or underaged plants, is common and has lasting, negative consequences for population growth (McGraw et al. 2010).

Examining the interaction of climate change and harvest is an important first step toward managing species, like ginseng, over the next century. Here, we used stochastic, population projection matrix modeling to ask whether the effect of harvest on extinction risk depends on climatic conditions.

## MATERIALS AND METHODS

### Study species

American ginseng (*Panax quinquefolius* L.) is an obligate understory species endemic to the eastern deciduous forest (McGraw et al. 2013). Within this habitat, populations occur on a variety of aspects and elevations (McGraw et al. 2003). While considered uncommon to rare, ginseng is widespread, existing in thousands of small populations from southern Quebec, Canada to northern Georgia in the United States, and west to the Mississippi River (Anderson et al. 1993). Particularly in the Appalachian region, harvest of ginseng is a traditional practice, and sale of ginseng in the medicinal plant trade is a source of supplemental income to rural, often low-income, residents (Robbins 2000).

### Census data

We located a total of 30 ginseng populations over a seven-year period (censuses initiated between 1998 and 2004). So as not to alter harvester behavior, all known individuals were cryptically tagged. Photographs, paired with notations of distances and azimuths, guided ginseng relocation. We censused ginseng populations twice annually. During the first annual census (1 May–15 June), we measured size-related traits, including stalk height and predictors of leaf area, leaflet length and width (Souther and McGraw 2010). Using a standardized protocol, we also conducted a search for new seedlings in a 2 m radius around each plant (Van der
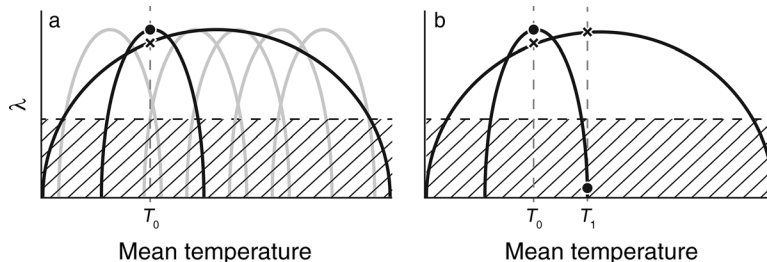
Fig. 1. Conceptual model of a generalist vs. locally adapted response to climatic warming. The cross-hatched region below the dashed horizontal line indicates the area where population growth rate ($\lambda$) is $<1$ and populations decline toward extinction. Panel (a) shows two hypothetical species occupying the same thermal distribution. The relationship between population growth and temperature of the generalist species is represented by the broad black curve, whereas narrow gray curves illustrate temperature response of locally adapted populations. At initial temperature conditions ($T_0$), $\lambda$ values for populations of both the generalist species (x) and locally adapted species (black circle) are $>1$. (b) When temperature increases ($T_1$), the generalist population persists, while the locally adapted population is extirpated. In this warming scenario, all populations of the locally adapted species would fall below replacement levels, whereas for the generalist species, only populations at the warm end of the temperature range would decline.

Voort 2005). Because ginseng seeds are readily counted within the fruit (1–3 seeds per berry), we obtained complete fertility measures during the second annual census (1 August–31 August).

For this study, we selected 12 populations that had $N > 100$ for at least five consecutive censuses (Fig. 2). We chose populations with large $N$ to assure accurate parameterization of projection matrices (Souther and McGraw 2011). Study populations were located in a variety of environments, representative of the range of aspects, elevations, and plant community types occupied by ginseng as a species (Table 1). Populations occurred across six states (Indiana, Kentucky, New York, Pennsylvania, Virginia, West Virginia), and spanned a range of latitudes (36°54′ N–42°38′ N) and longitudes (74°05′ W–84°05′ W; Fig. 2; Souther and McGraw 2011). Exact locations of populations are withheld to prevent targeted harvest.

### Seed cage experiments

Seed bank dynamics are frequently ignored in demographic modeling, but their presence can add significant delays between seed production and recruitment. Ginseng seeds may persist in the soil for up to four years. To estimate germination and survival rates of seed cohorts of different ages, we conducted a seed cage experiment at each field site. We obtained 7200 seeds from a grower of "wild-simulated" ginseng in West Virginia. The term "wild-simulated" refers to a method of ginseng cultivation in which plants are derived from wild stock and grown in "natural" wooded conditions. Ginseng seeds require an 18-month stratification period before germination. Therefore, prior to seed cage deployment, we bulk stratified ginseng seeds in mesh bags in sand at a forested site having a natural ginseng population. We created seed cages by affixing plastic mesh to the base of 8.5 cm diameter by 8 cm long segments of black polyvinyl-chloride pipe. For each population, three groups of four cages (total cages = 12)

were placed in three locations evenly distributed across the site. After filling seed cages with native soil, we manually dispersed 50 seeds atop the soil in each cage, and then covered cages with a wide-gauge plastic mesh hardware cloth, thus allowing germination, while preventing seed escape and granivory. Annually, after counting germinants, we removed three, randomly selected cages, one from each of the three locations, in order to test seed viability using tetrazolium staining ($N = 3$; Roistacher et al. 1953).

### Population projection matrices

Census and seed cage data were used to parameterize population projection matrices (**A**) representing the set of probabilities characterizing rates of survival, growth, and reproduction from one year to the next (Caswell 2001):

$$\mathbf{A} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & a_{16} & a_{17} & a_{18} \\ a_{21} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & a_{32} & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & a_{43} & 0 & 0 & 0 & 0 & 0 \\ a_{51} & a_{52} & a_{53} & a_{54} & a_{55} & a_{56} & 0 & 0 \\ 0 & 0 & 0 & 0 & a_{65} & a_{66} & a_{67} & a_{68} \\ 0 & 0 & 0 & 0 & 0 & a_{76} & a_{77} & a_{78} \\ 0 & 0 & 0 & 0 & 0 & a_{86} & a_{87} & a_{88} \end{pmatrix}.$$

The number of plants in each class consisted of all individuals present at the time of the first annual census. Population projection matrices included eight stages; the first four (1–4) were seed cohorts aged 9 months, 21 months, 33 months, and 45 months. Seed cohort ages were calculated from the time of seed maturation in August to the time of the first annual census in May. The final four stages (5–8) were stage/size classes of post-germination individuals. These stages consisted of seedling (one-leaf), juvenile (two-leaf), small adult, and large adult plants (Fig. 3). The number of stages used in this model was a trade-off between accurately characterizing groups of individuals
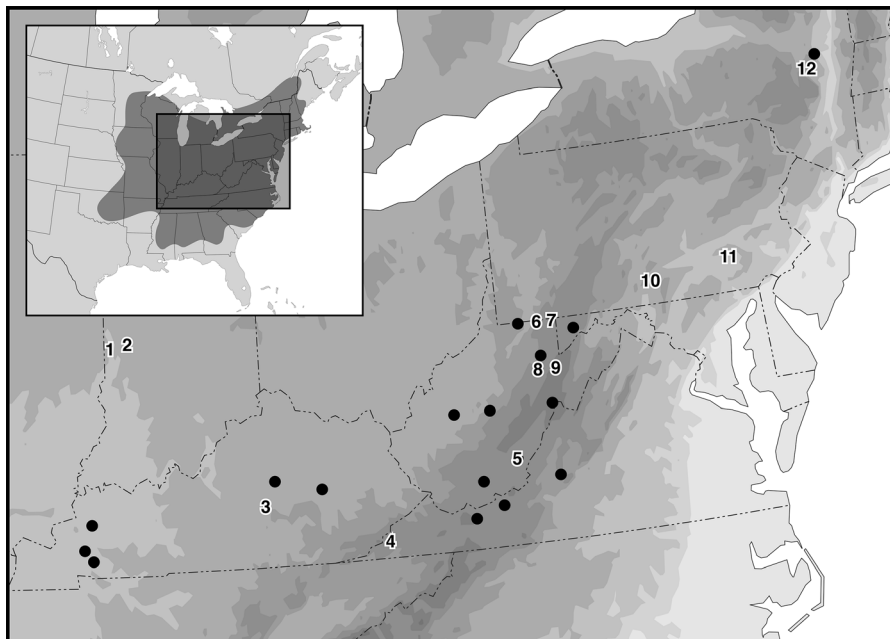
Fig. 2. Map of 30 census populations of American ginseng (*Panax quinquefolius* L.) in the context of ginseng's range. Census populations used in the model are indicated by numbers 1–12, while populations that were not used in the model are marked with black dots. Locations of populations are intentionally imprecise to prevent targeted harvest.

with similar survival and reproductive rates, and allowing adequate parameterization of transition probabilities to and from these classes. One-leaf seedlings exhibited high mortality rates and never produced seeds. After plants attained two leaves, survival was much higher, yet seed production was uncommon. Plants with more than two leaves (three to five-leaf plants) were considered adults, and demonstrated the highest survival and reproduction. Once adults, reproduction and survival were better explained by leaf area than leaf number, and consequently we used the median leaf area to divide the adult class into two, roughly

equal-sized stages (small and large adults). The large adult class had mean fertilities ~5- to 10-fold higher than the small adult class.

Population projection matrix models and their derivatives have become the standard approach to quantifying population growth for plant and animal species with complex life histories and size-dependent vital rates (Caswell 2001). Due to its "slow" life history, lack of vegetative reproduction, short-lived seed bank, large seed size, and consistent growth stages, ginseng is an ideal species for using this methodology. A relatively new approach to population projection studies, the

TABLE 1. Characteristics of American ginseng (*Panax quinquefolius* L.) study population sites.

| Population ID | N, 2008 | Land ownership | Elevation (m) | Dominant overstory species | Total growing-season precipitation, 1970–2001 (cm) |
|---|---|---|---|---|---|
| 1 | 203 | MR | 185 | AS–TA | 54.7 |
| 2 | 126 | SPF | 202 | AS–FG | 60.3 |
| 3 | 402 | NP | 287 | AS–QA | 59.3 |
| 4 | 207 | PL | 658 | AS–LT | 62.0 |
| 5 | 169 | PL | 630 | TA–F sp. | 51.6 |
| 6 | 140 | SPF | 470 | AS–LT | 55.8 |
| 7 | 431 | SPF | 520 | QR–LT | 55.8 |
| 8 | 141 | NF | 760 | AS–LT | 69.6 |
| 9 | 216 | NF | 789 | AS–TA | 69.6 |
| 10 | 552 | MB | 242 | LT–CT | 52.4 |
| 11 | 101 | PL | 221 | LT–CO | 56.6 |
| 12 | 372 | NP | 488 | AS–PG | 49.9 |

*Notes:* Land ownership abbreviations are: NP, nature preserve; PL, private land; PF, state park or forest; MB, military base; and NF, national forest. Species abbreviations are: AS, *Acer saccharum*; QA, *Quercus alba*; LT, *Liriodendron tulipifera*; CO, *Carya ovata*; TA, *Tilia americana*; F sp., *Fraxinus* sp.; PG, *Picea glauca*; CT, *Carya tomentosa*; QR, *Quercus rubra*; and FG, *Fagus grandifolia*. Browse history abbreviations are: L, low; M, medium; and H, high.
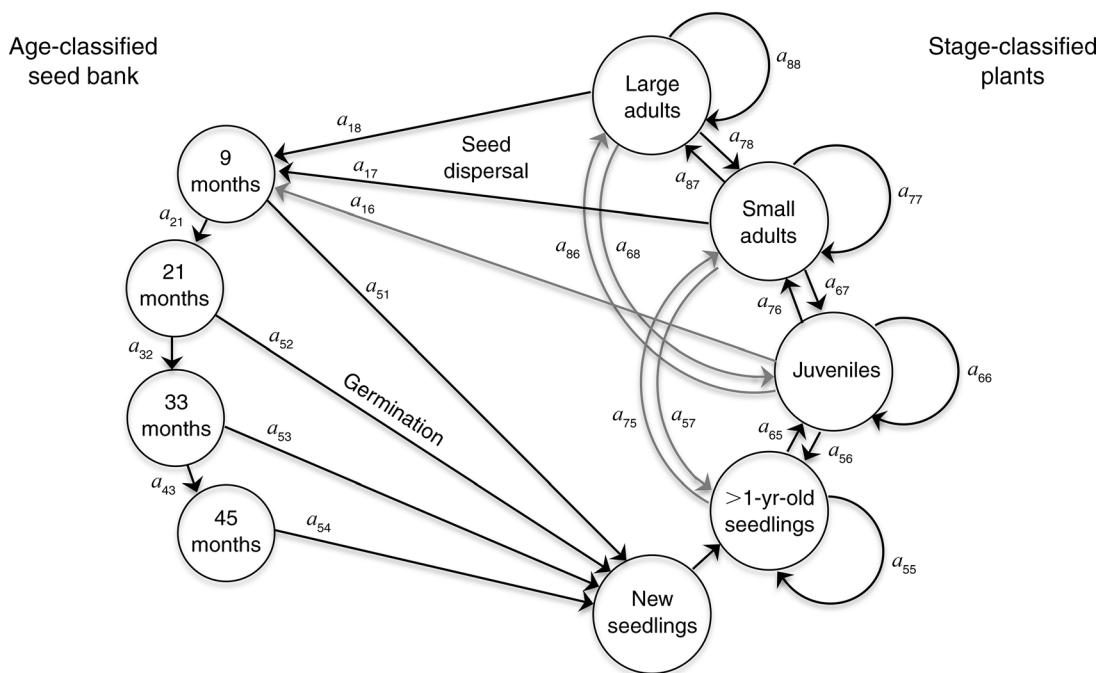
FIG. 3. Life cycle diagram depicting an age-classified seed bank and stage-classified plant population. Arrows and the transition elements $a_{ij}$ indicate possible transitions among stages for individuals within the population. Gray arrows specify transitions that are occasionally observed, but with less frequency than transitions indicated by black arrows. In this demographic model, new seedlings were pooled with seedlings aged more than one year.

integral projection model, treats size classes as a continuum. For ginseng, because of the existence of structurally and behaviorally discrete seed, seedling, juvenile, and adult classes, we chose to use the traditional stage-based approach (Caswell 2001). Indeed, differential life history behavior as a function of stage, above and beyond the size differences in these stages, suggested that discrete classes were preferable to continuous size classes used in integral projection models for this species.

Transition probabilities quantifying seed bank dynamics were calculated from the seed bank experiment. For 7 of the 12 populations, two sequential seed cage studies were performed, and for those, results were averaged across experiments. Seed survival ($a_{21}$, $a_{32}$, $a_{43}$) from year$_t$ to year$_{t+1}$ was estimated directly from seed viability tests, and was calculated as

$$a_{ij} = \frac{S_i}{S_j}$$

TABLE 1. Extended.

| Mean maximum growing-season temperature, 1970–2001 (°C) | Soil pH | Aspect | Known harvest history | Browse history |
|---|---|---|---|---|
| 25.1 | 6.6 | N | no | M |
| 24.9 | 5.4 | N | yes | M |
| 26.5 | 5.1 | NW | no | H |
| 24.9 | 5.7 | W | yes | L |
| 23.1 | 5.0 | NE | no | M |
| 23.3 | 4.6 | NW | yes | H |
| 22.3 | 4.1 | NE | yes | M |
| 20.9 | 4.1 | N | no | H |
| 21.1 | 4.2 | NW,E | no | M |
| 23.2 | 4.4 | E | no | M |
| 22.4 | 5.0 | S | yes | H |
| 22.4 | 4.4 | S | no | L |

where $i < 5$, $j = i - 1$, and $S$ was mean number of viable seeds remaining in the soil. Germination rates ($a_{51}, a_{52}, a_{53}, a_{54}$), quantifying the transition from viable seeds at time $t$ to one-leaf seedlings (stage 5) at time $t + 1$, were calculated as

$$a_{5j} = \frac{G_{t+1}}{S_j}$$

where $j = 1, 2, 3, 4$, $G$ was the number of germinants, and $S_j$ was the number of viable seeds in stage $j$.

Transition probabilities of post-germination stages included shrinkage ($a_{ij}$ where $i < j$), stasis ($a_{ij}$ where $i = j$), or growth ($a_{ij}$ where $i > j$), and were calculated directly from census data as the proportion of individuals in stage $j$ that transitioned to stage $i$ the following year. Plants missing at the time of the first annual census were assigned a stage corresponding to their stage prior to disappearance. Long-term root dormancy is rare, so death (stage 9) was retroactively assigned after two consecutive years of absence.

Fertility transitions ($a_{1j}$) represent the mean number of viable seeds in the soil at time $t + 1$ produced per individual in stage $j$ at time $t$. Fertilities for juveniles and adults were calculated as

$$a_{1j} = p \frac{\Sigma S_j}{n_j}$$

where $S_j$ is the number of seeds produced in stage $j$ in year $t$, and $n_j$ is the total number of individuals in stage $j$ ($j = 6, 7, 8$) in year $t$. The coefficient $p$ is the proportion of seeds produced in August of year $t$ that survived to May of year $t + 1$. This coefficient varied among sites due to variation in early seed mortality among sites (e.g., due to seed predation). Because we directly counted new seedlings and we knew "expected" rates of survival in the seed pool from seed cage data, we were able to estimate this coefficient, which was unique to each population, as follows:

$$p = \frac{\left(\dfrac{\overline{G_{obs}}}{0.90}\right)}{\overline{G_e}}$$

where $\overline{G_{obs}}$ is the mean number of observed, naturally occurring germinants over a three-year period (2008–2010), 0.90 is a correction factor to account for the estimated 10% of seeds that disperse beyond the 2-m search radius for germinants (McGraw and Furedi 2005), and $\overline{G_e}$ is the mean number of expected germinants 2008–2010 given prior seed production and seed bank transition probabilities. We calculated $G_e$ for each year as

$$G_e = \Big( (SD_{21} \times a_{51}) + (SD_{33 \times a_{21} \times a_{52}}) + (SD_{45 \times a_{32} \times a_{53}}) \\ + (SD_{57 \times a_{43} \times a_{54}}) \Big)$$

where SD is the total number of seeds produced 21, 33, 45, or 57 months prior to germination, $a_{21}, a_{32}, a_{43}$ are

age-related survival rates of seeds in the seed bank, and $a_{5j}$ (where $j = 1, 2, 3, 4$) is the germination rate for each cohort of seeds.

Projection matrices (**A**) were generated for each population over all transition years from 1998 to 2009, yielding a total of 75 matrices. The finite rate of increase ($\lambda$) for each matrix was determined from the dominant eigenvalue of the matrix (herein, deterministic $\lambda$ values will be denoted as $\lambda_d$). The 2009–2010 transition was not included, because the fate of missing plants was uncertain.

### Climate data

In a previous study, we found that mean daily maximum temperature during the growing season best explained variation in $\lambda$ among years for each population (Souther and McGraw 2011). Therefore, we used this climate statistic in all subsequent analyses (henceforth, temperature will refer to mean daily maximum growing-season temperature). We assembled temperature data from weather stations located within 50 km of each population. In 2007, we placed a HOBO pendant datalogger (Onset Computer Cooperation, Bourne, USA), suspended from a wooden stake, at a random location at each site, such that the datalogger faced north and was located at plant level (~20 cm above the soil surface). In order to infer population-specific temperatures, we regressed daily temperatures from HOBO dataloggers on those derived from climate station data for each population. We then used this regression equation to calculate annual mean growing-season temperatures (1 April–30 September), as well as a 30-year (1971–2000) mean growing-season temperatures from climate station records.

### Stochastic population growth rate

Stochastic lambdas ($\lambda_s$) were calculated for each population by both Tuljapurkar's approximation and by simulation in R 2.12.0 (R Development Core Team 2012). In order to derive $\lambda_s$ by the latter method, 50 000 simulations were performed with equal probability of selection of **A** matrices. For each population, we first calculated $\lambda_s$ for all transition matrices, and then found $\lambda_s$ for only those transition matrices in which a harvest event did *not* occur. In order to calculate a mean $\lambda_s$, **A** matrices were pooled across populations, and $\lambda_s$ calculated using the same procedure as described for calculating single population estimates ($N = 75$). We excluded harvest years and repeated the analysis to generate a "no harvest" mean $\lambda_s$ ($N = 62$).

### Model of extinction risk response to climate change and harvest

We obtained global climate model predictions of mean maximum temperature increase from the Program for Climate Model Diagnosis and Intercomparison (PCMDI) archive. The PCMDI data portal serves as a repository for data used in the Intergovernmental Panel

on Climate Change's (IPCC) fourth assessment report. In this report, climate models project temperature increase for several emissions storylines, described in the IPCC's Special Report on Emissions Scenarios (SRES; IPCC 2007). These emissions storylines describe different scenarios of fossil fuel use over the next century. For our analyses, we selected the A1B scenario, a mid-level estimate of greenhouse gas emissions that describes a world of rapid economic growth that relies on both fossil and non-fossil fuel based energy sources (IPCC 2007). We selected the National Center for Atmospheric Research's (NCAR) CCSM3.0 climate model, which provided climate projection data on a monthly basis in a spatially explicit, gridded format (cells = $1.4° \times 1.4°$). Compared to other modeling groups, the magnitude of temperature increase projected by the NCAR CCSM3.0's climate model is average to slightly above average (IPCC 2007). Using these model projections, we estimated mean annual temperature increase by regressing mean annual maximum growing-season (1 April–31 September) temperature on year, the slope of this line giving the mean temperature increase on a per annum basis. We averaged the slope of these regressions across grid cells in which censused populations were present, and across all four runs of the NCAR CCSM3.0 climate model, yielding an estimate of mean annual temperature increase for all populations.

To create stochastic climate projections to drive matrix selection during the population viability analysis, we randomly generated annual temperatures from a normal distribution based on mean temperatures projected by climate models, using the variance of temperatures observed at censused ginseng populations. We generated 1000, 70-year temperature runs for the A1B warming scenario. In order to examine the sensitivity of population viability to warming, we generated three additional climate scenarios: (1) a one-third reduction in warming rate, (2) a two-thirds reduction in warming rate, and (3) a 100% reduction in warming rate (no change from the 1970–2000 temperature mean; hereafter referred to as the "no warming" scenario).

In a regression of $\lambda_s$ on temperature, temperature did not explain variation in $\lambda_s$ across populations ($\lambda_s$, including harvest years, $R^2 = 0.1939$, $\beta = 0.0109$, $p = 0.1520$; $\lambda_s$, excluding harvest years, $R^2 = 0.0012$, $\beta = 0.0009$, $p = 0.9165$) as expected for a species in which populations are locally adapted to temperature. Based on this and the results from previous studies demonstrating local adaptation to temperature and a consistent thermal niche breadth among study populations (Souther and McGraw 2011, Souther et al. 2012), we pooled A matrices across temperature environments, expressing annual temperature associated with each A matrix in terms of standard deviation from a 30-year, population-specific mean. Metapopulation dynamics were not incorporated into the model, as studies of neutral genetic variation indicate negligible levels of gene flow among populations (Cruse-Sanders and Hamrick

2004a, b, Cruse-Sanders et al. 2005). An alternative modeling approach is to relate vital rates to temperature, and use these relationships to create matrices that represent demographic rates under future conditions. Instead, we elected the statistically conservative approach of sampling from a pool of observed matrices. By using observed matrices, we realistically preserved covariation of vital rates, and avoided incorporating additional error that could generate unrealistic matrices.

We performed simulations under each of the climate scenarios for two groups: (1) all matrices including years in which harvest occurred ($N = 75$) and (2) matrices excluding harvest years ($N = 62$). For simplicity, we refer to simulations in which harvest years were included as "harvest" simulations, though the pool of matrices used in these analyses includes years in which harvest did occur as well as years in which harvest did not occur, thus reflecting ambient harvest rates of sample populations. Similarly, "no harvest" simulations are those in which we excluded harvest years.

The population viability analysis was performed in MATLAB 2009b (Mathworks 2009). Stochastic population projections driven by each of the four climate change scenarios formed the basis of our population viability analysis. Starting from an initial population size ($N_i$), each simulation run consisted of a series of annual population projections as follows:

$$N_{(t+1)} = \mathbf{A}_i \times N_{(t)}$$

in which the matrix $\mathbf{A}_i$ corresponding to an annual temperature most similar to the temperature determined by the climate scenario was selected. Thus, as the mean climate warmed over time within any one run, matrices were increasingly selected from the right side of the distribution of temperature-years. Because temperatures were expressed in terms of deviation from 30-year averages for each population, this did not bias the matrix selection geographically; relatively warm years could be chosen from any population.

Each simulation run proceeded for 70 years, which corresponded with a 1°C mean increase in temperature from year 2000 to 2069. By limiting warming to 1°C, we prevented oversampling **A** matrices that corresponded to the "warmest" temperatures (circa +1.5°C from current mean temperatures) observed during the demographic census of ginseng populations.

For each simulation run, population response was binary, with the simulation resulting in either population extinction or persistence. The dynamics of small populations are governed by unique demographic and genetic factors (e.g., Allee effects, demographic stochasticity, erosion of genetic variation). Because the net effect of these factors reduces $N$, most populations enter a cycle that leads to extinction at some critically small $N$ that is often greater than zero (Morris and Doak 2002). For this reason, in most population viability analyses, a population is considered extinct once it drops below a quasi-extinction threshold ($N_{qe}$), i.e., where $N < N_{qe}$.

TABLE 2. Stochastic λ with 95% confidence intervals (CI) for 12 ginseng populations.

| Population | Stochastic λ including harvest | | | Stochastic λ excluding harvest | | |
|---|---|---|---|---|---|---|
| | Simulation | Lower CI | Upper CI | Simulation | Lower CI | Upper CI |
| 1[H] | 0.9723 | 0.9439 | 1.0001 | 0.9723 | 0.9439 | 1.0001 |
| 2[H] | 1.0024 | 1.0009 | 1.0057 | 1.0684 | 1.0028 | 1.135 |
| 3[H] | 0.9447 | 0.8856 | 1.0016 | 1.0121 | 1.0008 | 1.0248 |
| 4[H] | 0.9758 | 0.9508 | 0.9999 | 1.0182 | 1.0003 | 1.0364 |
| 5 | 1.0112 | 1.0008 | 1.023 | 1.0112 | 1.0008 | 1.023 |
| 6[H] | 0.997 | 0.9932 | 0.9992 | 1.0239 | 1.0008 | 1.048 |
| 7[H] | 0.9533 | 0.9048 | 1.0005 | 0.9598 | 0.918 | 1.0001 |
| 8 | 1.014 | 1.0006 | 1.0285 | 1.014 | 1.0006 | 1.0285 |
| 9 | 1.0664 | 1.0026 | 1.1311 | 1.0664 | 1.0026 | 1.1311 |
| 10 | 0.9943 | 0.9872 | 0.9986 | 0.9943 | 0.9872 | 0.9986 |
| 11 | 0.9118 | 0.8185 | 1.0032 | 0.9118 | 0.8185 | 1.0032 |
| 12[H] | 1.0385 | 1.0009 | 1.0765 | 1.0376 | 1.0007 | 1.0744 |
| All populations† | 0.9961 | 0.9911 | 0.999 | 1.0127 | 1.001 | 1.0262 |

*Note:* A superscript H indicates populations in which harvest events had occurred.

† Stochastic λ calculated by pooling **A** matrices across all populations.

We set the $N_{qe}$ for this population viability analysis (PVA) at 20 individuals because (1) in an experimental manipulation of ginseng population size, Allee effects were found to decrease λ in population sizes of $N < 20$ (Hackney and McGraw 2001, McGraw and Furedi 2005), and (2) demographic stochasticity imperils populations when $N < 20$ for many species (Morris and Doak 2002).

After 1000 simulation runs were performed, we calculated a probability of persistence (P) as

$$P = \frac{N_v}{1000}$$

where $N_v$ is the number of runs that resulted in persistence ($N > N_{qe}$ for 70 years), and extinction risk as $1 - P$. Probability of persistence was calculated for 99 initial population sizes (ranging from 20 to 1000 in 10-year increments) for both harvest and no harvest matrix pools under four climate scenarios (total P's calculated = 99 $N_{init} \times$ 2 harvest scenarios $\times$ 4 climate scenarios = 792).

### Life table response experiment (LTRE)

A life table response experiment (LTRE) was conducted in order to quantify how warm years and inclusion of harvest years affected individual transition elements ($a_{ij}$), which in turn, affected deterministic λ ($\lambda_d$). For each pool of matrices (those including harvest years and those excluding harvest years), we selected **A** matrices within ±0.5 standard deviations of each population's thermal "optimum," to represent "circum-optimal" years. We also selected **A** matrices that corresponded to "warm" years, defined as years in which the mean temperature was greater than 0.5 standard deviation above the 30-year mean ("optimal") temperature. Three mean matrix sets were compared pairwise to examine nonadditivity of effects: (1) no harvest, circum-optimal climate vs. no harvest plus harvest, circum-optimal climate (examining harvest effect alone), (2) no harvest, circum-optimal climate vs. no harvest, warm climate (examining climate effect alone), and

finally, (3) no harvest, circum-optimal climate vs. no harvest plus harvest, warm climate (examining the combined effects).

In each pairwise comparison, the mean matrix was calculated for the set of matrices that fell into each class, and then a vector was created representing the difference in corresponding $a_{ij}$ elements for the two mean matrices. To calculate the contribution of that matrix element to the difference in $\lambda_d$ between the two mean matrices, this difference was multiplied by its corresponding sensitivity ($s_{ij}$), calculated for each $a_{ij}$ element from the average matrix of the matrices used in each analysis (Caswell 2001). The overall difference in $\lambda_d$ between the two mean matrices sums across the component contributions of the matrix elements as follows:

$$\Delta\lambda = \sum_{ij} \left( a_{ij}^{(w)} - a_{ij}^{(o)} \right) \times \frac{\partial\lambda}{\partial a_{ij}} \bigg| \mathbf{A}^{(m)}$$

where $a_{ij}^{(w)}$ are the transition probabilities associated with the average matrix of warm years, $a_{ij}^{(o)}$ are the transition probabilities associated with the average matrix of "optimal" years, and where

$$\mathbf{A}^{(m)} = \frac{\left( \mathbf{A}^{(w)} + \mathbf{A}^{(o)} \right)}{2}.$$

$\mathbf{A}^{(w)}$ is the average matrix of warm years, and $\mathbf{A}^{(o)}$ is the average matrix of "optimal" years.

### RESULTS

#### Stochastic population growth rate

Calculations of population-level stochastic growth rate ($\lambda_s$) by Tuljapukar's approximation did not differ from results derived by simulation. Stochastic growth rate varied between 0.9118 and 1.0664 when harvest years were included, and between 0.9118 and 1.0684 when harvest years were excluded (Table 2). When harvest years were included, 25% of populations fell below replacement level, while this was the case for only
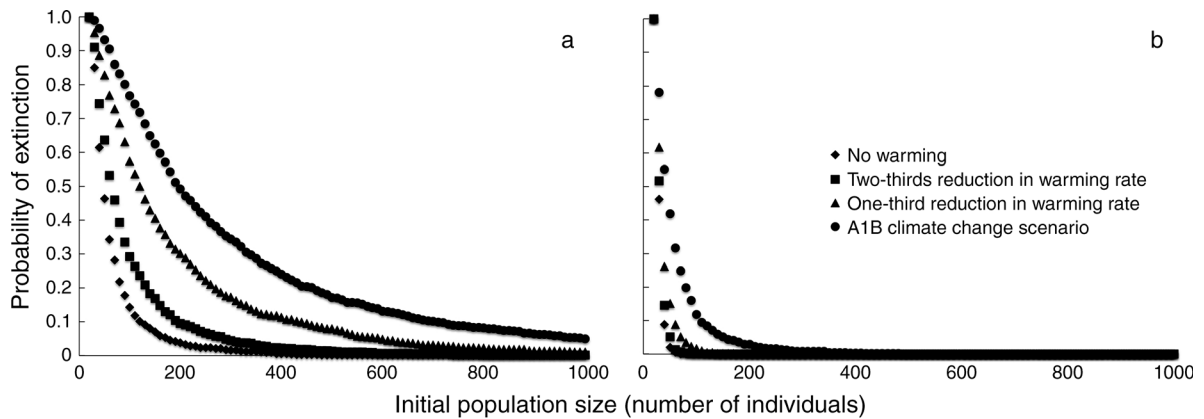
FIG. 4. Probability of ginseng extinction as a function of initial population size for (a) harvest and (b) no harvest simulations under four warming scenarios. For both (a) and (b), the result of individual population viability analyses (PVAs) for a particular climate scenario are indicated: A circle represents the A1B climate scenario, a triangle represents a one-third reduction in warming rate from the A1B scenario, a square represents two-thirds reduction in warming rate, and a diamond represents a no warming scenario. A1B is a mid-level estimate of greenhouse gas emissions that describes a world of rapid economic growth that relies on both fossil and non-fossil fuel based energy sources (IPCC 2007).

1 of the 12 populations (8%) when harvest years were excluded (Table 2). There was a general tendency for $\lambda_s$ values to increase when harvest years were removed, and populations 4 and 6 demonstrated significant increase (Table 2). The mean $\lambda_s$ across populations and including harvest years was slightly under replacement rate ($\lambda_s = 0.9961$; Table 2). For the no harvest simulation, the across population mean $\lambda_s$ increased above a $\lambda_s$ of 1 ($\lambda_s = 1.0127$; Table 2).

### Population viability analysis

As expected, the larger the initial population size, the lower the extinction risk over the 70-year simulation period, regardless of climate or harvest scenario (Fig. 4). For both simulations including and excluding harvest, extinction risk increased with level of warming (Fig. 4). Simulated climate warming elevated extinction risk above the standard cutoff of viability (viable =

extinction risk < 0.05) across all initial population sizes when simulations included harvest ($N = 20$–1000; harvest years included; Fig. 4a). For no harvest simulations, the climate change effect was observed only at smaller initial $N$ ($N < 150$) and was much less pronounced (harvest years excluded; Fig. 4b).

To illustrate the implications of the extinction risk curves in Fig. 4, we examined the extinction probability for the median size of populations in this study ($N = 140$) in a factorial manner (with and without warming, with and without harvest, in all combinations; Fig. 5a, b). At $N = 140$, there was a 0% likelihood of extinction for no warming, no harvest simulations (Fig. 5b). Individually, climate change and harvest increased extinction risk only slightly; the extinction risk under the A1B warming scenario when harvest was excluded was 6%, and the extinction risk for a "no warming" scenario including harvest was 8%. For simulations that included harvest
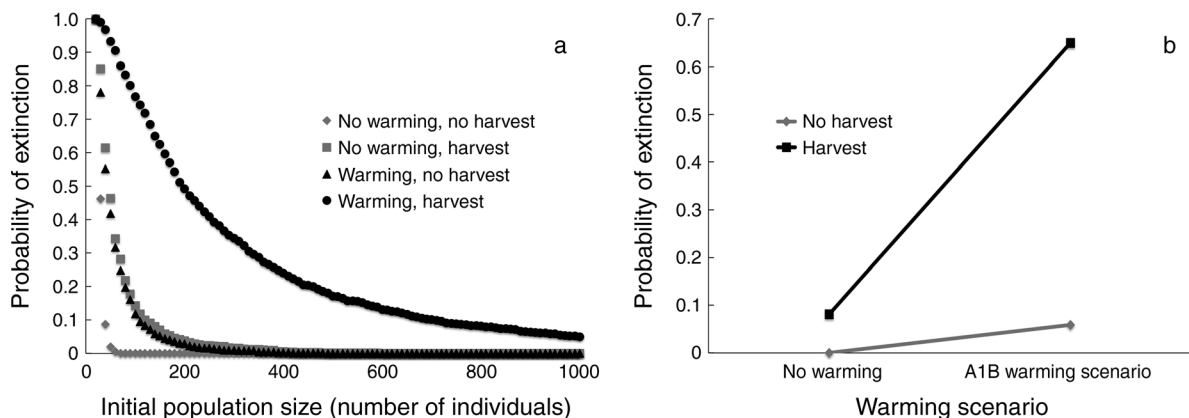


FIG. 5. PVAs conducted at (a) differing population sizes and extinction risks at an initial population size of 140 (median population size of census populations) and (b) for all combinations of two harvest and two climate scenarios. Both (a) and (b) show the interactive effect of climate change and harvest on extinction risk.
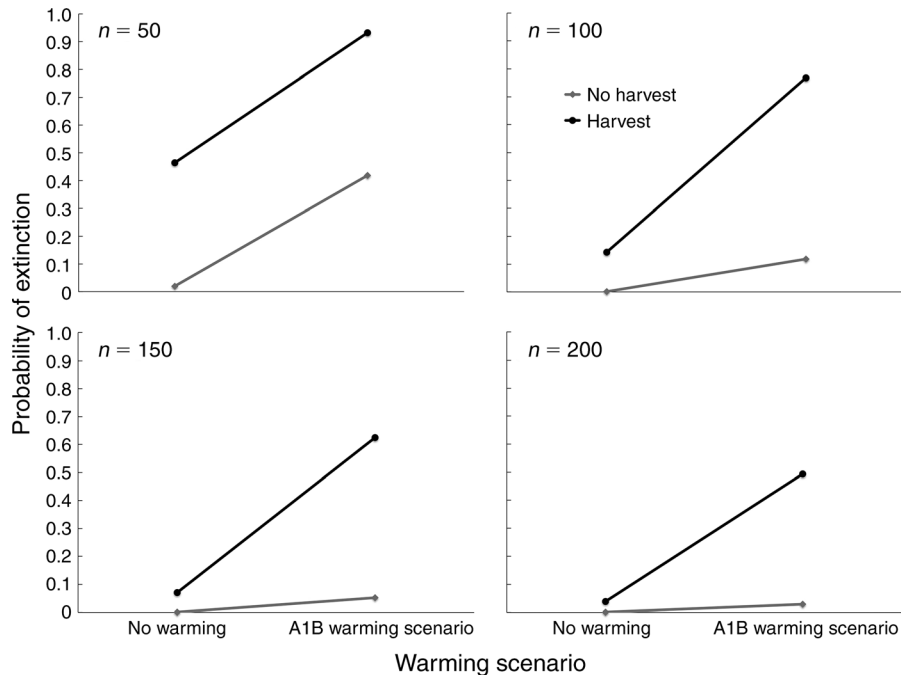
FIG. 6. Extinction probabilities under a no warming and A1B warming scenario both including and excluding harvest events for four initial population sizes ($N = 50, 100, 150, 200$).

and climate change, extinction risk increased to 65%, a percentage well above the additive effects of these two factors (Fig. 5b). When we examined extinction risk across a range of typical population sizes (50, 100, 150, 200 individuals), this same pattern of an interactive effect of harvest and climate warming on extinction probability was seen at all but the smallest population size. At $N = 50$, the effects of harvest and warming were approximately additive (Fig. 6).

### LTRE

The effects of harvest alone (comparison 1; Table 3) showed the expected reduction in population growth rate (from $\lambda_d = 1.033$ to 1.014) and the effects of warm years (comparison 2; Table 3) were of similar magnitude (from $\lambda_d = 1.033$ to 0.990). The population growth rate reduction due to both harvest and warm years (comparison 3; Table 3) was close to the additive effect of both single factors ($\lambda_d = 0.978$; "expected" $\lambda_d = 0.971$).

Effects of both harvest and warm years on reproduction, seed bank survival, and germination contributed negligibly to the change in $\lambda_d$ in all three pairwise comparisons (Table 3). For all pairwise comparisons, the reduction in growth to and stasis of large adults explained the largest portion of $\lambda_d$ decline. Transitions to the small adult stage compensated to a degree for the reduced transitions to the large-adult class between circum-optimal vs. warm years. Indeed, juveniles actually transitioned to small adults at a greater rate in warm years than in circum-optimal years, placing these individuals in a class with higher seed production. The

sum of the components of $\Delta\lambda_d$ in each pairwise comparison corresponded closely to observed $\lambda_d$ differences.

### DISCUSSION

#### Stochastic $\lambda$

In a previous analysis, we showed that the pattern of deterministic population growth rate response to inter-annual temperature variation suggested adaptation of ginseng populations to the local temperature regime (Souther and McGraw 2011). Here, we incorporated among-year variation in vital rates, deriving $\lambda_s$ estimates for 12 ginseng populations, as well as a mean estimate of $\lambda_s$ across populations. As expected for populations adapted to local thermal conditions, no range-wide relationship between $\lambda_s$ and temperature was detected. Generally, $\lambda_s$ increased when we removed years in which harvest occurred from analyses; a finding consistent with previous studies that have demonstrated negative impacts of harvest on population growth and viability (Nantel et al. 1996, Van der Voort and McGraw 2006, Farrington et al. 2009). Among harvested census populations, average harvest rates ranged from 0.9% to 3.3% of the population per year, and the overall harvest rate across populations was 1% (Table 4). To give some context for these numbers, harvest rates of censused populations were consistently lower than the 4.9% harvest rate estimated for West Virginia, which ranks in the top seven states in terms of total harvest yields (McGraw et al. 2003, Kauffman 2006). Despite low harvest rates, harvest decreased $\lambda_s$. Harvester

TABLE 3. Life table response experiment (LTRE) for pairwise comparisons of population growth rate (λ) response to harvest and climate.

| | | Effect of interest | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Harvest | | | Climate | | | Harvest and climate | | |
| $a_{ij}$ | Transition type | $\Delta a_{ij}$ | $s_{ij}$ | $\Delta\lambda$ | $\Delta a_{ij}$ | $s_{ij}$ | $\Delta\lambda$ | $\Delta a_{ij}$ | $s_{ij}$ | $\Delta\lambda$ |
| $a_{21}$ | seed bank survival | 0.0045 | 0.0579 | 0.0003 | 0.041 | 0.0499 | 0.002 | 0.0301 | 0.0514 | 0.0015 |
| $a_{32}$ | seed bank survival | −0.0071 | 0.0058 | 0 | 0.0165 | 0.004 | 0.0001 | 0.0072 | 0.0046 | 0 |
| $a_{43}$ | seed bank survival | −0.0141 | 0 | 0 | −0.0231 | 0 | 0 | −0.0122 | 0 | 0 |
| $a_{16}$ | reproduction | 0.0042 | 0.0748 | 0.0003 | −0.0005 | 0.069 | 0 | −0.0022 | 0.0744 | −0.0002 |
| $a_{17}$ | reproduction | 0.0065 | 0.0309 | 0.0002 | −0.0294 | 0.0367 | −0.0011 | −0.0502 | 0.0379 | −0.0019 |
| $a_{18}$ | reproduction | −0.0185 | 0.0599 | −0.0011 | −0.0814 | 0.054 | −0.0044 | −0.0915 | 0.0552 | −0.0051 |
| $a_{51}$ | germination | −0.0146 | 0.0982 | −0.0014 | −0.0376 | 0.0903 | −0.0034 | −0.0238 | 0.0903 | −0.0022 |
| $a_{52}$ | germination | 0.0323 | 0.034 | 0.0011 | −0.0421 | 0.0333 | −0.0014 | −0.0198 | 0.033 | −0.0007 |
| $a_{53}$ | germination | 0.0627 | 0.0061 | 0.0004 | −0.0401 | 0.0064 | −0.0003 | −0.0077 | 0.0063 | 0 |
| $a_{54}$ | germination | 0 | 0.0004 | 0 | 0 | 0.0004 | 0 | 0 | 0.0004 | 0 |
| $a_{65}$ | growth | −0.0056 | 0.3644 | −0.002 | −0.0269 | 0.3629 | −0.0098 | −0.0164 | 0.3599 | −0.0059 |
| $a_{75}$ | growth | −0.0019 | 0.4724 | −0.0009 | −0.0094 | 0.4698 | −0.0044 | −0.0096 | 0.4628 | −0.0045 |
| $a_{76}$ | growth | −0.0024 | 0.3362 | −0.0008 | 0.0596 | 0.3269 | **0.0195** | 0.0528 | 0.3345 | **0.0177** |
| $a_{86}$ | growth | −0.0066 | 0.4438 | −0.0029 | −0.0411 | 0.437 | **−0.018** | −0.0473 | 0.4498 | **−0.0213** |
| $a_{87}$ | growth | −0.0186 | 0.1833 | −0.0034 | −0.0823 | 0.2324 | **−0.0191** | −0.0894 | 0.2293 | **−0.0205** |
| $a_{56}$ | regression | 0.0071 | 0.1152 | 0.0008 | 0.0198 | 0.1074 | 0.0021 | 0.0176 | 0.1134 | 0.002 |
| $a_{57}$ | regression | 0.0021 | 0.0476 | 0.0001 | −0.0016 | 0.0571 | −0.0001 | −0.0018 | 0.0578 | −0.0001 |
| $a_{67}$ | regression | −0.0233 | 0.1072 | −0.0025 | −0.0063 | 0.1343 | −0.0008 | −0.0148 | 0.1326 | −0.002 |
| $a_{68}$ | regression | −0.0102 | 0.2075 | −0.0021 | −0.0318 | 0.1977 | −0.0063 | −0.0263 | 0.1929 | −0.0051 |
| $a_{78}$ | regression | 0.014 | 0.2689 | 0.0038 | 0.0795 | 0.2559 | **0.0203** | 0.0665 | 0.2481 | **0.0165** |
| $a_{55}$ | stasis | −0.0052 | 0.1619 | −0.0008 | 0.011 | 0.1543 | 0.0017 | −0.0021 | 0.1569 | −0.0003 |
| $a_{66}$ | stasis | −0.009 | 0.2594 | −0.0023 | −0.0564 | 0.2525 | **−0.0142** | −0.0473 | 0.2601 | **−0.0123** |
| $a_{77}$ | stasis | 0.0225 | 0.1389 | 0.0031 | 0.0761 | 0.1738 | **0.0132** | 0.0737 | 0.1705 | **0.0126** |
| $a_{88}$ | stasis | −0.0238 | 0.3549 | −0.0084 | −0.0516 | 0.3421 | **−0.0177** | −0.0665 | 0.3337 | **−0.0222** |
| Total Δλ component | | | | −0.0185 | | | −0.0421 | | | −0.054 |

*Note:* Boldface type indicates a substantial contribution to Δλ, i.e., |Δλ| > 0.01.

behavior may explain the negative influence of harvest on $\lambda_s$, despite low harvest frequency and intensity. All populations in which harvest occurred experienced at least one event in which harvesters removed undersized plants, and population 7 was repeatedly harvested illegally prior to onset of harvest season (Table 4). Illegal harvest is extremely detrimental to ginseng populations, because it often results in removal of individuals before they have replaced themselves within the population (Van der Voort and McGraw 2006, McGraw et al. 2010, 2013).

### Model results

Individually, harvest and warming both increased extinction risk, especially at small population sizes. These findings are consistent with previous studies that

TABLE 4. Harvest history of ginseng populations.

| Population ID | Percentage of population harvested† | Average harvest rate | Frequency of harvest‡ | Harvested at a legal date?§ | Harvested at a legal location?§ | Proportion of harvested plants legally sized† |
|---|---|---|---|---|---|---|
| 1 | 0 | 0 | 0/9 | NA | NA | NA |
| 2 | 0.0238–0.0775 | 0.0330 | 4/6 | yes | no | 0.1818–1.0000 |
| 3 | 0.1304 | 0.0217 | 1/6 | yes | no | 0.8542 |
| 4 | 0.0050–0.0987 | 0.0287 | 6/8 | yes | yes | 0.6667–1.0000 |
| 5 | 0 | 0 | 0/5 | NA | NA | NA |
| 6 | 0.0075–0.1628 | 0.0253 | 4/9 | yes | no | 0.0000–0.5000 |
| 7 | 0.0379–0.0620 | 0.0173 | 4/11 | no | no | 0.6000–0.7895 |
| 8 | 0 | 0 | 0/9 | NA | NA | NA |
| 9 | 0 | 0 | 0/8 | NA | NA | NA |
| 10 | 0 | 0 | 0/5 | NA | NA | NA |
| 11 | 0 | 0 | 0/5 | NA | NA | NA |
| 12 | 0.0441 | 0.0088 | 1/5 | yes | no | 0.6000 |

† When harvest occurred in multiple years, the range of values was reported; NA indicates data not applicable.

‡ Number of years in which harvest occurred over total number of census years.

§ For all populations, the legality of harvest date and location were consistent among years; NA indicates data not applicable.

have shown that harvest reduces population viability and growth (Charron and Gagnon 1991, Nantel et al. 1996, Van der Voort and McGraw 2006, Farrington et al. 2009), and with an experimental investigation of thermal tolerance in ginseng that demonstrated a reduction in growth and reproduction when ginseng populations were transplanted to a "future" (warmer) temperature treatment (Souther et al. 2012). Harvest and warming individually increased extinction risk to a similar magnitude, and the effects of both factors on likelihood of extinction rapidly decreased with increasing population size.

At most initial population sizes, climate change in conjunction with harvest increased extinction risk beyond the sum of the individual effects of these factors. This result is consistent with PVA analyses showing nonlinear responses of extinction probability as a function of time horizon of the simulations (Morris and Doak 2002). With λ very close to 1 or greater than 1, and a time horizon of 70 years, and realistic initial population sizes, stochastic simulations showed that most populations would not reach the pseudo-extinction threshold. However, the compounding effects of harvest and a gradually warming climate were sufficient to reduce population sizes below the pseudo-extinction threshold with a high probability. Extending the time horizon would likely reduce these differences, as warming effects would eventually result in extinction regardless of harvest rates, but in the short term, harvest exacerbates the negative effects of climate.

Notably, despite the fact that ginseng is widespread, occurring across a ~1500-km latitudinal gradient that spans a ~10°C gradient in mean summertime temperature, a small degree of warming (1°C) is sufficient to increase extinction risk of an average ginseng population both including and excluding harvest (the precise extinction risk for any given population will depend on various factors, such as population size and site quality). These results demonstrate the repercussions of population-level, climatic specialization on extinction risk as directional warming occurs, and are consistent with both transplant experiments that show a reduction in fitness when populations are introduced into climatic environments to which populations are not adapted (Turesson 1930, Linhart and Grant 1996), and also with theoretical models of the consequences of local climatic adaptation in the context of climate change (Atkins and Travis 2010).

To our knowledge, this is the first demographic model to demonstrate a harvest by climate change interaction with respect to extinction risk. However, Mora et al. (2007) derived a similar result experimentally using *Brachionus plicatilis*. Researchers performed experimental warming and culling over several generations of this short-lived rotifer species, and speculated that the interactive effect on population growth was due to a reduction in genetic diversity, which decreased rotifer resilience to warming. Over the long term, harvest of

ginseng may reduce genetic diversity of ginseng populations both directly through removal of individuals from the population and indirectly through legacy effects of population size reduction on per capita reproductive rates and inbreeding levels (Hackney and McGraw 2001, Cruse-Sanders and Hamrick 2004a, Mooney and McGraw 2007). Similar to *B. plicatilis*, a decrease in genetic diversity could reduce resilience to warming as well as the adaptive capacity of the species (Etterson and Shaw 2001, Hampe and Petit 2005, Jump and Penuelas 2005). Here, we did not explicitly incorporate reduction of genetic variability in simulations, though such a reduction could further reduce ginseng viability.

Model simulations were based on data from 12 populations. We acknowledge that 12 populations is a small sample from which to extrapolate to a range-wide scale, but argue that this extrapolation is valid. Study sites represent populations occurring across a large geographic area (McGraw et al. 2010), though there is a tendency to underrepresent populations at the range margins, which may respond differently to warming than populations at the range center (Hampe and Bairlein 2000, Jansson and Dynesius 2002, Santamaria et al. 2003, Hampe and Petit 2005). Populations are distributed among a wide range of land-use histories, and encompass a diversity of environments that vary in elevation, overstory composition, mean precipitation and temperature conditions, soil pH, harvest, and browse history (Table 1). Compellingly, data from this diverse group of populations yielded a consistent, population-level relationship between temperature and growth rate (Souther and McGraw 2011). Studies of neutral genetic variation that sampled extensively across ginseng's range suggest that genetic differentiation of populations (high fixation index, $F_{ST}$) is the norm for this species (Cruse-Sanders and Hamrick 2004a, Grubbs and Case 2004).

The current analysis focused on effects of warming and harvest, however, other environmental factors are changing concomitantly with temperature increase, and may affect the long-term persistence of ginseng. Increased carbon dioxide levels could partially compensate for decreased photosynthetic rates caused by high temperatures, thus ameliorating the negative effects of warming on ginseng population growth (Ainsworth and Long 2005, Norby and Zak 2011). Alterations to precipitation regime will likely affect ginseng demography (Souther and McGraw 2011); however, changes in precipitation as a function of climate change are difficult to predict, and therefore, this remains a source of uncertainty in these projections (IPCC 2007). Biotic factors, like browsing by deer, also impact viability (McGraw and Furedi 2005, Farrington et al. 2009). Insomuch as biotic factors co-varied with temperature, they have been implicitly incorporated into our population viability projections of ginseng response to climate change.

### Life table response experiment

The life table response experiment necessarily compared effects of climate and harvest in a different way than the stochastic simulations: While stochastic simulations gradually ratcheted up the probability of encountering warm years over a 70-year period, the LTRE compared a set of circum-optimal years with a set of warm years. In addition, the LTRE examined the causes for differences in $\lambda_d$, whereas stochastic simulations modeled change in $N$ over time incorporating stochasticity. Nevertheless, the LTRE allowed us to search for differential responses to warm climate years as a function of harvest presence in the population. No such differences were evident. In fact, the overall effects of warming were remarkably similar in the absence and in the presence of harvest.

### Potential spatial and evolutionary response to climate change

Dispersal to northern and upland regions as well as in situ adaptation to novel climatic conditions may rescue species threatened by climate change (Aitken et al. 2008). Studies of pollen and seed dispersal in ginseng, along with analysis of among-population genetic differentiation suggest short dispersal distances (Hackney 1999, Cruse-Sanders and Hamrick 2004b, Van der Voort 2005), and hence, restricted ability for ginseng to track rapid climate change by means of a spatial response. Studies of neutral genetic variation in naturally occurring ginseng populations find low within-population genetic variation (Cruse-Sanders and Hamrick 2004a, b), a common attribute of populations with high levels of selfing (Linhart and Grant 1996). Genetic variation is further reduced in populations with a history of harvest (Cruse-Sanders and Hamrick 2004a). Because adaptation requires genetically based phenotypic variation, low within-population genetic variation may indicate low adaptive potential, and suggests that harvest may further reduce the ability of populations to adapt to changing climatic conditions (Cruse-Sanders and Hamrick 2004a).

### Harvest in the context of climate change

Long-term sustainability of ginseng harvest may be contingent not only on slowing the pace of climatic warming, but also on adapting current harvest regulations to promote resilience as global temperature increases over the next century (Hannah et al. 2002a, b). Though further research is needed to structure climate change-integrated harvest regulations, in general, policies should promote stewardship-style harvest behavior that increases the likelihood of replacement prior to harvest (Van der Voort and McGraw 2006, McGraw et al. 2010, 2013). Ensuring replacement maintains abundance and may preserve adaptive genetic variation, a prerequisite for adaptation to novel climatic conditions (Cruse-Sanders and Hamrick 2004a). Among harvested populations used in analyses presented here,

all experienced at least one harvest event characterized as illegal (i.e., the harvest event included the culling of undersized plants, occurred out of season, or occurred on protected land). Creative strategies to prevent illegal harvest are urgently needed, as warmer conditions will amplify the consequences of irresponsible harvest behavior.

### Conclusions

Ecological context alters demographic impact of harvest in complex and sometimes nonlinear ways (Farrington et al. 2009, Gaoue and Ticktin 2010, Mandle and Ticktin 2012). In some cases, the influence of environmental factors on harvest effects may not be intuitive. For example, one study found that deer browse ameliorated demographic consequences of harvest by "hiding" ginseng from harvesters (Farrington et al. 2009). Here, the combined effects of climate change and harvest pushed ginseng populations past a demographic tipping point, elevating extinction risk above the additive effect of either factor alone. While this model specifically examined the influence of ginseng harvest in the context of climate change, the implications of these results apply broadly to other harvested species. Current management strategies, which assume stable climatic conditions, may not sufficiently protect species in a dynamic climate (Halpin 1997, Hannah et al. 2002a, b, Hulme 2005, Hannah 2008). Given the possibility of interactive effects among factors, the use of models to evaluate current management strategies under future climatic conditions may be critical for species conservation, as model outcomes may allow for modification of species or habitat management prior to the occurrence of environmental conditions that elicit rapid population decline.

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