Introduced herbivores and the Allee effect in animal-pollinated plants

Diego P Vázquez ✉

Instituto Argentino de Investigaciones de las Zonas Áridas, Centro Regional de Investigaciones Científicas y Tecnológicas, CONICET, Mendoza, Argentina

Abstract. Interspecific interactions can be modulated by the community context in which they occur. In this paper I focus on plant–pollinator interactions and their modulation by introduced herbivores through changes in plant population density. I first develop a mathematical model that relates the population density of an animal-pollinated plant species with pollinator visitation frequency, pollination, reproduction and *per capita* growth rate. This model allows me to investigate how several pollination-related parameters—including relative abundance of the focal plant species, pollinator specialization, pollination quantity and quality and pollen limitation of reproduction—influence the relationship between *per capita* growth rate and population density. I then use this theoretical framework to discuss two case studies that have addressed the density-mediated effects of introduced herbivores on plant reproduction. This exercise allows me to point out several limitations of previous studies and to suggest avenues for future research.

[Keywords: abundance, Allee effect, density dependence, introduced herbivores, mutualism, plant reproduction, pollination, pollinator specialization and generalization, population dynamics]

Resumen. **Herbívoros introducidos y el efecto Allee en plantas polinizadas por animales**: Las interacciones interespecíficas pueden ser moduladas por el contexto comunitario en el que ocurren. Este artículo estudia las interacciones planta-polinizador y su modulación por herbívoros introducidos mediante cambios en la densidad poblacional de las plantas. En primer lugar desarrollo un modelo matemático que relaciona la densidad poblacional de una planta polinizada por animales con la frecuencia de visitas por polinizadores, la polinización, la reproducción y la tasa *per capita* de crecimiento poblacional. Este modelo me permite investigar la influencia de varios parámetros relacionados con la polinización—incluyendo la abundancia relativa de la especie focal, la especialización de los polinizadores, la cantidad y la calidad de la polinización y la limitación por polen de la reproducción—sobre la relación entre la tasa *per capita* de crecimiento y la densidad poblacional. Luego utilizo este marco teórico para discutir dos estudios de caso que han evaluado los efectos mediados por la densidad de los herbívoros introducidos sobre la reproducción de las plantas. Este ejercicio me permite señalar algunas limitaciones de los estudios previos y sugerir direcciones para investigaciones futuras.

[Palabras clave: abundancia, efecto Allee, densodependencia, herbívoros introducidos, mutualismo, reproducción de plantas, polinización, especialización y generalización de polinizadores, dinámica poblacional]

✉ Instituto Argentino de Investigaciones de las Zonas Áridas, Centro Regional de Investigaciones Científicas y Tecnológicas, CONICET, CC 507, 5500 Mendoza, Argentina.
dvazquez@lab.cricyt.edu.ar

Introduction

One of the basic principles of ecology is the densodependent regulation of populations (considered a "law" by some; Lawton 1999; Turchin 2001). Population regulation results from the density dependence of demographic parameters (Hixon et al. 2002), imposing bounds on population abundance and allowing long-term persistence. On one extreme, an upper bound may be imposed by competition for resources and other biological interactions that limit population abundance, so that there is a negative correlation between population density or size and individual fitness. This kind of negative density-dependent regulation has received much attention since the origin of ecology as a discipline. For example, population regulation was the basis of Malthus' argument in his essay on the limits of human population growth (Malthus 1798), which was later used by Darwin (1859) as an inspiration for his idea of the struggle for survival as the mechanism underlying natural selection. Likewise, Verhulst (1845) incorporated density-dependent regulation in his now classic logistic model of population growth.

On the other extreme of the population abundance continuum, several mechanisms may impose a lower bound to population abundance, under which the population is unable to sustain itself and goes extinct. For many populations it is unrealistic that there will be negative density-dependence at low densities if there is facilitation among conspecifics, including mating in sexually reproducing organisms and cooperation in colonial or social organisms. In these cases, there may be an inverse density dependence at low densities (i.e., a positive correlation between population density or size and individual fitness), usually termed Allee effect (after W. C. Allee, who first noted the phenomenon; Allee et al. 1949; Dennis 1989; McCarthy 1997; Courchamp et al. 1999; Stephens & Sutherland 1999).

Animal-pollinated plants are particularly likely to suffer from Allee effects. At low population density or size, pollinators may visit individual plants less frequently and bring lower-quality pollen than at higher densities;

lower pollination performance can in turn lead to lower reproductive success, particularly when reproduction is pollen limited (Rathcke 1983; Kunin 1993; Ghazoul 2005). Consideration of Allee effects is particularly important when investigating the population ecology of rare plants, either naturally so or made rare by human impact to ecosystems including habitat fragmentation, habitat degradation such as that produced by fire or livestock grazing, biological invasions and selective harvesting (Bond 1994; Ghazoul 2005; Aizen & Vázquez 2006; Traveset & Richardson 2006). However, the Allee effect is not a necessary consequence of decreased population density, and its strength may vary substantially among species; this variation will depend on several pollination-related factors, including the relative abundance of the focal plant species, pollinator specialization, the density dependence of pollination quality, the strength of pollen limitation of reproduction and the breeding system.

One situation in which plants can suffer from Allee effects is when their abundance is decreased following the introduction of exotic herbivores. Introduced herbivores, particularly large mammalian species, can lead to fundamental changes in species composition, habitat structure and ecosystem processes in the habitats they invade (de Vos et al. 1956; Ebenhard 1988; Vázquez 2002). By directly affecting plant population abundance, herbivores can also affect indirectly plant pollination and reproductive success through Allee effects (Vázquez & Simberloff 2004; Traveset & Richardson 2006).

Here I develop a mathematical model that includes a mechanistic Allee effect incorporating pollinator visitation, pollination and reproduction into a logistic model of population dynamics. I use the model heuristically, as a tool to generate qualitative hypotheses about how different aspects of plant–pollinator interactions and plant reproductive biology affect the density dependent regulation of animal-pollinated plants. I then exemplify the use of the model by applying it to two case studies. Although I have developed this model in the context of one type of ecosystem perturbation, introduced herbivores, it can be applied to other types of perturbations that operate

through increased mortality; this would include, for instance, harvesting and fire, but would exclude habitat fragmentation (provided that it does not increase mortality of the plant). Even in the latter case, if any conditions of the ecosystem change with fragmentation (e.g., relative abundance or the degree of specialization of pollinator; see Aizen & Feinsinger 1994a 1994b) in spite of no added mortality, the model could be used to compare these contrasting scenarios. Using this kind of mechanistic model could thus be useful to understand the varying responses of different plant species to decreased population abundance (Ghazoul 2005).

MODELLING THE ALLEE EFFECT IN ANIMAL-POLLINATED PLANTS

Prolegomena

I start with the discrete-time logistic equation to model the population dynamics of an animal-pollinated plant species,

$$N_{t+1}=N_t+rN_t(1-N_t/K)\,,\qquad(1)$$

where N_t and N_{t+1} are population abundances at time intervals t and $t+1$, r is the intrinsinc population growth rate and K is the carrying capacity (Kot, 2001). The *per capita* growth rate (the number of adults produced per adult) is then a linearly decreasing function of population density

$$N_{t+1}/N_t=1+r(1-N_t/K)\,.\qquad(2)$$

The discrete-time logistic model is appropriate for unitary (non-modular) organisms with discrete, non-overlapping generations and no age structure. Although many plant species are not represented by this type demography, the simplicity of the model allows me to use it heuristically to explore how different pollination and reproductive parameters modulate the density-mediated effects of introduced herbivores on the population dynamics of animal-pollinated plants. More complexity can be added, for example by incorporating a transformation for modularity (Crawley 1997) or age structure (Caswell 2001).

The basic model described by eq. 1 assumes that *per capita* reproductive rate is a linearly decreasing function of population size (the straight line in Figure 1). Although this form of density dependence may be a reasonable assumption when conspecific individuals compete strongly for resources and there is no facilitation, it is not appropriate when individuals facilitate each other's reproduction at low densities, as may occur with animal-pollinated plants. The most commonly used form of the logistic equation incorporating the Allee effect is

$$N_{t+1}=N_t+rN_t(N_t\text{-}K_0/K)(1\text{-}N_t/K)\,,\qquad(3)$$

where K_0 is a critical density below which the population cannot reproduce (Courchamp et al. 1999; Kot 2001; Stephens & Sutherland 1999). The term $N_t\text{-}K_0/K$ increases linearly with density and causes the *per capita* growth rate to increase at low densities, peaking at intermediate densities (Figure 1). Albeit simple, this form of Allee effect has several limitations, particularly the lack of flexibility in the shape of the per-capita growth rate curve (it is symmetric) and the fact that it is not mechanistic, in the sense that it does not specify how the increase in reproductive success at low densities occurs (Stephens & Sutherland 1999). Hence, here I develop a different form of Allee effect, one which varies non-linearly with density and which allows me to incorporate mechanistically the density-mediated effects of herbivores on pollination and reproduction.

I assume the focal plant species is pollinated mainly by one pollinator species (or by several species that have similar characteristics). Although many plant species are quite generalized in their interactions with pollinators (Waser et al. 1996; Waser & Ollerton 2006), we know that pollinator effectiveness varies widely among pollinator species, and usually one or a few species provide a large proportion of the total pollination service (Morris 2003; Vázquez et al. 2005); thus, the simplifying assumption that the focal plant is pollinated by one pollinator species seems reasonable. Pollinators can themselves vary in their degree of specialization on plant species, which have important implications for pollination quantity and quality (Rathcke 1983; Kunin 1993;
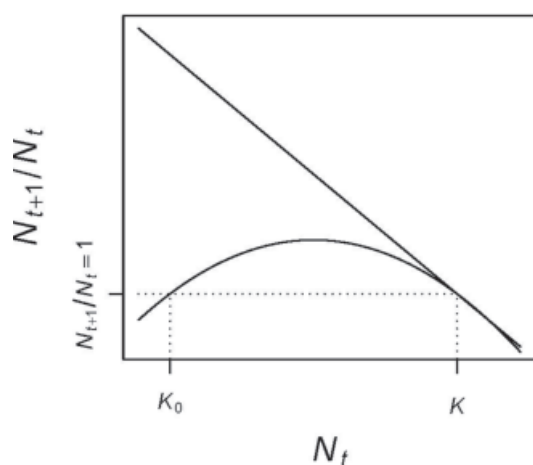
Figure 1. *Per capita* growth rate as a function of population abundance. Straigth line: basic model with no Allee effect (eq. 2); hump-shaped curve: basic model with Allee effect (eq. 3). Dotted lines indicate K (vertical line, right), K_0 (vertical line, left) and the minimum growth rate for population persistence (horizontal line).

Figura 1. Tasa *per capita* de crecimiento poblacional en función de la abundancia poblacional. Línea recta: modelo básico sin efecto Allee (eq. 2); línea curva: modelo básico con efecto Allee (eq. 3). Las líneas punteadas indican K (línea vertical, derecha), K_0 (línea vertical, izquierda) y la tasa de crecimiento mínima para la persistencia de la población (línea horizontal).

Vázquez & Simberloff 2004). In the model, degree of generalizaton of pollinators is governed by one parameter, g, which ranges from 1 (extreme pollinator generalization) to 0 (extreme specialization). I thus take pollinator specialization as a given, rather than evaluating how it varies with absolute and relative abundance of the focal plant species. Although this assumption is surely a simplification given the complex dynamics that pollinator specialization can exhibit (Kunin & Iwasa 1996), doing so allows me to focus on the dynamics of focal plant species without adding too much unnecessary complexity to the model.

I use a series of saturating functions that link plant absolute and relative density, pollinator visitation, pollination and reproductive success. These functions have the general form of a rectangular hyperbola, a saturating function of the form $y= \alpha x/\beta+x$, where x and y are the variables of interest and α and β are param-

eters controlling the saturation point and the velocity with which this point is reached, respectively. Although it has the drawback of having more parameters than the simple model presented in eq. 3, my modelling approach allows more flexibility to incorporate a mechanistic Allee effect into the logistic equation (see also Stephens & Sutherland 1999).

In the next five sections I describe the different components of the mechanistic model relating plant abundance, pollinator visitation, pollination, reproduction, *per capita* growth rate and herbivore-induced mortality. Main variables and parameters of the model are summarized in Table 1.
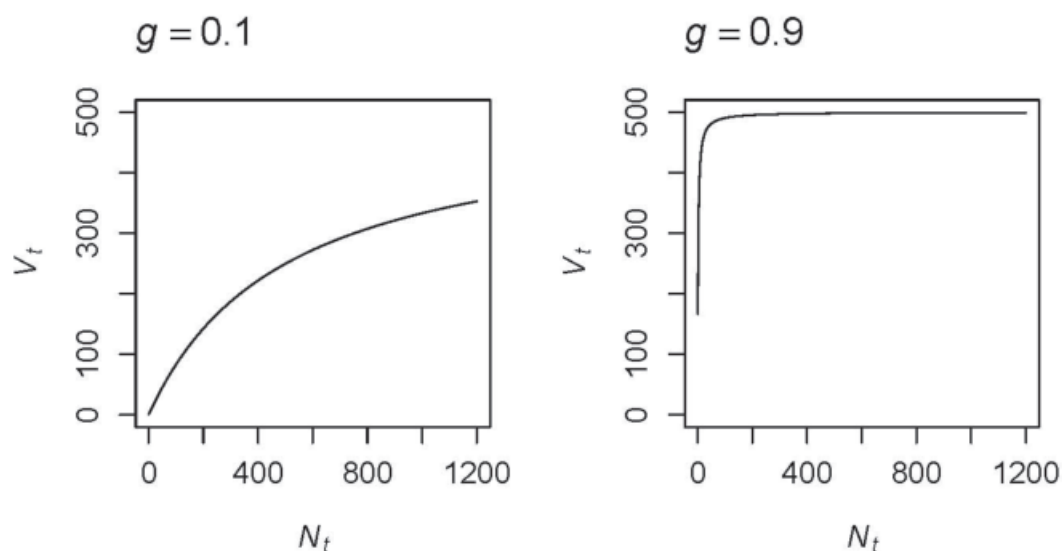
Pollinator visitation

I model pollinator visitation rate per plant at time t, V_t, as a function of population density of the focal plant, N_t:

$$V_t = \alpha_v N_t/\beta_v + N_t. \qquad (4)$$

Here the slope parameter is defined as $\beta_v \equiv (\beta_v')^{1-g}$. Thus, the influence of N_t is modulated by the degree of generalization of pollinators, g. When pollinators are specialized, $g \approx 0$ and $(\beta_v')^{1-g} \approx \beta_v'$, and eq. 4 saturates slowly with increasing population density (Figure 2a). In contrast, when pollinators are generalized $g \approx 1$ and $(\beta_v')^{1-g} \approx 1$, and eq. 4 saturates rapidly, attaining maximal visitation rate thoughout most of the range of population abundances (Figure 2b). In other words, when pollinators are specialized on the focal plant their visitation frequency is strongly density dependent, affecting the quantity component of pollination; in contrast, when they are generalized they can visit other plants in the community and thus are not affected strongly by variations in the density of the focal plant (see Kunin 1993; Vázquez & Simberloff 2004). I am assuming here that generalist pollinators have no preferences for the plants they visit, and so they visit any individual plant they encounter. Under this scenario, individuals of rare plant species should be visited at the same rate that individuals of abundant species. Conversely, if pollinators are specialists, they have strong preferences for the plant they are specialized

Table 1. Definition of variables and parameters used in the model.

Tabla 1. Definición de variables y parámetros utilizados en el modelo.

Notation	Definition
N_t	Population size of focal plant species at time t.
V_t	Pollinator visitation rate at time t.
C_t	Number of conspecific pollen grains deposited by pollinators at time t.
H_t	Number of heterospecific pollen grains deposited by pollinators at time t.
P_t	Proportion of conspecific pollen grains deposited by pollinators at time t.
Q_t	Quality of conspecific pollen received at stigma at time t.
F_t	Fecundity (fruit or seed production) of focal plant species at time t relative to maximum attainable by the population.
ρ	Relative density of focal plant species.
g	Degree of generalization of pollinators.
i	Degree of interference of fertilization by heterospecific pollen.
β_f	Strength of limitation of reproduction by pollen quantity.
β_q	Strength of decrease of pollen quality with decreasing population density.
K	Carrying capacity.
s	Degree of self-incompatibility.
b	Intrinsic birth rate.
d	Intrinsic death rate.
δ	Herbivore-induced death rate.

Figure 2. Pollinator visitation frequency to the focal plant species as a function of population density when pollinators are specialized (g=0.1) or generalized (g=0.9). Other parameter values: α_v=500, β_v'=1000.

Figura 2. Frecuencia de visitas de los polinizadores a la especie de planta focal en función de la densidad poblacional cuando los polinizadores son especialistas (g=0.1) o generalistas (g=0.9). Valores de otros parámetros: α_v=500, β_v'=1000.

on, but at low densities they may be unable to encounter them, so they may leave the patch.

Pollination

Deposition of conspecific and heterospecific pollen (C_t and H_t, respectively) are modelled as functions of both visitation rate and relative abundance of the focal plant. Conspecific pollen deposition is described by

$$C_t = \alpha_c V_t / \beta_c + V_t, \qquad (5)$$

where α_c and β_c are saturation and slope parameters as in eq. 4. Saturation point parameter is defined as $\alpha_c \equiv \alpha_c'(1-g)^{1-p}$, where $\rho = N_t/(N_t + O_t)$ is relative abundance (i.e., abundance of the focal plant N_t relative to all other coflowering species in the community, O_t). Notice that because I do not model the dynamics of other species in the community, I consider ρ as a parameter rather than a variable, evaluating how different values of r influence the behavior of the model. The influence of saturation point parameter α_c is modulated by $(1-g)^{1-p}$. Thus, when pollinators are specialized, $g \approx 0$, $(1-g)^{1-p} \approx 1$ and $\alpha_c \approx \alpha_c'$, independently of relative abundance. In contrast, when pollinators are generalists, $g \approx 1$ (not exactly equal to 1 but slightly lower), and relative abundance parameter ρ will have a strong influence on the value of α_c. At high relative abundances, $\rho \approx 1$, $(1-g)^{1-p} \approx 1$ and $\alpha_c \approx \alpha_c'$. However, at low relative abundances ρ will be close to 0 (but not exactly so) and $\alpha_c << \alpha_c'$. Thus, all else being equal, when pollinators are generalized and relative population density of the focal plant is low, the amount of conspecific pollen deposited at stigmas will be substantially lower than when relative abundance is high and/or pollinators are specialized (Figure 3).

Likewise, heterospecific pollen deposition is given by

$$H_t = \alpha_h V_t / \beta_h + V_t, \qquad (6)$$

where α_h and β_h are parameters as in eq. 4. Saturation point parameter is defined as $\alpha_h \equiv \alpha_h' g(1-g)^p$. Here, when pollinators are specialized, $g \approx 0$ and thus $\alpha_h \approx 0$, independently of relative abundance. Therefore, heterospe-

cific pollen deposition is always low when pollinators are specialized. In contrast, when pollinators are generalists, $g \approx 1$ (not exactly equal to 1 but, slightly lower), and relative abundance parameter ρ will have a strong influence on the value of α_h. At high relative abundances, $\rho \approx 1$, $(1-g)^p \approx 0$ and $\alpha_h \approx 0$. Thus, again, heterospecific pollen deposition is low when pollinators are generalized and the focal plant population is at high relative density. In contrast, at low relative abundances, $\rho \approx 0$, $(1-g)^p \approx 1$ and $\alpha_h \approx \alpha_h'$ (Figure 3). Thus, all else being equal, when pollinators are generalized and relative population density of the focal plant species is low, the amount of heterspecific pollen deposited on stigmas will be substantially higher than when relative abundance is high and/or pollinators are specialized (Figure 3).

We can also use eqs. 5 and 6 to study the density dependence of pollen purity, defined as the proportion of conspecific pollen deposited at stigmas,

$$P_t = C_t / (C_t + H_t). \qquad (7)$$

When pollinators are specialized, P_t is high throughout the entire range of densities. Likewise, when pollinators are generalized and relative abundance is high, P_t is also high. In contrast, when pollinators are generalized and relative abundance is low, P_t is low (Figure 3). Thus, at low relative densities, generalist pollinators are bringing a greater proportion of heterospecific pollen. This is the quality component of pollination (see Rathcke 1983; Kunin 1993, 1997a).

Reproduction

I model reproductive success as the number of seeds produced per individual relative to the maximum attainable by the population (i.e., relative fitness). This relative reproductive success, F_t, is a function of the quantity and quality of pollen deposition:

$$F_t = (\alpha_f C_t / \beta_f + C_t)^s, \qquad (8)$$

where α_f and β_f are parameters as in previous equations. Saturation point parameter is defined as $\alpha_f \equiv P_t^i Q_t$. Parameter *i* controls the in-
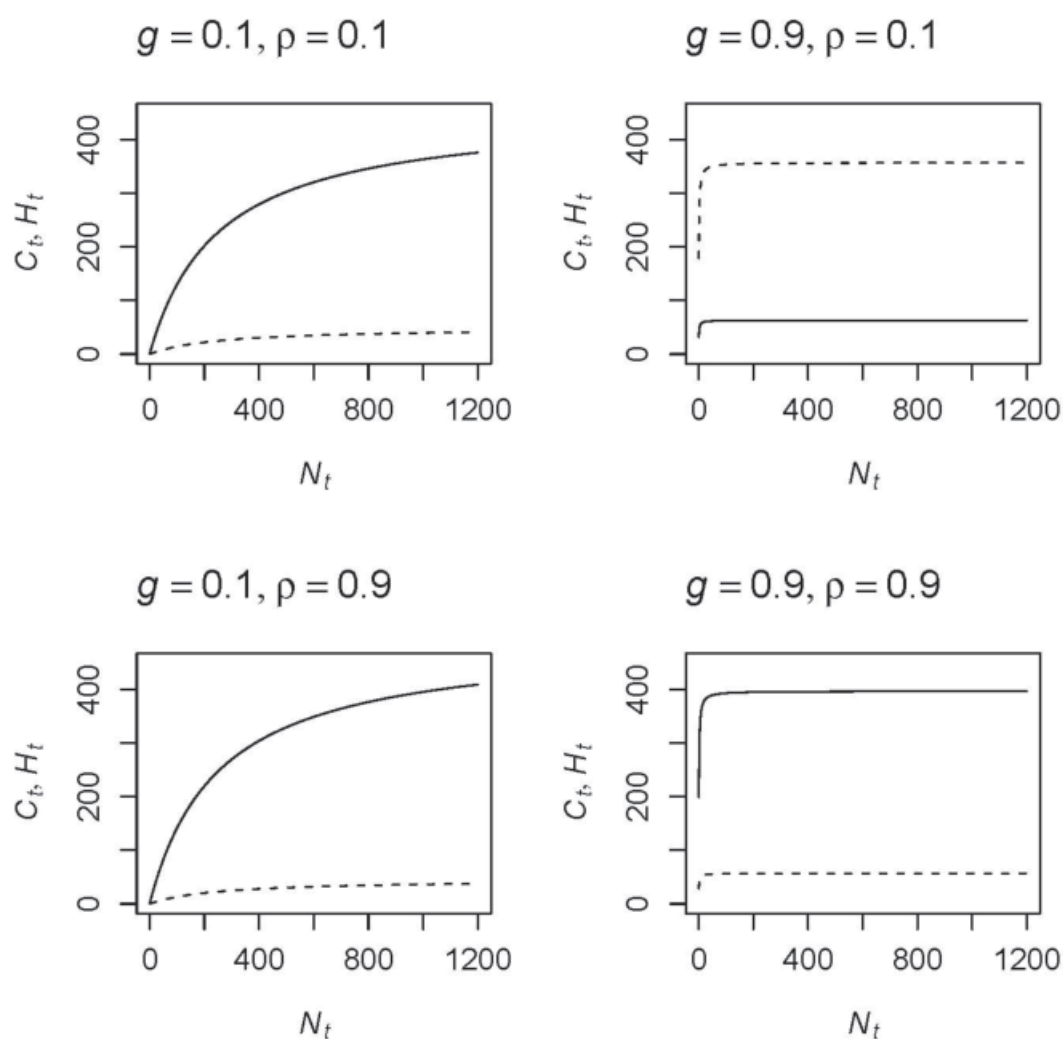
Figure 3. Conspecific (continuous line) and heterospecific (dashed line) pollen deposition as a function of population density when pollinators are specialized (g=0.1) or generalized (g=0.9) and relative density is low (ρ=0.1) or high (ρ=0.9). Other parameter values: $\alpha_c'=\alpha_h'=1000$, $\beta_c=\beta_h=500$; parameter values for V_t as in Figure 2.

Figura 3. Depósito de polen conespecífico (línea continua) y heteroespecífico (línea a rayas) en función de la densidad poblacional cuando los polinizadores son especialistas (g=0.1) o generalistas (g=0.9) y la densidad relativa es baja (ρ=0.1) o alta (ρ=0.9). Valores de otros parámetros: $\alpha_c'=\alpha_h'=1000$, $\beta_c=\beta_h=500$; valores de parámetros para V_t como en la Figura 2.

fluence of pollen purity on pollination; it can be interpreted as a measure of the extent of interference of heterospecific pollen on fertilization by conspecific pollen. When $i\approx0$, $P_t^i\approx1$ and thus it has no effect on eq. 8. Conversely, when i is large (≥1) and purity is low ($P_t<1$), assymptotic reproductive success will be lower because of interference by heterospecific pollen. Considering what we discussed above for

eqs. 5 and 6, this effect will be important when pollinators are generalized and relative density is low (Figure 4). Slope parameter β_f can be interpreted as regulating the strength of limitation of reproduction by pollen quantity; the larger the value of β_f, the stronger pollen limitation of reproduction. Parameter s represents the breeding system of the focal plant species, specifically the degree of self-compatibility;

when $s=1$ the plant is strictly self incompatible (or dioecious) and reproductive success depends strongly on pollen deposition; on the other extreme of the spectrum, when $s=0$ the plant is apomictic and reproductive success is independent of pollen deposition. For simplicity, I assume $s=1$ throughout the paper. Finally, because not only pollination quantity but also quality may determine reproduction (Aizen & Harder 2007), I include a component Q_t that controls the quality of conspecific pollen and is itself a function of density

$$Q_t = X_t/\beta_q + X_t, \qquad (9)$$

where $X_t = N_t/K$, and β_q is a saturation parameter as in previous equations. Thus, quality varies between 0 at low densites to 1 at high densities in a saturating fashion, so that low densities mean more self pollination and thus lower quality of conspecific pollen. When $\beta_q=0$ quality of conspecific pollen is always high (i.e., $Q_t=1$) regardless of population density; when $\beta_q>0$ quality of pollen decreases at low absolute densities of the focal plant species (Figure 4).

Population dynamics

Finally, I model population dynamics as

$$N_{t+1} = N_t + bN_tF_t(1 - N_t/K) - dN_t, \qquad (10)$$

and *per capita* growth rate as

$$N_{t+1}/N_t = 1 + bF_t(1 - N_t/K) - d. \qquad (11)$$

where b is the intrinsic birth rate and d is the intrinsic death rate (i.e., I have decomposed the intrinsinc population growth rate, r, into its birth and death components). Here, F_t (eq. 8) produces the mechanistic Allee effect we wanted to model (Figure 5). As before, the influence of F_t on *per capita* growth rate depends on the degree of pollinator specialization and the relative abundance of the focal plant population (Figure 5). It also depends on the strength of density dependence of pollen quality (Q_t, eq. 9). When there is no density dependence of pollen quality (continuous line in Figure 5) and pollinators are generalists, there is virtually no Allee effect, and *per capita* growth rate is

high at low densities and decreases linearly with increasing density. Conversely, when there is density dependence of pollen quality (dashed line in Figure 5) and pollinators are generalists, there is a stronger Allee effect, so that *per capita* growth rate increases at low densities up to a maximum and then decreases gradually as density continues to increase. When pollinators are specialists, there is always an Allee effect, but *per capita* growth rate is always higher when there is no density dependence of pollen quality.

It is important to point out here that many studies of density dependence of reproduction and growth rate in animal-pollinated plants (e.g., Kunin 1993; Aizen & Feinsinger 1994a; Kunin 1997b; Aguilar & Galetto 2004; Vázquez & Simberloff 2004; see Ghazoul 2005 for review) estimate seed production as a measure of plant reproductive success. However, because pollination quality can affect seed viability and vigor even if it does not affect seed production, these studies may be missing the Allee effects for reproductive success and *per capita* growth rate shown in Figures 4 and 5, wrongly concluding that there is no effect of density on reproductive success.

Adding herbivore-induced mortality

We can add the effect of herbivores to the model by incorporating a term that removes a portion of the population due to herbivore-induced mortality:

$$N_{t+1} = N_t + bF_tN_t(1 - N_t/K) - dN_t - \delta N_t. \qquad (12)$$

So now *per capita* growth rate becomes

$$N_{t+1}/N_t = 1 + bF_t(1 - N_t/K) - (d+\delta), \qquad (13)$$

where δ is the proportion of the population that is removed by herbivores. The addition of herbivore-induced mortality results in *per capita* growth rate now exhibiting a higher threshold density, under which the population cannot replace itself and goes extinct; the equilibrium density is also lower than K, and the maximum *per capita* growth rate is substantially lower than in the absence of herbivores (dotted line in Figure 5).
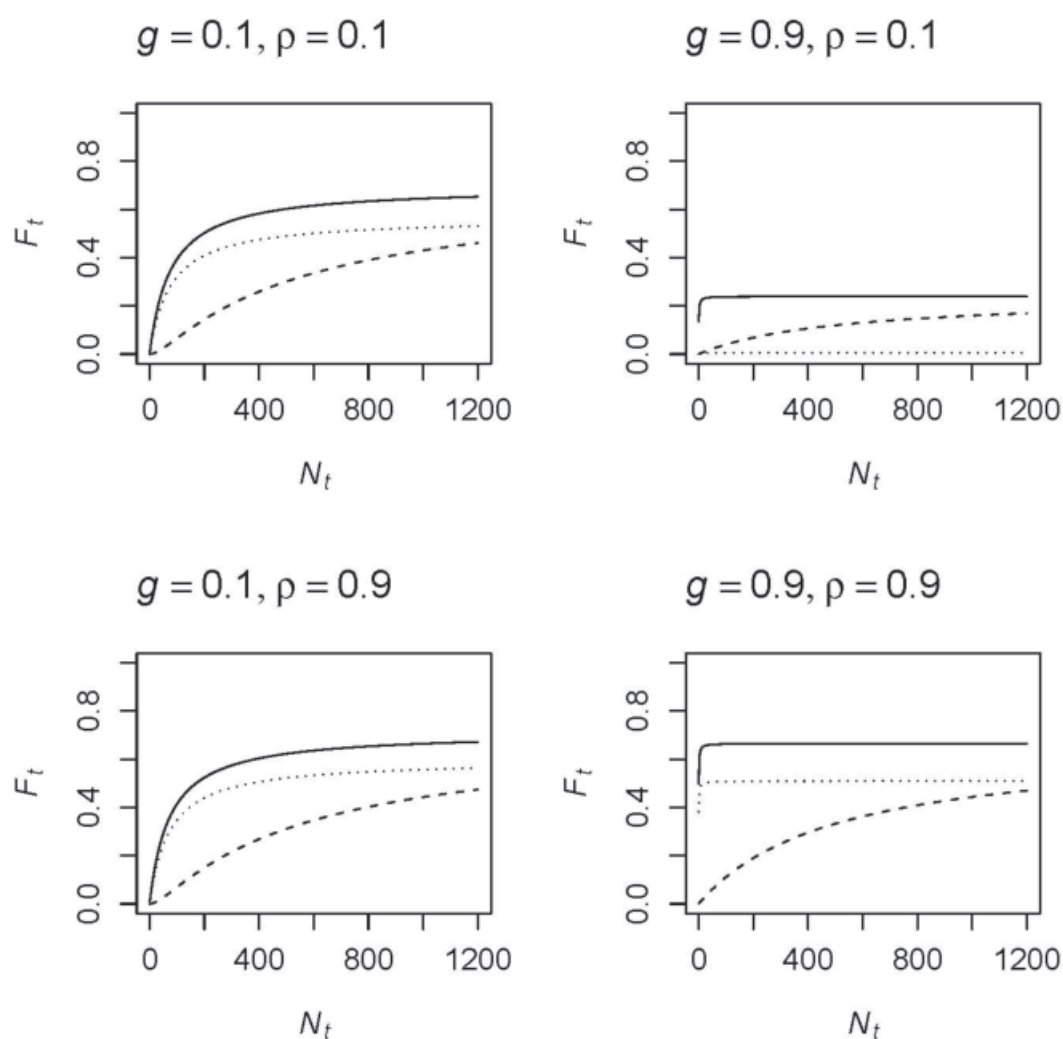
Figure 4. Reproductive success as a function of population density when pollinators are specialized (g=0.1) or generalized (g=0.9) and relative density is low (ρ=0.1) or high (ρ=0.9). Line types: continuous line, no effect of heterospecific pollen (i=0), no density dependence of conspecific pollen quality (β_q=0); dotted line, negative effect of heterospecific pollen (i=2), no density dependence of conspecific pollen quality (β_q=0); dashed line, no effect of heterospecific pollen (i=0) and moderate density dependence of conspecific pollen quality (β_q=0.5). Parameter values for C_t and H_t as in Figure 3; β_f=200.

Figura 4. Éxito reproductivo en función de la densidad poblacional cuando los polinizadores son especialistas (g=0.1) o generalistas (g=0.9) y la densidad relativa es baja (ρ=0.1) o alta (ρ=0.9). Tipos de línea: continua, sin efecto del polen heteroespecífico (i=0), sin densodependencia de la calidad del polen (β_q=0); punteada, efecto negativo del polen heteroespecífico (i=2), sin densodependencia de la calidad del polen conespecífico (β_q=0); a rayas, sin efecto del polen heteroespecífico (i=0) y con densodependencia moderada de la calidad del polen conespecífico (β_q=0.5). Valores de los parámetros para C_t y H_t como en la Figura 3; β_f=200.
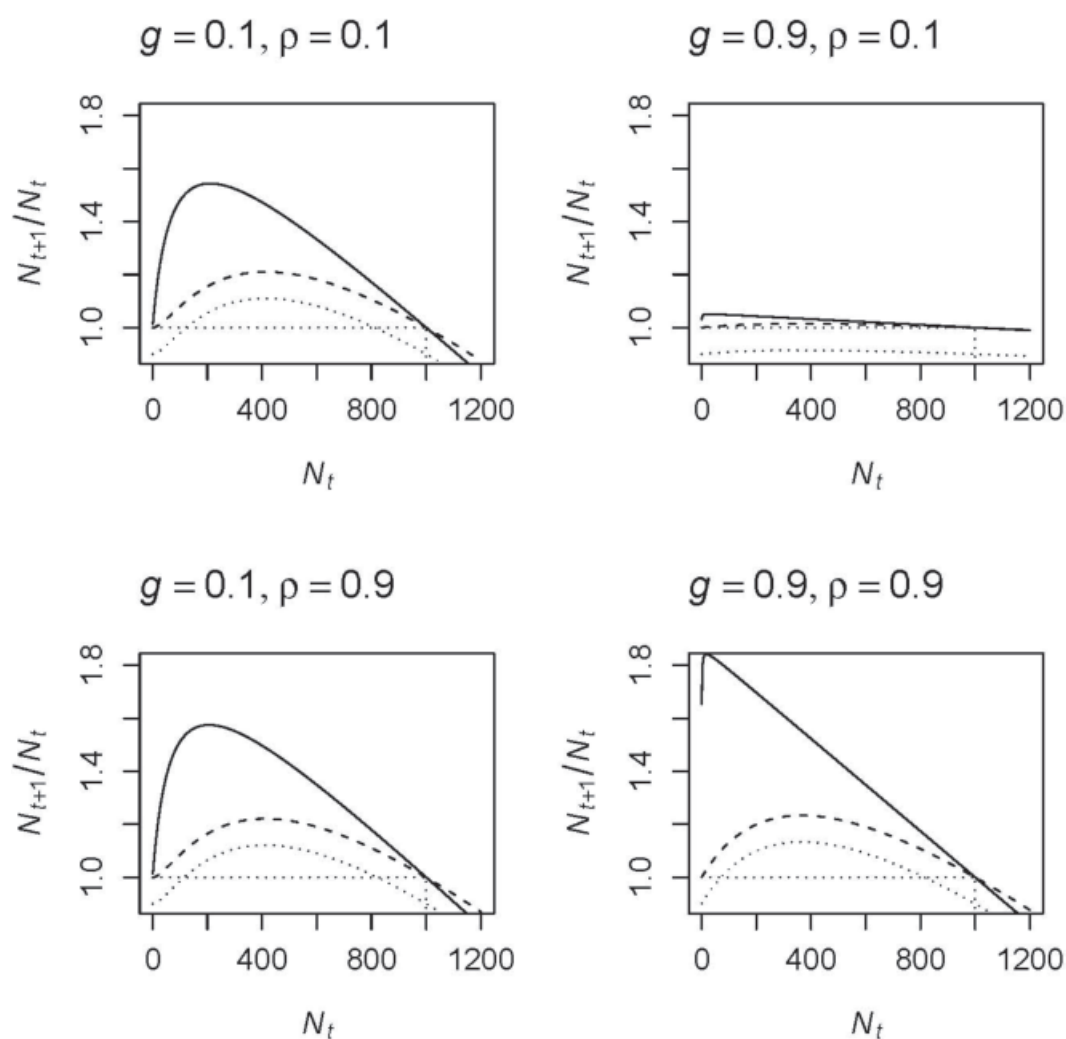
Figure 5. *Per capita* growth rate as a function of population density when pollinators are specialized (g=0.1) or generalized (g=0.9) and relative density is low (ρ=0.1) or high (ρ=0.9). Line types: continuous line, no density dependence of pollen quality (β_q=0); dashed line, moderate density dependence of conspecific pollen quality (β_q=0.5); dotted line, moderate density dependence of conspecific pollen quality (β_q=0.5) and herbivore-induced mortality (δ=0.1). The straight dotted horizontal line indicates N_{t+1}/N_t=1, and the straight dotted vertical line indicates K. Other parameters as in previous figures, except i=1.

Figura 5. Tasa *per capita* de crecimiento poblacional en función de la densidad poblacional cuando los polinizadores son especialistas (g=0.1) o generalistas (g=0.9) y la densidad relativa es baja (ρ=0.1) o alta (ρ=0.9). Tipos de línea: continua, sin densodependencia de la calidad del polen (β_q=0); a rayas, densodependencia moderada de la calidad del polen conespecífico (β_q=0.5); punteada, densodependencia moderada de la calidad del polen conespecífico (β_q=0.5) y con mortalidad inducida por los herbívoros (δ=0.1). La línea recta punteada horizontal indica N_{t+1}/N_t=1, y la línea recta punteada vertical indica K. Otros parámetros como en figuras anteriores, excepto i=1.

Notice, however, that the threshold is not equally high in all cases (Figure 5). When pollinators are specialized, the threshold for population persistence is relatively high. This threshold increases with the severity of the effect of herbivores. In contrast, when pollinators are generalized and there is no density dependence of pollen quality, there is virtually no threshold for population persistence. Finally, when there is density dependence of pollen quality ($\beta_q > 0$) there is a threshold even if pollinators are generalists. This finding sheds some light on Ghazoul's (2005) conjecture, "the existence of thresholds remains uncertain for most species, but where they occur they will probably be mediated by the type of pollinator involved". The present model suggests that degree of pollinator specialization on the plant can determine the severity of such threshold.

In the next section I illustrate the use of the model by applying it to two case studies.

Case studies

I consider two case studies that have addressed the density-mediated effects of introduced herbivores on plant pollination and reproduction. These two case studies are contrasting in terms of the details of the ecology of plant-pollinator interactions, and serve to show how the model can be used to generate mechanistic predictions about the effects of introduced herbivores.

Alstroemeria aurea in Nahuel Huapi

The first case study I will discuss is *Alstroemeria aurea* (Alstroemeriaceae) in Nahuel Huapi National Park, in the temperate forest of the southern Argentine Andes. *A. aurea* is a summer-flowering perennial herb from this region. It dominates the understory in some forest types (Aizen 1997; 2001; Vázquez & Simberloff 2004). Although it is self compatible, pollination and seed production are pollinator-dependent because of the plant's pronounced protandry (Aizen & Basilio 1995). Its main pollinator is the native bumblebee *Bombus dahlbomii* and, increasingly, the exotic

bumblebee *B. ruderatus* (Aizen 2001; Vázquez & Simberloff 2002; Morales 2007); both bumblebee species are highly generalized (Morales & Aizen 2002; Vázquez & Simberloff 2002). *A. aurea* is highly susceptible to trampling by ungulates, and both its absolute and relative densities decrease sharply in native forest sites with cattle or deer, compared to ungulate-free sites (Vázquez & Simberloff 2004). This effect on density does not have a detectable effect on pollinator visitation frequency, but it does affect pollination, with decreased deposition of conspecific pollen and increased deposition of heterospecific pollen in grazed sites (pollinators appear to bring a lower proportion of conspecific pollen grains per visit); this effect on pollination in turn results in decreased reproductive success in the presence of herbivores (Vázquez & Simberloff 2004).

Let's now parameterize the model, to see what it can tell us about the effect of cattle on *A. aurea*. The parameter values I will use are not quantitative estimates, but only "qualitative guesses" based on what we know about this species; but these guesses will be enough to allow us to make some qualitative predictions. First, given it is pollinated by highly generalized pollinators, we set g=0.9. There is only weak density dependence of pollen quality, with high levels of heterozigocity a few meters away from individual ramets (Souto et al. 2002); so we set β_q=0.1. We don't know how much heterospecific pollen grains interfere with pollination; I assume one heterospecific pollen grain excludes one conspecific grain, and so we set i=1. We know cattle affects this species disproportionately to other species; so we will compare a situation of high relative abundance in the absence of cattle (ρ=0.9) with one with moderate relative abundance when cattle are present (ρ=0.5). Finally, we assume that herbivores kill 10% of the population when it is at K; thus, δ=0.1 in the presence of cattle, and δ=0 in the absence of them.

The model tells us that when the focal plant species is pollinated by generalists, decreased absolute density will not lead to decreased pollinator visitation (Figure 2). It also tells us that if relative abundance decreases, deposition of conspecific pollen will decrease and that of heterospecific pollen will increase (Fig-

ure 3), leading to decreased pollen purity and thus lower pollination quality. Lower pollination quality in turn results in lower reproductive performance (Figure 4). All this agrees with the findings of Vázquez and Simberloff (2004) described above. The model also allows us to make a prediction about what would happen with *per capita* growth rate; although we have no estimates of intrinsic birth rates b and d for this species and thus won't be able to contrast the model with reality, qualitative predictions will be unaffected by the specific value of these parameters used. *Per capita* growth rate will exhibit a threshold density in the presence of cattle, under which the population cannot replace itself and goes extinct (Figure 6). The equilibrium density will be lower than K, and the maximum *per capita* growth rate will be substantially lower than in the absence of disturbance. The existence of a threshold for *per capita* growth rate suggests that populations of *A. aurea* in areas with cattle may be doomed to local extinction, even though there may still be some seed production. The likelihood of this scenario will depend on the severity of the threshold and the strength of other factors not considered in the model that could affect small populations, such as demographic stochasticity or inbreeding depression (Lande 1988).

Prosopis flexuosa in Ñacuñán

The second case study contrasts with the previous one in some crucial aspects of the pollination ecology of the focal species. *Prosopis flexuosa* (Leguminosae) is the dominant tree species in the Central Monte Desert of Mendoza, Argentina; it is functionally important in this ecosystem (Campos & Ojeda 1997; Rossi & Villagra 2003; Milesi & López de Casenave 2004). It represents an important source of wood and its pods are a rich food source for both man or cattle. Its wood has been overexploited during the first half of the 20th century. It is self-incompatible (Masuelli & Balboa 1989), and is pollinated by several insect species that are mostly restricted to *P. flexuosa* during its flowering season (thus behaving as functionally specialized; V. Aschero and D. P. Vázquez, *unpubl. data*). The perimeter of Ñacuñán Biosphere Reserve was fenced in the early 1970s, thus excluding cattle ranch-

ing and wood and pod harvesting; although wood harvesting is currently banned by provincial authorities, ranching and pod harvesting continue to date in the private land surrounding the reserve. Thus although adult trees are protected, human activities still have the potential to affect seedling and sapling survivorship and adult fecundity. Working in six pairs of 1 ha plots inside and outside the reserve, V. Aschero and I (unpubl. ms.) have found that absolute density of *P. flexuosa*, pollinator visitation frequency and seed production all tend to be lower outside the reserve.

As in the previous case study, to parameterize the model we need to make some guesses, but that will not affect the general qualitative predictions. First, based on what we know about the flower visitors, we will assume the pollinator is relatively specialized; so we set g=0.1. Because pollinators are specialized, the value of parameter i (heterospecific pollen interference) is irrelevant (see eq. 8); so we set it again at the arbitrary value of 1. We also assume there is a moderate density dependence of pollen quality; thus β_q=0.1. Again because the pollinator is relatively specialized, its relative density is irrelevant (see eqs. 5 and 6); so we set r at the arbitrary value of 0.5. Finally, we assume that disturbance kills 20% of the population when it is at K; thus, δ=0.2 in the presence of cattle and δ=0 in the absence of them. *Per capita* growth rate again exhibits a threshold density, under which the population cannot replace itself and goes extinct, and the equilibrium density is also lower than K (Figure 7). However, in this case the effect results from entirely different mechanisms than the previous case study: it results solely from the increased mortality caused by cattle, not by a change in the functional relationship between F_t and N_t; in fact, this relationship is unchanged by cattle. The presence of cattle simply keeps the population at a lower density, and this lower density results in lower visitation frequency, pollination quantity, reproductive success and lower *per capita* growth rate.

So what?

You may be asking yourself: so what? Arguably, many of the qualitative predictions com-
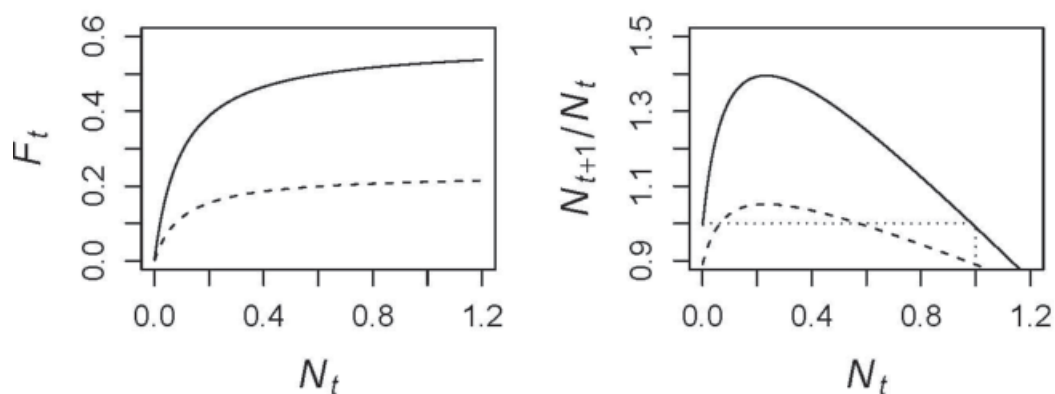
Figure 6. Model results for reproductive success and *per capita* growth rate as functions of population density, with the model parameterized for the *Alstroemeria aurea* case study in the presence (dashed line) and absence (continuous line) of cattle. See text for parameter values. In the abscissas, N_t is expressed relative to *K*.

Figura 6. Resultados del modelo para el éxito reproductivo y la tasa *per capita* de crecimiento poblacional en función de la densidad poblacional, con el modelo parametrizado para el estudio de caso de *Alstroemeria aurea* en presencia (línea a rayas) y en ausencia (línea continua) de ganado. Ver texto para los valores de los parámetros. En las abscisas, N_t está expresado en términos relativos a *K*.
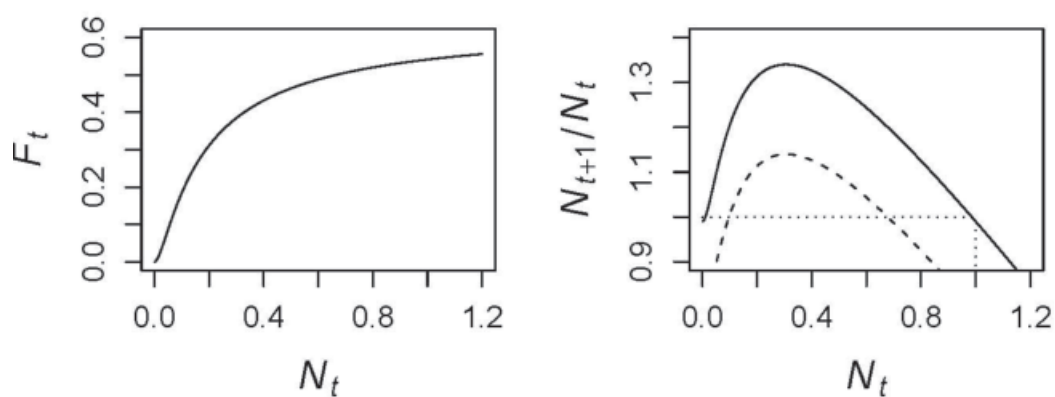

Figure 7. Model results for reproductive success and *per capita* growth rate as functions of population density, with the model parameterized for the *Prosopis flexuosa* case study in the presence (dashed line) and absence (continuous line) of cattle. See text for parameter values. In the abscissas, N_t is expressed relative to *K*.

Figura 7. Resultados del modelo para el éxito reproductivo y la tasa *per capita* de crecimiento poblacional en función de la densidad poblacional, con el modelo parametrizado para el estudio de caso de *Prosopis flexuosa* en presencia (línea a rayas) y en ausencia (línea continua) de ganado. Ver texto para los valores de los parámetros. En las abscisas, N_t está expresado en términos relativos a *K*.

ing from the model I have developed above could be made without it (and actually had been made repeatedly in the literature). However, putting together all the information needed to make such predictions is not simple, and the model can be useful as a tool to formalize them. How strong will be the Allee effect generated by introduced herbivores on a particular plant species if, for example, the plant is pollinated by a generalized pollinator, is self-compatible, there is no density dependence of conspecific pollen quality, and its relative abundance decreases sharply in the presence of herbivores? What if, all else being equal to the previous case, there is now moderate density dependence of conspecific pollen quality and relatively abundance does not change? The model can aid us to investigate these scenarios and provide testable predictions that can be evaluated in field observational or experimental studies.

Predicting Allee effects of introduced herbivores on animal-pollinated plants requires knowledge on several aspects of the pollination ecology and reproductive biology of the focal plant species, some of which are not available in the case studies discussed above (this applies, in fact, to the majority of studies of Allee effects in animal-pollinated plants). For example, we need not only knowledge of the richness and relative importance of pollinators, but also of the degree of specialization of pollinators on the focal plant species, something that is not available in many studies (see also Ashworth et al. 2004). In cases when pollinators are not specialized on the focal plant species, we also need to know what happens with both the absolute and relative densities of the focal plant population. Likewise, we should not only evaluate reproductive success as seed production but also in terms of seed viability an germination potential. The model developed here could be used to generate a checklist of the variables to be measured in studies of Allee effects in animal-pollinated plants.

As I argued in the introduction, this model could be applied to other types of perturbations besides introduced herbivores that operate through increased mortality. This kind of

modelling approach can thus provide a quantitative framework that complements the conceptual framework proposed recently by Aizen & Vázquez (2006). Together, these tools can be useful guides for the design of process and mechanism-oriented studies of the effects of anthropogenic habitat disturbance on plant pollination and reproduction.

ACKNOWLEDGMENTS

REFERENCES

AGUILAR, R & L GALETTO. 2004. Effects of forest fragmentation on male and female reproductive success in *Cestrum parqui* (Solanaceae). *Oecologia*, **138**:513–520.

AIZEN, MA. 1997. Influence of local floral density and sex ratio on pollen receipt and seed output: empirical and experimental results in dichogamous *Alstroemeria aurea* (Alstroemeriaceae). *Oecologia*, **111**: 404–412.

AIZEN, MA. 2001. Flower sex ratio, pollinator abundance, and the seasonal pollination dynamics of a protandrous plant. *Ecology*, **82**: 127–144.

AIZEN, MA & A BASILIO. 1995. Within and among flower sex-phase distribution in *Alstroemeria aurea* (Alstroemeriaceae). *Canadian Journal of Botany*, **73**:1986–1994.

AIZEN, MA & P FEINSINGER. 1994a. Forest fragmentation, pollination, and plant reproduction in a Chaco dry forest, Argentina. *Ecology*, **75**: 330–351.

AIZEN, MA & P FEINSINGER. 1994b. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine Chaco Serrano. *Ecological Applications*, **4**:378–392.

AIZEN, MA & LD HARDER. 2007. Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. *Ecology*, **88**:271–281.

AIZEN, MA & DP VÁZQUEZ. 2006. Flower performance in human-altered habitats. Pp. 159–179 in: LD Harder & SCH Barrett (eds). *Ecology and Evolution of Flowers*. Oxford University Press.

ALLEE, WC; AE EMERSON & O PARK. 1949. *Princples of Animal Ecology*. W.B. Saunders Co., Philadelphia.

ASHWORTH, L; R AGUILAR; L GALETTO & MA AIZEN. 2004. Why do pollination generalist and specialist plant species show similar reproductive susceptibility to habitat fragmentation? *Journal of Ecology*, **92**:717–719.

BOND, WJ. 1994. Do mutualisms matter? Assessing the impact of pollinator and disperser disruption on plant extinction. *Philosophical Transactions of the Royal Society of London Series B*, **344**:83–90.

CAMPOS, CM & RA OJEDA. 1997. Dispersal and germination of *Prosopis flexuosa* (Fabaceae) seeds by desert mammals in Argentina. *Journal of Arid Environments*, **35**:707–714.

CASWELL, H. 2001. *Matrix Population Models: Construction, Analysis, and Interpretation*. Sinauer Associates, Suntherland, MA.

COURCHAMP, F; T CLUTTON-BROCK & B GRENFELL. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution*, **14**:405–410.

CRAWLEY, MJ (ed). 1997. *Plant Ecology*. Second ed. Blackwell Science, Oxford.

DARWIN, C. 1859. *The Origin of Species by Means of Natural Selection*. Bantam, New York, U.S.A.

DE VOS, A; RH MANVILLE & RG VAN GELDER. 1956. Introduced mammals and their influence on native biota. *Zoologica (New York Zoological Society)*, **41**:163–194.

DENNIS, B. 1989. Allee effects: population growth, critical density, and the chance of extinction. *Natural Resource Modeling*, **3**:481–538.

EBENHARD, T. 1988. Introduced birds and mammals and their ecological effects. *Swedish Wildlife Research (Viltrevy)*, **13**:1–107.

GHAZOUL, J. 2005. Pollen and seed dispersal among dispersed plants. *Biological Reviews*, **80**:1–31.

HIXON, MA; SW PACALA & SA SANDIN. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology*, **83**:1490–1508.

KOT, M. 2001. *Elements of Mathematical Ecology*. Cambridge University Press.

KUNIN, W & Y IWASA. 1996. Pollinator foraging strategies in mixed floral arrays: density effects and floral constancy. *Theoretical Population Biology*, **49**:232–263.

KUNIN, WE. 1993. Sex and the single mustard: population density and pollinator behavior effects on seed-set. *Ecology*, **74**:2145–2160.

KUNIN, WE. 1997a. Population biology of rarity: on the complexity of density dependence in insect-plant interactions. Pp. 150–173 in: WE Kunin & KJ Gaston (eds). *The Biology of Rarity*. Chapman and Hall, London.

KUNIN, WE. 1997b. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology*, **85**:225–234.

LANDE, R. 1988. Genetics and demography in biological conservation. *Science*, **241**:1455–1459.

LAWTON, JH. 1999. Are there general laws in ecology? *Oikos*, **84**:177–192.

MALTHUS, TR. 1798. *An essay on the Principle of Population, as it affects the future improvement of society, with remarks on the speculations of Mr. Godwin, M. Concorcet, and other writers*. J. Johnson.

MASUELLI, R & O BALBOA. 1989. Self-incompatibility in *Prosopis flexuosa* D.C. *Plant Cell Imcompatibility Newsletter*, **21**: 44–48.

MCCARTHY, M. 1997. The Allee effect, finding mates and theoretical models. *Ecological Modelling*, **103**:99–102.

MILESI, FA & J LÓPEZ DE CASENAVE. 2004. Unexpected relationships and valuable mistakes: nonmyrmecochorous *Prosopis* dispersed by messy leaf-cutting ants in harvesting their seeds. *Austral Ecology*, **29**: 558–567.

MORALES, CL. 2007. Introducción de abejorros (*Bombus*) no nativos: causas, consecuencias ecológicas y perspectivas. *Ecología Austral*, **17**: 51-65.

MORALES, CL & MA AIZEN. 2002. Does invasion of exotic plants promote invasion of exotic flower visitors? A case study from the temperate forests of the southern Andes. *Biological Invasions*, **4**: 87–100.

MORRIS, WF. 2003. Which mutualists are most essential? Buffering of plant reproduction against the extinction of pollinators. Pp. 260–280 in: P Kareiva & SA Levin (eds). *The Importance of Species: Perspectives on Expendability and Triage*. Princeton University Press, Princeton.

RATHCKE, B. 1983. Competition and facilitiation among plants for pollination. Pp. 305–329 in: L Real (ed). *Pollination Biology*. Academic Press, London.

ROSSI, BE & PE VILLAGRA. 2003. Effects of *Prosopis flexuosa* on soil properties and the spatial pattern of understorey species in arid Argentina. *Journal of Vegetation Science*, **14**:543–550. Article.

SOUTO, CP; MA AIZEN & AC PREMOLI. 2002. Effects of crossing distance and genetic relatedness on pollen performance in *Alstroemeria aurea* (Alstroemeriaceae). *American Journal of Botany*, **89**:427–432.

STEPHENS, PA & WJ SUTHERLAND. 1999. Consequences

of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology & Evolution*, **14**:401–405.

Traveset, A & DM Richardson. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends in Ecology & Evolution*, **21**: 208–216.

Turchin, P. 2001. Does population ecology have general laws? *Oikos*, **94**:17–26.

Verhulst, PF. 1845. Recherches mathématiques sur la loi d'accroissement de la population. *Nouveaux Mémoires de l'Académie Royale des Sciences et Belles-Lettres de Bruxelles*, **18**:3–38.

Vázquez, DP. 2002. Multiple effects of introduced mammalian herbivores in a temperate forest. *Biological Invasions*, **4**:175–191.

Vázquez, DP; WF Morris & P Jordano. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. *Ecology Letters*, **8**:1088–1094.

Vázquez, DP & D Simberloff. 2002. Ecological specialization and susceptibility to disturbance: conjectures and refutations. *American Naturalist*, **159**:606–623.

Vázquez, DP & D Simberloff. 2004. Indirect effects of an introduced ungulate on pollination and reproduction. *Ecological Monographs*, **74**:281–308.

Waser, NM; L Chittka; MV Price; NM Williams & J Ollerton. 1996. Generalization in pollination systems, and why it matters. *Ecology*, **77**:1043–1060.

Waser, NM & J Ollerton (eds.). 2006. *Plant–Pollinator Interactions: From Specialization to Generalization*. University of Chicago Press.