

10 Considering Interactions: Incorporating Biotic Interactions into Viability Assessment

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10.1 Introduction

Most analyses of population viability focus on changes in numbers of the focal species independent of other members of their community or any other biotic interactions. It is difficult to incorporate all relevant factors into a viability analysis, but leaving out biotic interactions may be a critical flaw in some analyses. While single-species population viability analyses (PVAs) implicitly incorporate the effect of species interactions on population growth rate parameters (i.e., vital rates), models that explicitly consider changes in species dynamics as ecological conditions change may be needed. Unfortunately, these models will significantly increase data requirements. Because robust data sets are notoriously difficult to acquire even for single-species PVAs, it is important to evaluate the relative importance of species interactions before considering development of a PVA model that incorporates them explicitly. In this chapter, we discuss the various kinds of interactions that plants are involved in, evaluate when species interactions are likely to matter, consider strategies for deciding when to incorporate these interactions into PVA models, and discuss relevant modeling approaches.

10.2 What Kinds of Interactions Are Plants Involved in?

The major categories of species interactions that plants are involved in include typically negative interactions such as competition, parasitism, seed predation, and herbivory – and typically positive interactions such as pollination, seed dispersal, protection (e.g., ant guards), and nutrient exchange (e.g., nitrogen-fixing bacteria and mycorrhizal fungi; Boucher et al. 1982).

Although we can define major categories of interactions, the outcome of species interactions is often dynamic (Thompson 1988). Thus, while negative and positive effects may seem like clear-cut distinctions, interactions are not always easily categorized (Thompson 1988). For example, the interaction between *Lasius niger* ants and *Aphis fabae* aphids can range from mutualism to predation depending on the abundance of alternative sugar sources (Offenberg 2001). Similarly, relationships between plants and mycorrhizal fungi (Kretzer et al. 2000) can range from mutualism to parasitism due to differential costs and benefits (Johnson et al. 1997; Lapointe and Molard 1997).

Although usually a strictly negative interaction, herbivory can also have positive effects on plant growth (e.g., Mattson and Addy 1975). For example, Simberloff et al. (1978) reported that branching induced in aerial roots by root-boring isopods and insects might increase the stability of mangrove plants and their resistance to being pushed over. Such observations have created interest in discovering examples of overcompensation by plants in response to herbivory, which may increase their fitness (e.g., Inouye 1982; Paige and Whitham 1987; see also the review of ecology of tolerance to consumer damage by Stowe et al. 2000). Another plant-related example of an interaction with a range of outcomes from positive to negative is that between seed predation and successful seed dispersal by the same seed predator (e.g., Levey and Byrne 1993; Norconk 1998). Unfortunately, our understanding of how these effects balance out is limited, because most attention has been given to situations in which animals act primarily as only predator or disperser. An analogous situation occurs in brood-site pollination mutualisms, such as between yuccas and yucca moths, in which effects can span a continuum from positive to negative depending on the fraction of seeds consumed (Addicott 1986). Other seemingly negative events such as nectar robbing can also have a range of effects, because many “robbers” may also act as pollinators (Maloof and Inouye 2000). These studies emphasize that the distinction between positive and negative interactions is not always obvious or even static.

Where variation in the outcome of species interactions is context dependent, the term “conditionality” has been used (Cushman and Addicott 1991; Bronstein 1994). Conditionality in species interactions can qualitatively change the predictions of PVAs if the ecological context is changing. Recent research dealing with species interactions in plants emphasizes this spatiotemporal variability. For example, plant herbivory can induce plant defenses, which in turn influence the population dynamics of herbivores (Karban and Myers 1989; Karban and Kuc 1999; Underwood 1999). In cotton, herbivory can induce production of extrafloral nectar that in turn attracts a defensive ant guard (Wackers and Wunderlin 1999). In addition to the better-known induction of chemical defenses, morphological defenses like spines can also be induced (Young and Okello 1998), and although best known for herbaceous species, induced defenses have also been reported in trees (Wold

and Marquis 1997). These plant-herbivore relationships and their effects on plant fitness can be quite intricate, involving multiple herbivore species (e.g., Agrawal 1999), temporal variation (Underwood 1998), and even transgenerational effects (Agrawal and Laforsch 1999). Such intricacies suggest that it may be complicated to incorporate the effects of herbivory – and species interactions in general – into PVA models.

On the other hand, there is no doubt that species interactions can potentially influence both population and community dynamics. For example, the effects of mycorrhizal mutualisms can influence tri-trophic interactions with herbivores (Borowicz 1997; Gange and Nice 1997; Gehring et al. 1997), and recent work has implicated mycorrhizal fungi as a potentially important agent of community structure by creating linkages among different plant species (Zelmer and Currah 1995). Thus, an important preliminary question becomes whether including species interactions in PVAs is likely to influence estimates of extinction risk or the development of management strategies.

10.3 When Are Species Interactions Likely to Matter?

Probably 90 % of the estimated 250,000 species of flowering plants (Heywood 1993) require the services of pollinators for sexual reproduction (Buchmann and Nabhan 1996), and as many as 300,000 species of animals visit flowers as pollinators (Nabhan and Buchmann 1997). Multiple species of pollinators may visit a single plant species, with widely varying degrees of pollinating effectiveness (e.g., Kearns and Inouye 1994). The details of pollination relationships are well known for only a small number of plants, and the threats facing many plant-pollinator relationships (Kearns et al. 1998; Chaps. 2, 3, this Vol.) suggest that these relationships are changing and that we may have a limited amount of time to learn about some of them. Although plant-pollinator interactions can involve many physiological, genetic, and behavioral factors for both pollinator and plant, these intricacies can sometimes be ignored in PVAs as long as the bottom line – successful production of seeds – is known (Chap. 3, this Vol.).

Ecologists distinguish between realized and intrinsic growth rates. Whereas the intrinsic growth rate represents the theoretical rate of increase for a population as it approaches zero density, the realized growth rate represents the observed rate of increase for a given population. Similarly, all realized parameters are the value of their corresponding intrinsic parameters after modification by environmental factors– including modification by species interactions. For example, estimates of seed production will incorporate the degree of pre-dispersal seed predation. Most PVAs implicitly include the effects of species interactions in realized parameter estimates of vital rates, and for some systems such inclusion is sufficient. For example,

community effects (e.g., competition among plant species, Chap. 3, this Vol.) may be adequately accounted for by the ordinary population growth rate parameters used in a PVA. However, such will *not* be the case if the identities and/or distributions of neighboring plants – or of other interacting organisms – are themselves changing significantly. In this latter case, it may be necessary to explicitly incorporate these changes in the PVA to produce a model with predictive value.

In general, we suggest that incorporating species interactions into PVAs will be especially important if: the population dynamics of the focal plant species are strongly influenced by the species interaction; the outcome of the species interaction is strongly dependent on ecological conditions; and the ecological conditions are likely to change. We begin by addressing the following conditions: (1) strong community effects; (2) density-dependent species interactions, including the Allee effect; and (3) critical interactions that might break down.

10.3.1 Community Effects

If a focal plant species is strongly affected by its neighborhood composition – and neighborhood composition is changing – any PVA of the focal species will be unreliable unless neighborhood effects and changes in neighborhood are taken into account. One obvious example of this is in plant communities undergoing succession, where failure to model the effects of vegetative succession will result in unreliable PVAs for affected species (e.g., Oostermeijer 2000).

In many cases it may be necessary to know the focal species' competitive position vis-à-vis prevalent neighboring heterospecifics – and the distribution of those heterospecifics – to predict the focal species' likelihood of persistence. If large portions of the habitat suitable for and accessible to the focal species are occupied by dominant competitors, or populations are threatened by invasive species, failure to recognize this can result in unrealistic predictions. Interestingly, although the invasion potential of exotic plants has been modeled extensively (Reeves and Usher 1989; Goodwin et al. 1999; Parker 2000; Zalba et al. 2000), and a few studies have quantified the impact of exotic species on the population dynamics of threatened plants (e.g., Lesica and Shelly 1996; Carlsen et al. 2000; Chaps. 2, 3, this Vol.), we are unaware of any studies that have incorporated competition from exotics into PVAs.

The surrounding plant community may also affect plant species persistence in a number of less obvious ways, by affecting interactions between the focal species and its herbivores, pollinators, seed predators, and seed dispersers. For example, even though fragmentation may result in lower numbers of a focal frugivore-dependent plant species, the presence of neighboring fruiting plants may enable the rarer focal species to still receive regular

visits (Whelan et al. 1998; see also Sect. 10.3.2). Similarly, structural or chemical properties of neighboring heterospecifics may make it easier or more difficult for interacting species to find the focal species, or may affect the survivorship or behavior of species interacting with the focal species. Such effects have been reported with neighboring heterospecifics impacting focal plant species by decreasing herbivory (Holmes and Jepson-Innes 1989; Ham-bäck et al. 2000; Chap. 3, this Vol.), increasing herbivory (Karban 1997; White and Whitham 2000), and increasing pollination (Lavery 1992). Seed predation can also be affected by the identity of neighboring plants and the interactions in which those plants are involved. For example, rodent seed predators have shown neighborhood-dependent seed preferences (Thompson 1985), as have granivorous birds (Willson and Harmeson 1973). Further, primates may serve as either seed predators or dispersers depending on the abundance of fruit (Gautier-Hion et al. 1993; Kaplan 1998).

In another example of the effects of plant community on species interactions, infestation by a shared pre-dispersal dipteran seed predator has been found to increase in one plant species with proximity to a heterospecific ant-defended plant. While prior research showed that seed predation on the montane sunflower *Helianthella quinquenervis* was decreased for focal plants by the activities of its ant partners (Inouye and Taylor 1979), recent research suggests that this displacement of flies causes them to oviposit in nearby non-ant-tended host plants. As a result, individuals of one alternate host plant species experienced a nine-fold increase in fly infestation rates when growing near ant-tended plants compared to those growing near plants from which ants had been excluded (Leigh, unpubl. data). These higher rates of fly infestation correlate with increased amounts of seed predation, and suggest that the identities and species interactions of heterospecific neighbors may have a significant effect on focal plants.

10.3.2 Density-Dependent Species Interactions

Incorporating species interactions such as competition and mutualism into PVA models increases in importance where the per-capita effect of the interaction depends on the density of either species. Density dependence in species interactions could affect estimates of population growth rate parameters in a variety of ways [e.g., pollination rates are a combined function of the density and effectiveness of pollinators as plant density changes (Jennersten and Nilsson 1993)], and ignoring this density dependence could significantly bias estimates of mean vital rates and their variance (Chap. 7, this Vol.).

In general, the influence of density-dependent interactions on estimates of mean vital rates will depend on the functional form of the interaction – that is, the per-capita effect of species A on focal plant species B as a function of B's density (Sih and Baltus 1987; Morales 2000; Holland and DeAngelis 2001). For

example, where interactions are characterized by a monotonically saturating curve (type II, Fig. 10.1), the mean interaction effect will increase relative to a model that assumes density-independent interaction (Fig. 10.1 and legend). Where interactions are characterized by an S-shaped curve (type III, Fig. 10.1), the direction of change in mean interaction effect will depend on the density of the focal population relative to the range of the functional form (Fig. 10.1 and legend). Both types II and III functional forms are common in species interactions, including examples from pollination and seed dispersal

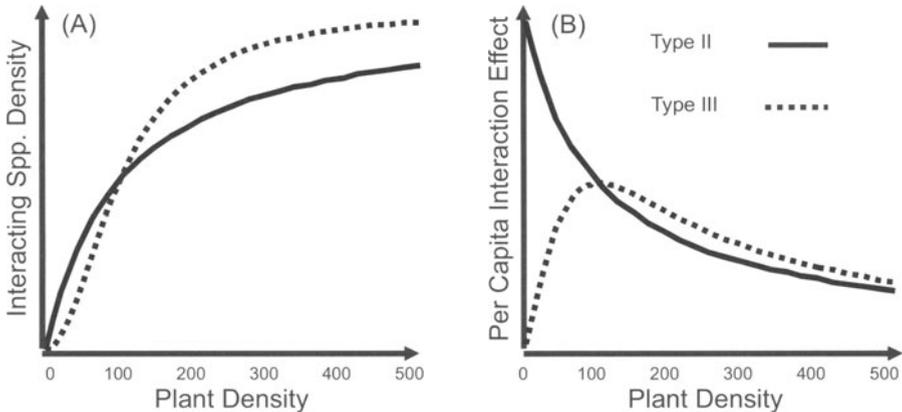


Fig. 10.1. Recruitment/functional response (A) and per-capita benefit to plants (B) as a function of plant density (P) for type II and III species “interactors” (e.g., seed predators, pollinators):

$$\frac{\alpha_i P}{P + \beta} \text{ Type II}$$

$$\frac{\alpha_i P^2}{P^2 + \beta^2} \text{ Type III}$$

where α_i is the interaction coefficient and β is the density of plants at which the effect of interacting is one-half the maximum (i.e., the half-saturation constant). The maximum per-capita interaction effect is at low or intermediate plant densities for a type II or III response, respectively. Note that small differences in the total density of interacting species generate large differences in patterns of per-capita benefit ($\alpha=1$, $\beta=100$ in the example above). Because a type II response is a decelerating function of plant density, the mean interaction effect is greater than the interaction effect at the mean plant density (assuming symmetric variation around the mean plant density). In other words, at any point along the type II curve in B (call this point the mean interaction effect), reducing plant density by some amount will cause a greater change in the interaction effect than augmenting plant density by the same amount. For a type III response, the change in mean interaction effect will depend on whether plant density is at the accelerating or decelerating portion of the response curve (i.e., in A)

systems (Howe and Kerckove 1979; Sih and Baltus 1987; Sargent 1990), although other functional forms are possible.

A special case of density dependence is the Allee effect, defined as a decrease in growth rate at low densities (i.e., positive density dependence). For plant species, Allee effects can result from species interactions in at least two ways. First, the response of pollinators (or other mutualists) to low plant densities can result in declines or even complete losses of seed production (Lamont et al. 1993; Widén 1993; Groom 1998; Cunningham 2000a, b; Hackney and McGraw 2001). In particular, where the effectiveness or density of mutualists (i.e., pollinators, seed dispersers, or ant defenders) is an S-shaped function of plant population density (Fig. 10.1), plant populations will show an Allee effect in the vital rates affected by those mutualists (Morales 2000). Whether this translates into an Allee effect in overall growth rate depends on the relative importance of the mutualism to the population dynamics of the focal plant population (Stephens et al. 1999; Chaps. 2, 3, this Vol.). Accordingly, a decrease in mutualist visitation rate or effectiveness in fragmented host populations is increasingly cited as a possible mechanism that may contribute to the decline of these populations (Rathcke and Jules 1993; Aizen and Feinsinger 1994a; Kunin and Gaston 1997; Groom 1998; Cunningham 2000b). For example, Sargent (1990) demonstrated that the amount of fruit around a fruiting plant affects fruit removal, such that fragmentation could depress seed dispersal rates. Unfortunately, while empirical support is increasing for the hypothesis that habitat fragmentation may disrupt host-visitor mutualisms (Aizen and Feinsinger 1994b; Groom 1998; Steffan-Dewenter and Tschardt 1999; Cunningham 2000b), the impact of this disruption on the persistence of host plant populations is largely unknown.

Allee effects will also be seen in populations of plant species that support and require the services of obligate mutualists. A consistent prediction arising from models of obligate-obligate mutualism is the existence of a threshold density (defined as the density of species A required to offset the extinction rate of species B), below which species will show a deterministic decline to extinction (Wolin 1985). For obligate plant species that interact with facultative mutualists and have a monotonically saturating benefit function (e.g., type II), there may or may not be a threshold density, depending on the values of the parameters. On the other hand, if the benefit function is S-shaped (e.g., type III), there will always be a threshold density for biologically reasonable parameter values (Morales 1999). This results in part because a threshold density of mutualists is required to offset the extinction rate of plants; however, where visitors show an S-shaped recruitment response, a threshold density of plants is also required to attract this threshold density of mutualists (Fig. 10.2). A potential example of this was found in Groom's study of the annual herb *Clarkia concinna* (Groom 1998), in which she documented complete reproductive failure of small and isolated populations of the herb due to their inability to attract pollinators.

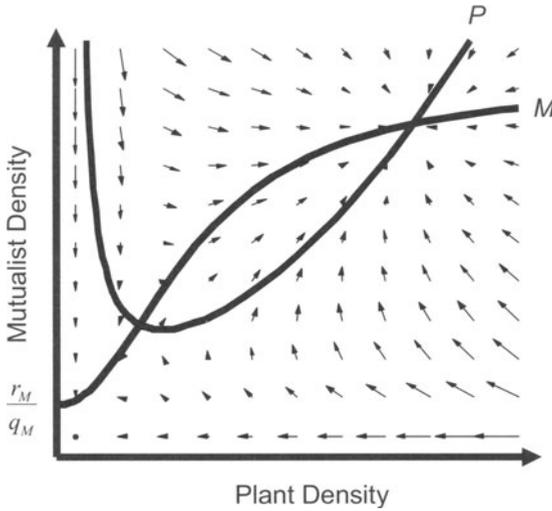


Fig. 10.2. Phase-plane graph of obligate-facultative mutualism with a type III benefit response, where plants (P) are obligate and mutualists (M) are facultative. Model equations are:

$$\frac{dP}{dt} = r_P P - q_P P^2 + \frac{\alpha_P P^2 M}{P^2 + \beta^2} \quad \text{Plant}$$

$$\frac{dM}{dt} = r_M M - q_M M^2 + \frac{\alpha_M P^2 M}{P^2 + \beta^2} \quad \text{Visitor}$$

where r is the intrinsic growth rate in the absence of the mutualist, and q is the slope of the growth rate as density increases (α and β are defined in the legend for Fig. 10.1). Because the benefit function has an inflection point at the half-saturation constant β , the host isocline curves upwards at this host density. Thus, there is always a low-density unstable equilibrium if a biologically reasonable solution to these equations exists (arrows indicate the population growth vectors for a given density combination)

10.3.3 Critical Interactions and Feedback Dynamics

Even where the per-capita effect of species interactions is density-independent, the *total* interaction effect could change if the density of either species changes. For generalist species, changes in interaction effect will be buffered to the extent that alternate species compensate for changes in the densities of each other. For example, reproductive success of *Dinizia excelsa* (Mimosaceae) in Amazonian forest fragments is maintained by introduced Africanized honeybees in the absence of its native pollinators (Dick 2001). On the other hand, plants that are involved in highly-specific, obligate interactions will be sensitive to changes in the density of their partner (Aizen and Feinsinger 1994a; Kearns and Inouye 1997; Chap. 3, this Vol.). For example, fig trees

depend exclusively on highly species-specific fig wasps for pollination, while fig wasps require figs for brood development (Janzen 1979). Because fig wasps are short-lived, they require continuous production of figs to maintain their populations. Recent droughts in Borneo associated with El Niño resulted in the almost complete absence of flowering fig trees from January to March 1998, leading to the local extinction of fig wasps associated with eight species of dioecious fig trees. As of April 1999 – over 1 year after the drought – fig wasps still had not recolonized four species of fig trees. Given the high level of endemism in Borneo and the species-specific nature of fig pollination systems, these fig wasp extinctions may ultimately result in the extinction of their associated fig trees (Harrison 2000).

For seed dispersal, the importance of feedback dynamics on plant population viability seems to exist primarily at the guild level (Fleming 1991). Except for a few examples, like phainopepla (*Phainopepla nitens*) and mistletoe (*Phoradendron californicum*) (e.g., Walsburg 1975; Larson 1996), most animal-dispersed plants rely on a variety of species for dispersal, although the relative efficacy of the various partners is rarely known (Livingston 1972; Howe and Primack 1975; Herrera and Jordano 1981; Murray 1998). Given this pattern of generalization, it may not be necessary to model separately each of the species involved in dispersal of a particular plant (an exception to this may be differences in seed dispersal agents that swallow seeds and then defecate them; see Traveset et al. 2001). On the other hand, it *will* be important to consider how disperser services change at the guild level. For example, habitat fragmentation may alter overall rates of fruit removal (see Sect. 10.3.2). Similarly, invasive species may change dispersal effectiveness by altering community composition (see Sect. 10.3.1). In the extremely diverse South African fynbos, up to 30 % of plants rely on ants for seed dispersal – a dispersal system known as myrmecochory. Ant dispersal is essential to these plants because they protect the seeds from rodent seed predators and fire. The recent invasion by Argentine ants (*Linepithema humile*) in these areas has displaced native ant species that preferentially disperse large-seeded plants, which may be causing a shift in plant composition away from these large-seeded plants following fire disturbances (Christian 2001).

10.4 Strategies for Evaluating the Importance of Species Interactions

In the sections above, we outlined characteristics of species interactions that suggest those interactions will be important when modeling PVAs. Below, we present approaches to evaluating the importance of species interactions for specific PVAs.

Although it might seem as though seed production, for example, would be a crucial aspect of plant population biology to model, there have been few

experimental studies comparing seed input with seedling establishment or other stages of the life cycle to determine effects on plant population size and structure (however, see Louda and Potvin 1995; Ackerman et al. 1996; Maron and Simms 1997). Seed predation can certainly be substantial, as evidenced by reported predation levels of 60 % (Inouye and Taylor 1979), 80 % (Snow and Snow 1986), and as high as 100 % of total seed production (Crawley 1992, and references therein). However, simply measuring the percentage of seeds consumed by seed predators may not be relevant to predictions of extinction risk, because recruitment may not be affected by seed predation (e.g., Sousa and Mitchell 1999; Alcantara et al. 2000). Rather, populations of some species may be limited by suitable microsites for seedling establishment (Turnbull et al. 2000), or may be able to offset seed predation, at least temporarily, by relying on seed banks for recruitment (Crawley 1992).

One approach to evaluating the importance of seed predation is through a series of experiments designed to assess the effect of seed predators relative to autecological factors (Schemske et al. 1994). Consideration of spatiotemporal effects will also be important, because different seed predators show different patterns of abundance and may handle food items in different ways (Holthuijzen et al. 1993; Diaz et al. 1999). For example, migratory granivorous birds may only have brief access to a plant population's seeds in the fall (Diaz et al. 1999); rodents, on the other hand, may exert more constant pressure, with a high amount of annual variation due to population cycles. Furthermore, different predators may search for food items in different microhabitats, and some seed predators may act as seed dispersers if they cache seeds and fail to recover them (Crawley 1992; Diaz et al. 1999).

The dispersal shadow (where the majority of seeds land) is also an important element to consider for at least two reasons. First, some studies have shown that distance from the parent plant or a conspecific adult may be an important variable affecting seed predation pressure (Janzen et al. 1976; Augspurger 1984; Holthuijzen et al. 1993; Terborgh et al. 1993). Second, microhabitats may differ significantly in their rates of seed mortality (Schupp et al. 1989; Terborgh et al. 1993; Diaz et al. 1999; however, see Whelan and Willson 1991). Optimally, one would measure how far seeds travel from the parent plant and how many seeds fall into different microhabitats (e.g., gap, forest interior, edge) when calculating dispersal success.

Finally, multiyear investigations are preferable, because the effects of seed predators vary annually (Schupp 1990; Whelan and Willson 1991). The need for multi-year investigations is even greater with herbaceous perennials, which may produce highly variable numbers of seeds each year (Crawley 1992). Similarly, multiyear investigations are essential for masting plants, since masting may affect the degree of seed predation during years of extensive fruit production (Curran and Leighton 2000; Kelly et al. 2000; see also Sect. 10.3.2).

10.4.1 Evaluating the Importance of Species Interactions: Matrix Modeling Approaches

A complementary approach for evaluating the importance of species interactions is based on matrix models. This is illustrated by the example of seed dispersal of wild ginger (*Asarum canadense*). Like many spring-flowering herbs in eastern North America, wild ginger is a myrmecochore, i.e., its seeds are dispersed by ants (Beattie 1985). The interaction between ants and wild ginger satisfies many of the properties outlined in the opening of this chapter. First, seed dispersal of wild ginger by ants increases as its relative and absolute density decreases (Smith et al. 1989; i.e., significant density dependence). Second, as has been shown in an ecologically similar system of myrmecochory (Morales and Heithaus 1998), the food reward to ants from wild ginger (elaiosomes) may increase the output of queen ants (i.e., positive feedback on ant populations). Finally, habitat fragmentation has been shown to decrease significantly the density of those ant species that are the most effective seed dispersers (Pudlo et al. 1980: i.e., significant community effects).

Even though the properties outlined above are satisfied, it may not be necessary to explicitly model this species interaction in a PVA. Development of matrix models followed by elasticity or sensitivity analysis can provide insight into the importance of species interactions to the persistence of a given population by examining the relative contributions of stage-specific transitions to overall growth rate (Caswell 2000; Chap. 6, this Vol.). For example, ants significantly benefit wild ginger primarily by reducing post-dispersal seed predation by mice (Heithaus 1981). Using elasticity analysis, Damman and Cain (1998) showed that seed germination success has relatively little impact on the population dynamics of this species – a result that is supported by simulation models of the same system (Heithaus 1986). These results suggest that even if ants were included in a dynamic model with wild ginger, predictions of population persistence would remain relatively unchanged.

Within a matrix modeling framework, life table response experiments (LTREs) provide the best approach to assess the relative importance of species interactions (Caswell 2000). For example, one could manipulate seed dispersal by ants to evaluate its effect on stage-specific vital rates. LTREs are important because the stage-specific effect of species interactions must be well established for elasticity analysis to identify accurately the relative importance of species interactions.

LTREs that have examined the stage-specific contribution of ants for other species of myrmecochorous plants have found that ants can increase seedling survivorship by dispersing seeds to suitable microsites (Hanzawa et al. 1988). In the case of wild ginger, there is no obvious indication of microsite enhancement (Heithaus 1986), although this has not been tested experimentally. How-

ever, because elasticity analysis identified seedling limitation as an important predictor for the long-term persistence of wild ginger (Damman and Cain 1998), future studies should examine the role of ants in seedling performance for this species. This example illustrates the utility of matrix modeling approaches combined with sensitivity analysis to identify the potential importance of species interactions, and in focusing future research on stage-specific effects of species interactions.

The use of matrix modeling approaches to investigate the effect of species interactions on plant population viability can also include human impacts such as harvesting or trampling (Chap. 6, this Vol.). For example, Nantel et al. (1996) used stochastic matrix projection models (see below) to evaluate the impact of various harvesting regimes on the population persistence of American ginseng (*Panax quinquefolius*) and wild leek (*Allium tricoccum*). This approach could be extended to species interactions more broadly.

10.5 Modeling Species Interactions in PVAs

Much of the information in this chapter emphasizes the variable or conditional nature of species interactions. Nevertheless, this variation presents a larger problem to understanding the effects of species interactions on plants than it does to modeling those effects. One approach to handling conditionality is to have multiple transition matrices, each reflecting a different set of conditions, or by using Markov chain approaches (Caswell 2000; Chaps. 6, Chap. 11, this Vol.). Stochasticity can be included by using bootstrap approaches or by sampling parameter estimates from a probability distribution (Caswell 2000; Chaps. 6, 11, this Vol.). For dynamic models (see below), stochastic and conditional variation can be explicitly modeled by sampling parameters from an underlying process or probability distribution (Hilborn and Mangel 1997).

Although matrix modeling approaches provide valuable insight into the influence of species interactions for the persistence of plant populations in many cases, these approaches do not come without limitations. In particular, matrix modeling approaches analyze the *current* properties of a given population (Caswell 2000). Where state variables such as population size are likely to change significantly, these analyses may no longer apply. In addition to quantitative changes, qualitative differences may also arise, especially if interactions are strongly density-dependent or where obligate interactions are involved (see above). For example, wild ginger reproduces both sexually and vegetatively, so loss of its seed disperser is not necessarily catastrophic, at least in the short term. In contrast, fig trees depend exclusively on species-specific fig wasps for their pollination. Models of obligate mutualism predict a threshold density below which populations go extinct, and for these systems it will

be necessary at a minimum to evaluate the risk of partner loss. In general, matrix modeling approaches will not work well where the effect of species interactions is likely to strongly influence the dynamics of both species.

One approach to modeling the persistence of strongly interacting populations is to consider the interaction while ignoring internal dynamics. An example of this can be found in two-species metapopulation models, used to examine minimum viable patch densities (Nee et al. 1996). Although these models are probably not useful for PVA per se, these analyses have generated useful predictions. For example, metapopulation models of obligate mutualists predict a threshold density of patches below which the metapopulation will go extinct (Nee et al. 1996). Interestingly, this prediction is supported by phenology-based models developed for the interaction between figs and fig wasps (Bronstein et al. 1990; Anstett et al. 1995, 1997).

In general, monoecious fig trees show within-tree synchrony and between-tree asynchrony in flowering. This phenological pattern maximizes outcrossing and increases the likelihood that brood-site resources are available to fig wasps throughout the year (Fig. 10.3, and discussion above – Sect. 10.3.3). However, as the number of fig trees decreases, the probability of a temporal

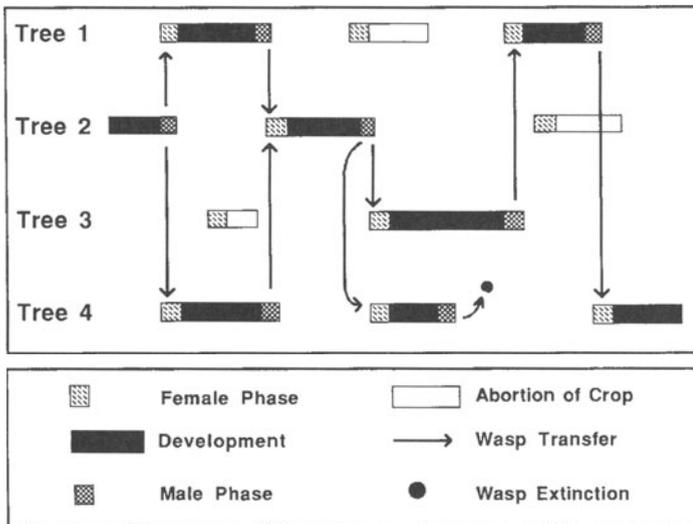


Fig. 10.3. Phenology of flowering and pollination for fig trees and fig wasps. Female wasps oviposit in figs during female-flowering phase. Wasp broods emerge, mate within figs, and female wasps exit after collecting pollen during the fig’s male-flowering phase. For fig trees that are in female-flowering phase during periods when no adult wasps are available, fruit crops are aborted (e.g., tree 3). If female wasps do not find trees in female-flowering phase, that brood goes extinct (e.g., tree 1). In this example, the population of wasps persists through the sequence 4→2→5→2→3. A temporal break in this sequence would result in total wasp extinction, followed by local extinction of the fig tree population in the absence of re-colonization by wasps. (Bronstein et al. 1990)

gap in flowering increases – which can cause a local extinction of fig wasps if the temporal gap is longer than the short life span of ovipositing fig wasps (Bronstein et al. 1990).

Several models have been developed that predict the critical or minimum viable population size of fig trees required to sustain a local population of fig wasps (Bronstein et al. 1990; Anstett et al. 1995, 1997). These analyses are based on the density of trees necessary to produce continuously overlapping periods of wasp emergence and receptive figs. Parameterized solely from observed phenology, these models generate estimates for the minimum population density of fig trees required for the long-term persistence of both fig tree and fig-wasp populations. Even though these models do not incorporate any information on the population dynamics of figs or fig wasps (e.g., the models assume 100% colonization success), such simplifications may produce fairly accurate predictions. In particular, leaving out the population dynamics of fig wasps from these models is probably appropriate, since the population dynamics of fig wasps operate on a time scale that is orders of magnitude faster than the population dynamics of fig trees. Consistent with this assumption, recent work has documented extreme resilience following disturbance for the interaction between figs and fig wasps in southern Florida (Bronstein and Hossaert-McKey 1995).

On the other hand, if species interactions are likely to affect the population dynamics of both populations, more complicated models will be needed. While we are unaware of any PVA models that incorporate dynamic species interactions for plant focal populations, analogous approaches are available for animal systems. For example, Hochberg et al. (1992, 1994) have examined the persistence of big blue butterflies (*Maculinea arion*) as a function of their interaction with host plants and ants (on which the larvae sequentially feed). Unfortunately, there are no available computer programs that allow researchers to model these systems; rather, individualized models must be developed on a case-by-case basis. Given the complexity required for dynamic interaction models, theoretical studies that consider the importance of species interactions in PVA are needed. For example, empirical and theoretical work suggests that mutualisms characterized by a type III benefit function merit special consideration, because these systems are likely to show Allee effects and associated increased risks of extinction (see discussion of Allee effects, Sect. 10.3.2).

10.5.1 Genetic Consequences of Species Interactions

So far, we have only considered the effect of species interactions on plant population dynamics. However, pollination and seed dispersal interactions also may have important consequences for the *genetic* structure of plant populations (Young 1996; however, see Holsinger and Gottlieb 1991; Chaps. 2, 3, this

Vol.). Currently available PVA packages can incorporate inbreeding as a function of population size for animal systems, and analogous approaches are possible for plant systems – but unlike animals, there is no simple relationship between inbreeding and population size in plants. In pollination systems, the degree of self-pollination (including geitonogamy) will vary as a function of pollinator behavior, pollen carryover (the pattern of self vs. outcross pollen deposition), and breeding system (Snow et al. 1996). Furthermore, pollinator communities may vary temporally, such that there may be no consistent relationship between plant density and inbreeding even for a single plant population. Finally, the consequences of inbreeding are likely to be extremely variable among plant species due to inherent differences in breeding systems (Chap. 3, this Vol.). For example, as plant population density declines, self-incompatible species may experience reduced seed-set, while most obligately selfing species will remain genetically unaffected.

Currently, few PVA models have explicitly considered the genetic consequences of interactions with pollinators or seed dispersers on the persistence of plant populations. One exception is a PVA of *Gentiana pneumonanthe* (Gentianaceae) (Oostermeijer 2000). Oostermeijer used a stochastic matrix modeling approach to examine the effects of ecological and genetic factors on the viability of restored *G. pneumonanthe* populations in “late” successional stages. Small populations of *G. pneumonanthe* experience increased selfing (and thus inbreeding depression) due to a decrease in insect pollination, and adding inbreeding depression to the PVA significantly decreased the predicted time to extinction in populations as large as 250 individuals. More models of this kind are needed.

10.6 Conclusions

Currently, species interactions are rarely included in models used to evaluate the risk of extinction for plant populations. The information summarized in this chapter underscores the complex ways in which species interactions may influence plant populations. Unfortunately, knowing when to explicitly include these dynamics may not always be obvious. In many cases, while we may suspect that such interactions exist and are important, they have not been studied enough to permit quantitative estimates to be incorporated into models. The kinds of models currently in use may not be able to incorporate our growing knowledge of such interactions, and more sophisticated models may be needed in the future.

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