

Population viability analyses in plants: challenges and opportunities

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Population viability analyses (PVAs) provide assessments of population persistence (or extinction risk) based on a combination of empirical data and modeling scenarios. PVAs can consider several classes of threats, including systematic trends, environmental stochasticity, catastrophes, demographic stochasticity and genetic stochasticity¹ (Box 1). Consequently, PVAs have been influential in conservation and management².

Review of plant PVAs

Recent reviews of PVAs have included few plant studies (e.g. for Refs 2–4, two of 136, zero of 166, and three of 58 records, respectively). Is it really true that plant PVAs are rare? The answer, of course, depends on the definition of a PVA. In this review, I use a broad definition for a PVA, considering a study a PVA if it includes

empirical data on the entire life cycle of a wild population and if it uses quantitative modeling to project future populations [e.g. the finite rate of increase (λ), extinction probability, time to extinction, or future population size or structure]. Most PVAs use matrix projection methods (Box 2).

I was able to find 95 plant PVAs in the ecological literature. The earliest plant PVA calculated λ for age-structured data derived from a Scots pine (*Pinus sylvestris*) forest⁵. The classic study of buttercups (*Ranunculus* spp.) by Sarukhán and Gadgil did a great deal to bring matrix methods to the attention of plant ecologists⁶. Some other notable plant PVAs are listed in Table 1. Increasing numbers of studies have been published over time, with the peak years (through 1998) being 1997 and 1998, each with 13 articles.

Unlike animal PVAs, most plant PVAs are based on stage- or size-classified matrices (Table 2). Some studies have contrasted projections based on populations classified by stage and by age, independently⁷. Recent analytical methods allow the estimation of age-based parameters from stage-based matrices⁸ (Box 3), which is likely to lead to more plant studies integrating stage and age approaches⁹. Simulations of stage-based populations can also be used to estimate age-related parameters, such as life span¹⁰.

Most plant PVAs have been of short duration, have been formed on a single species and have considered only a few populations (Table 2). The mean, median and modal length of a PVA is about four years (similar to typical dissertation and grant study periods); it is an open question whether such short periods of study can result in PVAs that genuinely represent a species' population dynamics¹¹. Most studies also consider just a few populations (mean 3.4, median 2.0 and mode 1.0), but because populations within species vary widely

This review of 95 plant population viability analyses (PVAs) reveals that most studies consider one species, only a few populations and are based on data collected for less than five years. Only five studies referred to themselves as PVAs. Plants offer numerous challenges, such as seed banks and periodic recruitment, but these can be answered with suitable data collection and modeling. New approaches, such as metapopulation models, inclusion of disturbance cycles, and integration of genetics and demography, are producing more realistic PVAs. Although exact solutions are fraught with limitations, plant PVAs can be useful in comparing management regimes, populations and microhabitats, and in using these results to guide conservation and management.

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in demographic parameters, studies based on only a few populations would seem incomplete at best. Demographic variation over time (environmental stochasticity) is only weakly correlated among populations^{12,13}, which argues that multiple populations need to be followed for several years.

Most assessments of plant PVAs have used deterministic approaches and have calculated λ , population size and population structure. Few have calculated a stochastic population growth rate^{14,15}. Many other deterministic parameters have been calculated, with elasticities¹⁶ (Box 1) among the most common. However, because elasticities within species vary across space and time^{12,17,18}, interpretations of elasticities need to be made with caution. In particular, elasticities of declining populations differ from those of increasing populations.

Stochastic modeling and other complex approaches have been less commonly used in plant PVAs (Table 2). Demographic stochasticity^{10,19} (Box 1) is not considered as great a threat to population viability as systematic factors (such as continuing habitat loss) or other stochastic factors. More commonly, environmental stochasticity or various types of disturbance or catastrophe have been considered. Of the 21 studies using stochastic modeling to predict extinction, 19 reported extinction probabilities; others reported times to extinction or both. The time periods used for projecting extinction risk vary from 25 to 1000 years (many authors used several different periods), with 50, 100 and 200 years being the most frequently used time periods; thus, comparisons of extinction risk are difficult. Few studies presented risk analyses with full distributions of times to extinction; these full-time distributions are recommended because they are less misleading than single results².

Challenges to plant PVAs

Many aspects of plant life history can present obstacles when obtaining data for PVAs. These include plant and seed dormancy, periodic recruitment and clonal growth.

Plant dormancy

Many plants exhibit prolonged dormancy, which presents a difficult challenge for plant population studies²⁰. In addition to the logistical challenge of keeping track of dormant individuals, only longer-term studies can be expected to provide reliable statistics on plant dormancy. Short-term studies are likely to inflate mortality estimates²⁰. An explicit treatment of plant dormancy in modeling requires

Box 1. An annotated glossary of plant PVA terms

Demographic stochasticity: variation in population dynamics owing to chance events affecting individuals¹; modeled by applying demographic rates to each individual or using a binomial distribution to introduce variation. Demographic stochasticity increases extinction risks only in small populations¹⁹.

Elasticities: proportional changes in finite rates of increase resulting from proportional changes in individual demographic parameters (matrix elements). Because elasticities sum to one, they can be used to compare various life histories. However, elasticities not only vary among species, but also among populations of a species and across time within individual populations^{17,18}.

Environmental stochasticity: variation in demographic parameters caused by environmental (*sensu lato*, including competitors, disease, etc.) variation affecting whole populations¹. Increasing environmental stochasticity increases extinction risk¹⁹. Catastrophes (disturbances) can be seen as particularly extreme, episodic or discrete types of environmental stochasticity.

Extinction probability: the proportion of simulations producing extinction (or quasi-extinction) of a population in a given time. Generally based on many (e.g. 1000) separate stochastic simulations using identical sets of starting conditions and sampling from the same range of demographic parameters.

Finite rate of increase (λ): exponential rate of population growth in a density-independent, deterministic environment. [This is also given as the natural log (ln) of r , the intrinsic rate of increase.] A λ of 1 projects a stable population; larger values represent growing populations; smaller values project declining populations. λ can be calculated as the dominant eigenvalue of a projection matrix or can be determined by simulation.

Genet: genetic individual or product of an independent colonization event (see ramet).

Megamatrix models: complex models where individual matrices describing the behavior of individual populations are linked into aggregate matrices that include transitions representing shifts among environmental states, successional stages, etc.^{12,32,33}.

Metapopulation: an assemblage of discrete local populations linked by movement of individuals among populations⁴⁴. Earlier, narrower definitions, defining metapopulations as characterized by recolonizations and extinctions, are now usually regarded as special cases. Metapopulation viability can be modeled using data on individual movements or using incidence function models³⁸.

Ramet: a unit of clonal or plant growth that is potentially capable of independent physiological existence. For many plants, ramets consist of a stem with associated roots and leaves. Ramets are a useful level for demographic study in plants. See also genet.

Seed bank: a reserve of viable, ungerminated seeds, usually in the soil⁴⁵. Persistent seed banks hold seeds dormant until the second (or later) germination season, and must be studied and modeled explicitly in most population viability analyses. Seed banks can buffer species with vulnerable above-ground stages from extinction.

Stage- or size-classified matrices and/or projections: summaries and model results based on populations with demographic parameters a function of stage (e.g. dormant seeds, seedlings, flowering plants) and/or size (Lefkovich matrix), as contrasted with age-based approaches (Leslie matrix). Stage classifications are usually more convenient for plants (Box 2).

Stochastic population growth rate: mean stochastic growth rate of all realizations of stochastic growth. Because ending population sizes are log-normally distributed, this stochastic population growth rate will be lower than the growth rate of the average projection matrix. Stochastic growth rates can be calculated numerically^{14,15}.

Time to extinction: median or mean number of years to extinction or quasi-extinction. Has a skewed distribution, thus cumulative probability of ending population sizes can be a less misleading result of population viability analyses².

classifying stage class(es) for dormant individuals, and careful data collection on individuals entering and leaving a dormant state. Dormant plants can be divided into classes based on their size when they were last seen²¹ or based on both pre-dormancy size and length of dormancy²².

Seed dormancy

Seed banks (Box 1) are a key phase of plant life histories: they can buffer environmental variation, reduce extinction risk²³ and conserve genetic variation. However, data on seed dormancy and seed banks are often fragmentary, even for species with many years of survival and growth data. Kalisz and McPeck created experimental seed banks to obtain two years of data on the annual blue-eyed Mary (*Collinsia verna*), then used simulations to examine what proportion of the demographically-favorable year would be required for long-term population viability²³. Such experiments are often missing from plant demography studies.

Periodic recruitment

Episodic seedling recruitment is characteristic of many species and habitats. Modeling seedling recruitment rates as constants, as implied by the calculation of finite rates of increase, does not capture this variation. Episodic seedling recruitment in royal catchfly (*Silene regia*) has been modeled by constructing matrices representing years with and without recruitment, calculating the proportion of years with recruitment for various management classes, and then modeling extinction probabilities²⁴. Fire management of *S. regia* populations promotes more frequent seedling recruitment and reduces extinction probabilities.

Clonal growth

Many perennial plants spread clonally, and consist of populations of both genets and ramets (Box 1). Ramet and genet dynamics differ greatly in the clonal woodland herb wild ginger (*Asarum canadense*)¹⁰. In late-successional woodlands, genets tend to increase in numbers even as ramet numbers decline, and genet and ramet minimum viable population (MVP) sizes differ widely. Although knowledge of both ramet and genet dynamics provides a more complete picture, data collection and modeling are usually most practical at the ramet level because genets cannot always be easily identified. Because new clonal ramets often have different demographic parameters than similar-sized plants derived from seedlings, separate stages are preferable in modeling ramet demography²¹.

New approaches and opportunities

Environmental stochasticity and matrix element correlation

Environmental stochasticity creates variation in demographic parameters over time and tends to decrease projected growth rates and increase extinction risk¹⁹. There are a myriad of ways to model environmental stochasticity. Stochastic analyses often assume (owing to lack of data) that elements within matrices have no correlation with each other, and that there is no autocorrelation over time. However, demographic parameters are often positively correlated across environments¹², thus creating more extreme year-to-year outcomes and increased extinction risks¹⁵. Many ecologists prefer to retain elements within the original matrices and select these matrices probabilistically over time to represent environmental stochasticity^{25,26}. This matrix selection preserves (or perhaps exaggerates) correlation structure and produces a more

conservative risk assessment than letting matrix elements vary independently²⁷ (see also Box 2).

Authors of future plant PVAs should collect data quantifying the correlation structures among matrix elements and among populations, because these affect extinction risks. In the absence of data, modeling the effects of correlation structure on extinction risk would help determine the most conservative risk assessments. Further long-term data sets need to be analysed for correlation structure so that modeling based on short-term data can be realistic.

Stochastic growth rates

Increasing attention has been paid to the calculation of the stochastic population growth rate (stochastic λ ; Box 1)^{14,15,28,29}. Stochastic λ s share an advantage with deterministic λ s: they are not tied to the particular time window (as are extinction probabilities) and thus can be compared across studies. Stochastic λ s provide a more conservative risk assessment than λ s estimated from mean matrices for species in fluctuating environments.

Modeling disturbance cycles

Disturbance is not only a factor that has important effects on the demography of plants, but also one that can often be manipulated to increase population growth rates and population sizes. For example, increased rates of canopy disturbance promoted population growth of the understory shrub spicebush (*Lindera benzoin*)³⁰. Population growth rates for an annual grass *Andropogon brevifolius* were fourfold higher in burned than in unburned savanna, particularly owing to higher fecundity in burned areas³¹.

Many plant species exist in environments that do not vary randomly, but instead vary cyclically. The effects of periodic disturbance and of subsequent recovery can be modeled by a combination of information about the disturbance cycle, the frequency and intensity of disturbance, and the demographic response to disturbance. These can be handled by a megamatrix approach (Box 1). Megamatrices have been used to show that open, post-hurricane environments supported the highest population growth rates for the tropical understory shrub marlberry (*Ardisia escallonioides*)³² and to model dynamics of the tropical forest gap specialist *Cecropia obtusifolia* in a shifting mosaic of canopy gaps in tropical rainforest³³. In the primrose *Primula vulgaris*, a forest herb, complex matrices were used to

Box 2. Example of projection matrix and demographic terms

Oostermeijer *et al.*¹⁸ collected demographic data on the rare iteroparous herb *Gentiana pneumonanthe* from ten sites for multiple years, generating a total of 35 matrices. Each matrix summarized transitions among five life history stages: seedlings, juveniles, vegetative adults, reproductive adults and dormant plants. Seeds were shown to be nondormant and not present at the time of the main census, thus they could be excluded from the stage model. Censuses in permanent plots with mapped plants provided much of the data needed to construct matrices. Fecundities were calculated as ratios of seedlings to reproductive adults in the year before. For species with seed dormancy, more involved measurements and experiments would be necessary to calculate fecundities.

An example of one matrix, combining information on one type of managed site (periodically sod-cut heath), is shown in the table below:

To	From				
	Seedling	Juvenile	Vegetative	Reproductive	Dormant
Seedling	–	–	–	0.443	–
Juvenile	0.267	–	–	0.165	–
Vegetative	0.167	0.675	0.553	0.251	0.379
Reproductive	–	0.123	0.172	0.657	0.159
Dormant	0.021	0.049	0.039	0.024	0.296

(Online: Table 1)

The two fecundity terms are shown in bold. Transitions with dashes are either impossible (structural zeros) or did not occur during the study (normal zeros). Each non-zero non-fecundity transition represents a proportion of plants moving from one stage to another in a year. For example, 67.5% of juvenile plants become vegetative, 12.3% become reproductive and 4.9% become dormant; approximately 15.3% of juvenile plants die (this number is not shown in the matrix). Each transition term has a calculated standard error (not shown).

The finite rate of increase (λ) can be calculated by formula or by simulation, and is 0.922 for the example shown, suggesting a population declining by about 8% per year if conditions remain the same. The transition contributing the most to the finite rate of increase, as measured by elasticities (Box 1), is stasis of reproductive plants (i.e. remaining reproductive, explaining 37% of the variation in the finite rate of increase).

Because conditions do not remain the same in sod-cut heathlands, or anywhere else, stochastic simulations offer more realistic projections and management guidelines. There are several ways to introduce stochasticity, including varying individual matrix elements and alternating matrices representing different years or conditions. Because matrix alternation preserves the correlation structure, it is probably more realistic. It also creates a more conservative risk assessment²⁷.

In the case of *G. pneumonanthe*, periodic sod-cutting of the heath creates more favorable conditions for population persistence than leaving meadows uncut. A realistic simulation, incorporating successional change in the heath with time since sod-cutting, and associated demographic changes summarized in different matrices, suggest that the optimal return interval for sod-cutting is about ten years, depending on initial population size³⁵.

examine the impact of increased forest disturbance rates on metapopulation growth rates³⁴. Simulations varying disturbance frequency and plant demography in relation to the time since the last disturbance, have been used to predict optimal sod-cutting intervals for the gentian *Gentiana pneumonanthe*^{18,35} and to predict optimal fire return intervals for the Proteaceous shrub *Banksia attenuata*³⁶.

Finally, population viability models for another Proteaceous shrub *B. cuneata* consider fire frequency effects, environmental stochasticity and potential inbreeding³⁷. The fire frequency that maximizes population size does not minimize extinction, because it exposes vulnerable seedlings to the risk of catastrophic mortality during droughts. Minimizing extinction and maximizing population size do not always require the same conditions.

Metapopulation dynamics and spatially explicit modeling

Metapopulation approaches (Box 1) might be particularly relevant to understanding persistence in plants because many plant species have patchy distributions and occur on specialized, identifiable sites that can be censused for occupancy. Some additional patchiness is created by disturbances and by disturbance-specialized or disturbance-avoiding species. The dispersal of many species is limited so that suitable patches can remain unoccupied. The concepts of minimum viable metapopulation and minimum available suitable habitat³⁸ are likely to be applicable to many plant species.

Table 1. Some notable plant PVA studies

Authors	Year	Significance of study ^a	Refs
J. Sarukhán and M. Gadgil	1974	Finite rates of increase (λ) for three species	6
P.A. Werner and H. Caswell	1977	Age versus stage; transient analyses	7
P. Bierzychudek	1982	Environmental stochasticity	25
P.L. Fiedler	1987	Four congeners	46
J.M. van Groenendael and P. Slim	1988	Extinction times	47
E.S. Menges	1990	Extinction probabilities, metapopulations	26
M.A. Burgman and B.B. Lamont	1992	Genetics and disturbance frequencies	37
M.E. Cochrane and S. Ellner	1992	Age-based statistics from stage-based data	8
S. Kalisz and M. McPeck	1992	Seed banks and extinction dynamics	23
O. Eriksson	1994	Ramet and genet demography	48
J.M. Bullock <i>et al.</i>	1994	Experimental grazing treatments	49
E.R. Alvarez-Buylla	1994	Density dependence and gap dynamics	33
J. Ehrlén	1995	Effects of herbivory	28
P. Nantel <i>et al.</i>	1996	Harvesting, minimum viable population	43
T. Valverde and J. Silvertown	1997	Metapopulation modeling	34
R.A. Bradstock <i>et al.</i>	1998	Spatially-explicit fire spread	41
K. Gross <i>et al.</i>	1998	Managing fire and trampling	29
J.B. Pascarella and C.C. Horvitz	1998	Megamatrix and patch dynamics	32
H. Damman and M.L. Cain	1998	Environmental and demographic stochasticity	10
N.J. Enright <i>et al.</i>	1998	Fire return intervals, serotiny, weather variation	36
E.S. Menges and R.W. Dolan	1998	Fire management, genetics, population size	24
J.G.B. Oostermeijer	1999	Genetics and demography, disturbance rates	35

^aDefinitions of terms are given in Box 1.

Data on species presence or absence in suitable habitat patches have been used to infer metapopulation dynamics in 80 species of Florida scrub plants. For 25 species, with occupancy related to patch size, isolation or fire regime, an incidence-based metapopulation model was used to infer colonization and extinction rates³⁹. This work suggests that, as patch size decreases, herbs are more sensitive than woody plants to increased extinction risks.

Table 2. Characteristics of plant PVAs (n=95)

Characteristic	Alternative	% of studies
Classification method	Stage or size	80
	Age	68
	(Stage or size) and age	4
	Other	8
Length of study	1–5 years	70
	6–10 years	27
	>10 years	3
Number of species	1	84
	>1	16
Number of populations	0–5	82
	6–10	9
	>10	8
Calculated parameters	Finite rate of increase (λ)	84
	Population size and/or structure	73
	Elasticities	45
Advanced modeling features	Environmental stochasticity	24
	Stochastic modeling of extinction	23
	Disturbance and/or catastrophe	16
	Density dependence	12
	Spatially explicit models	5
	Demographic stochasticity	3
	Genetics	3
Metapopulation modeling	3	

More explicitly, dynamic metapopulation models have been formulated for primrose by linking individual population demography with transition probabilities among canopy stages, and by estimating colonization and extinction rates³⁴. Colonization was not estimated directly, but was modeled as varying fractions of seeds being dispersed away from individual populations, combined with data on plant densities and fecundities. Both seed dispersal and forest disturbance rates increased metapopulation growth rates. Metapopulation approaches have great potential for plant studies, but direct estimates of colonization, extinction and dispersal will always be difficult. Even when dispersal and colonization data cannot be obtained directly, the persistence of metapopulations can be modeled with

and without the assumption of environmental heterogeneity among populations¹³.

Spatially explicit PVAs are useful to predict the importance of individual patches in a landscape⁴⁰ and to predict how species can be affected by anthropogenic changes in landscapes. Spatially explicit models have been used to explore fire effects on extinction of functional plant groups in Australian shrublands⁴¹. Model parameters included burn size, randomness of ignitions and fire frequency. Extinction risks for resprouters were unaffected by fire, but obligate seeders were threatened by large, random fires⁴¹.

Relating genetics and demography

Reed and others have lamented that few studies have integrated demography and genetics in PVAs (Ref. 42). However, Beissinger and Westphal have recommended limiting the mixing of genetic and demographic approaches because of the paucity of information on how genetic variation affects demographic rates². In any event, for plants there are few examples integrating genetics and demography. Inbreeding effects have been included with many other demographic and environmental factors in exploring viability in the Australian shrub *B. cuneata*³⁷ and in the gentian *G. pneumonanthe*³⁵ (Box 2).

Minimum viable populations

PVAs can be used to define, given an assumption of the maximum risk to be tolerated (e.g. less than 5% risk of extinction in 100 years), a MVP that will forestall extinction. Deterministic and stochastic analyses, which incorporated harvesting pressure on wild ginseng (*Panax quinquefolium*) and wild leek (*Allium tricoccum*) in Quebec, Canada, were used to formulate MVPs (Ref. 43). However, many authors are hesitant to calculate MVPs, perhaps because of the uncertainty of data and modeling assumptions that go into PVAs, or because of a fear of giving the impression of PVA superiority over more qualitative

Box 3. Linking age- and stage-based demography

The demography of most plants is dependent on size and stage, whereas age might be a poor predictor of survival, growth or fecundity. Although stage-based analyses can provide useful projections, age-based statistics, such as life span, could not be provided directly until Cochrane and Ellner⁸ provided equations and (more usefully for most) a computer program. Their approach was to decompose stage matrices into separate birth, survival and fission matrices, and derive formulae for such age-based parameters as age-based survivorship, mean age at maturity, stable age distribution and generation time. In addition, they derived time-related characteristics of stage-based demography, such as the mean age of residence of each stage class and the expected life span for individuals in a stage class. A recent study of the cushion plant *Silene acaulis* used these formulae to estimate that larger plants might exceed 300 years in age⁹.

approaches; that is the 'fallacy of illusory precision'⁴². However, a series of MVPs, given for alternative scenarios and assumptions, could be useful by providing targets for management and by focusing efforts on potentially viable populations.

Using comparative PVAs to assess management

Plant PVAs will continue the trend towards providing more detailed results under a range of scenarios and assumptions¹³. Beissinger and Westphal² recommend that PVAs examine relative, rather than absolute, rates of extinction. This is an especially useful approach when contrasting alternative management strategies. For example, in a PVA of royal catchfly, λ s and extinction probabilities were compared among three groups of populations with contrasting management regimes²⁴. Comparisons among species can also be helpful in broadening the ecological context of specific results and in allowing comparisons of relative rates of extinction.

Prospects

This review has documented many of the limitations of the data that underpin plant PVAs; specifically the short duration of most studies, the small number of populations monitored, and the inherent difficulties in generating numbers for difficult parts of the plant's life cycle, such as dormancy and the occurrence of seed banks. De-emphasizing the exact values of λ and of extinction probabilities avoids some of the problems of uncertainty in demographic parameters. They provide the basis to continue or to expand potentially useful management regimes, which should continue to be monitored to allow the feedback of data to improve and update PVAs.

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Biological consequences of global warming: is the signal already

The prospect that increases in atmospheric concentrations of greenhouse gases will have measurable effects on the earth's climate over the next few decades has attracted a vast research effort. Climatologists have faced two main challenges. The first has been to distinguish the signal of human-induced climate change from the noise of interannual and decadal natural variability. The second has been to predict probable climate scenarios for the future. Climate monitoring over the past century and long-term reconstructions of climate over the past millennium indicate that the earth is indeed warming up (Fig. 1)¹. Moreover, the recent patterns of warming and of changes in precipitation are generally consistent with the patterns predicted by global circulation models (Box 1)^{1–7}. Physical features of the earth's surface, such as sea ice and glaciers, also appear to be responding in a predictable way to the warming trends (Box 2)^{8–11}.

For ecologists, physiologists and land managers, the challenge is to predict the effects of human-induced climate and atmospheric change on species and on

Increasing greenhouse gas concentrations are expected to have significant impacts on the world's climate on a timescale of decades to centuries. Evidence from long-term monitoring studies is now accumulating and suggests that the climate of the past few decades is anomalous compared with past climate variation, and that recent climatic and atmospheric trends are already affecting species physiology, distribution and phenology.

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communities. These predictions can be broadly summarized into four categories (Fig. 2):

(1) Effects on physiology: changes in atmospheric CO₂ concentration, temperature or precipitation will directly affect metabolic and developmental rates in many animals, and processes such as photosynthesis, respiration, growth and tissue composition in plants.

(2) Effects on distributions: a 3°C change in mean annual temperature corresponds to a shift in isotherms of approximately 300–400 km in latitude (in the temperate zone) or 500 m in elevation. Therefore, species are expected to move upwards in

elevation or towards the poles in latitude in response to shifting climate zones.

(3) Effects on phenology: life cycle events triggered by environmental cues such as degree days might be altered, leading to decoupling of phenological relationships between species.

(4) Adaptation: species with short generation times and rapid population growth rates might undergo microevolutionary change *in situ*.