

# Long-term ant-species-dependent dynamics of a myrmecochorous plant community

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**Abstract** Myrmecochory or seed dispersal by ants is a widely spread phenomenon, and myrmecochorous plants constitute a large portion of species in many ecosystems. Since the ant species complex in the ecosystem is continuously changing in time and space, the long-term effects of such ant–plant interactions on the plant community remained unclear. The manifold information obtained in numerous previous studies from one ecosystem in the deciduous forests of Central Ukraine allowed us to simulate the possible scenarios for plant survival and distribution in the ecosystem after a reduction in the number or local extinction of one of the ant species. The results of the virtual long-term experiment show that the abundance and spatial distribution of myrmecochorous plants strongly depends on both the abundance of ants and their species composition in the ecosystem. The positive role of ant species diversity for maintaining myrmecochorous plant

species diversity is shown. Competition between plant species for seed dispersers is influenced by the ant community in such a way that the disappearance of one ant species may lead to the reduction or even local extinction of a particular plant population.

**Keywords** Insect–plant interactions · Dispersal strategy · Modelling · Population · Spatial distribution · Survival

## Introduction

Myrmecochory or seed dispersal by ants is a widely spread phenomenon record in 3,000 species and nearly 80 families of plants (Beattie 1985; Giladi 2006). According to recent reports, it has evolved independently at least 100 times in angiosperms and is estimated to be present in over 11000 species, or in more than 4.5 % of all known angiosperm species (Lengyel et al. 2009). Myrmecochores are globally distributed, and constitute large portions of species in many ecosystems, for example, they account for up to 30–40 % or 40–50 % of spring-flowering herbs in temperate deciduous forests of North America (Handel et al. 1981; Beattie and Culver 1981; Beattie 1985) and Europe (Gorb and Gorb 2003), respectively.

Seeds of myrmecochorous plants bear specialized lipid-rich appendages, elaiosomes, for attracting ants (Sernander 1906). Ant workers collect the seeds and usually carry them to their nests (Fig. 1). Some seeds reach the nests, whereas others are dropped during transport (Hughes and Westoby 1992; Gorb and Gorb 1999a). In the nests, the energy-laden elaiosomes are removed and consumed, whereas intact and viable seeds are commonly deposited either in underground nest chambers or in “waste piles” outside the nest (Buckley 1982; Beattie 1985; Keeler 1989;

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Gorb et al. 2000). The ants benefit by receiving high quality food rich in fats, fatty acids, sugars, amino acids and proteins (Bresinsky 1963; Thompson 1973; Beattie 1985; Soukup and Holman 1987; Lanza et al. 1992; Fischer et al. 2008). Although mean dispersal distance is relatively short (Culver and Beattie 1978; Horvitz and Schemske 1986; Hughes and Westoby 1992; Gómez and Espadaler 1998; Ness et al. 2004), nevertheless myrmecochory provides plants with several selective advantages, such as protection of the seeds against predators and fire, avoidance of interspecific competition and reduction in the competition between the parental plant and its seedlings as well as among seedlings, or transportation of the seeds to sites suitable for germination and seedling development (see reviews (Beattie 1983, 1985; Giladi 2006; Rico-Gray and Oliveira 2007)).

For many plant species, seed dispersal by ants is the only dispersal method used (obligate myrmecochory). Another part of the myrmecochorous group of plants is composed of diplochorous species using another dispersal method, mostly autochory, in addition to ant dispersal (facultative myrmecochory) (Sernander 1906; Ulbrich 1928; Berg 1966; Beattie and Lyons 1975; Nakanishi 1994; Ohkawara and Higashi 1994; Gorb and Gorb 2003). Seeds, depending on their dimensions and elaiosome size (or elaiosome-to-seed ratio), are attractive to different ant species to a different extent and have different dropping rates during transport to/from the nest (Culver and Beattie 1980; Davidson and Morton 1981; Kjellsson 1985; Horvitz and Schemske 1986; Bond and Stock 1989; Oostermeijer 1989; Higashi et al. 1989; Hughes and Westoby 1990; Gorb and Gorb 1995, 1999a, 1999b; Mark and Olesen 1996; Gorb 1998; Garrido et al. 2002; Mayer et al. 2005; Edwards et al. 2006; Alcántara et al. 2007). These distinctions, together with differences

in the dimensions of the ant colony's territory, sizes of ant individuals, locations of waste piles and overall behaviour (e.g. foraging strategy) of the ants, presumably influence dispersal success, abundance, distribution and survival of myrmecochorous plants in the ecosystem.

The ant species complex in the ecosystem is continuously changing in time and space, and the long-term effects of ant–plant interactions on the plant community are still not clear. Knowing that fate and germination success of seeds as well as survival of seedlings depend on the biology of the seed dispersal agents (Davidson and Morton 1981; Hughes and Westoby 1992; Gorb and Gorb 2000, 2003; Gorb et al. 2000; Garrido et al. 2002; Cuautle et al. 2005; Giladi 2006; Rico-Gray and Oliveira 2007), the question arises about the effect of the spatial distribution of different ant species in the ecosystem on the number and distribution of myrmecochorous plants with different dispersal strategies. In the present study, we aim at modelling of the population dynamics of two myrmecochorous plants having various dispersal strategies in an ecosystem with two ant species differing in their seed preferences, colony territory size and location of their waste piles. The present model incorporates the interactions of only four species, while ant and plant communities are greatly more complex.

As a basis for the model, we used our observations and experimental data on ant–seed interactions obtained in the deciduous forest of the Central Ukraine (Gorb and Gorb 2003). This set of data contained information on the removal and dropping rates of ant-dispersed seeds (Gorb 1998; Gorb and Gorb 1995, 1999a, 1999b, 2000), seed dispersal distance (Gorb and Gorb 1999a), soil seed bank (Gorb and Gorb 2003) and seed-related ant behaviour (Gorb et al. 2000). This manifold information from one ecosystem allowed us to simulate possible scenarios of plant distribution within the ecosystem after the reduction in the abundance or local extinction of one of the ant species. We use the term “local extinction” here in the sense that the species disappeared in the visible forest area considered in the model. This does not mean that it is extinct globally.

The main goal of this study is to determine a correlation between the number of nests of different ant species and the stability of the ecosystem under consideration. Taking into account that survival of different plant species strongly depends on the location and number of the ant nests, one could expect that if one ant species would partially or totally disappear from the system, this could cause dramatic changes in the plant populations as well. To elucidate this, we performed a set of numerical experiments with different numbers of ant nests.



**Fig. 1** Ants *Formica polyctena* collecting elaiosome-bearing seeds of the violet *Viola odorata*

**Model and simulations**

To simulate time-dependent behaviour of the forest ecosystem under consideration, we applied the following combination of discrete and continuous model. A subsystem of ant nests is treated as two separate arrays of discrete points  $\{x_{jk}, y_{kj}\}$ . The nests are assumed to be randomly placed initially inside a fixed area in two-dimensional space  $[x, y]$ . Here, the indices  $\{k\}$  and  $\{j\}$  numerate two different species of ants  $k = 1, 2$  and a particular ant nest  $j = 1, \dots, N_k$  in each set of ant nests.

Index  $k = 1$  corresponds to the nest of larger ants having a larger foraging territory, and  $k = 2$  corresponds to smaller ants with a smaller territory. Initial numbers of the nests at  $t = 0$  are always fixed and equal to  $N_1 = 10$  and  $N_2 = 50$ , respectively. For simplicity in further simulations, we selected a square forest area of size  $L_x \times L_y$  with constant equal sides  $L_x$  and  $L_y$ :  $L_x = L_y = 50$  m.

Spatial distributions of the ant nests and the corresponding plant densities are developed by the system self-consistently as a result of a self-organized process and in general are unknown to us "ab initio". To get correct initial conditions, we have to start from some more or less natural random initial conditions and wait a transient time in order to get a self-organized structure. In this study, we applied this approach and used the initial positions for the ant nests at  $t = 0$  given by the following formulae:

$$x_{kj} = L_x \zeta_{kj}, \quad y_{kj} = L_y \zeta_{kj} \tag{1}$$

where  $\zeta_{kj}(x, y)$  are  $\delta$ -correlated random numbers  $\langle \zeta_{kj} \zeta_{k'j'} \rangle = \delta_{kk'} \delta_{jj'}$  uniformly distributed in the interval  $[-1/2 \div 1/2]$  along both spatial coordinates  $x$  and  $y$ . Briefly, one can say that original nests are distributed uniformly and independently in the square of forest domain. We do not force them to lie outside the territories of each other, but it naturally happens after transient time for subsequent generations.

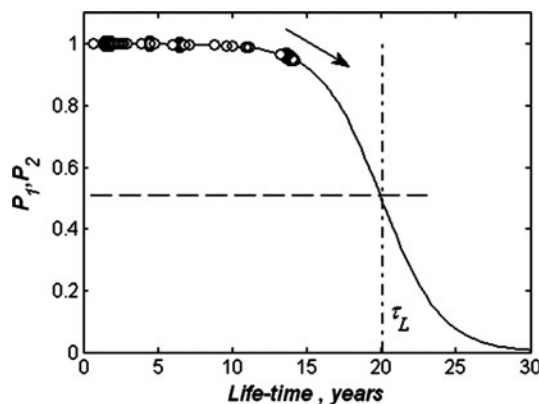
One of the most important sources for the dynamic behaviour of the populations presented here is the ants' ability, from time to time, to change the position of their nests, relocating (almost randomly) from one place to another within the forest. According to biological observations (Smallwood 1982; Brian 1983; Hölldobler and Wilson 1990), each nest exists for a limited time in a particular position  $\{x_{jk}, y_{kj}\}$ . This time is defined by the ant species, environmental conditions and other factors and can be approximately estimated to be around 15-20 years. During the main part of this period (let us call it "life-time"  $\tau_L$ ), the probability of finding  $P_k = P_k(t)$ ;  $k = 1, 2$  the ant nest in the same place is very close to the unit  $P_k = 1$  and is almost constant. Below for simplicity, we have assumed that the nests of both ant species have existed in fixed positions approximately for the same "life-time"  $\tau_L$ , which was set to

equal to 20 years. In the frame of the model, it means in fact that nests live an average of 20 years, with life-time chosen from the given distribution. The locations for the new nests are then chosen uniformly from the region, but excluding areas within the existing territories.

To simulate this process numerically, we applied the following procedure. For each time step  $t$  for both arrays of ant nests, we generated arrays of random numbers  $\zeta_{kj}(t)$ , uniformly distributed in the interval  $[0, 1]$ , and compared them with a smoothed step-like function  $P_k(\delta t_{kj}) = 1 / (\exp \frac{\delta t_{kj} - \tau_L^k}{0.1 \tau_L^k} + 1)$ , which has regulated the width of decay from 1 to 0 and is shown in Fig. 2.

The procedure is organized as follows. Instant "living time"  $\delta t_{kj}$  is calculated individually for every ant nest starting from the moment of its appearance in a given place. When a randomly generated number  $\zeta_{kj}(t)$  apparently exceeds the function  $P_k(\delta t_{kj})$ , a corresponding nest from the array  $k$  with the particular index  $j$  leaves its current place with the coordinates  $(x_{jk}, y_{kj})$  and randomly moves to a new one. At this time, we also reset its "living time"  $\delta t_{kj}$  to zero and its "life" begins in a new position from the beginning  $\delta t_{kj} = 0$ .

It is expected that each ant colony has its own territory (circle) with a radius  $R_k$  differing for large and small ants:  $R_1 = 5$ ;  $R_2 = 1$ . Formally, when an ant nest moves to a new place, its position can be randomly chosen within the entire forest area  $L_x \times L_y$ . However, one has to exclude the regions (circles) already occupied by a colony of the same ant species (Gorb et al. 2000). If, occasionally, a new ant nest position appears within an already existing circle, the programme repeats the random choice of a new position until a correct place in an empty region is found.



**Fig. 2** Dependence of the probability of an ant nest to remain in the same position ("survive") in a forest in a "life-time", during which the nest already exists in this place. *Small and large circles* mark positions of the instant "life-times" for two different ant species, respectively. The *arrow* shows the direction along the curve, in which these positions move with time. When the ant nest leaves its current place and moves to another one in the forest, the corresponding circle jumps back to its initial point at zero time

To simulate the ability of the ants to disperse plant seeds, each ant nest is assumed to have, around its current position, a region with positive impact on the probability  $z_k^{k'}(x, y)$  of the plants to survive and produce new seeds for the next generation. Here, we use the subscripts  $k = 1, 2$  to numerate the nests of different ant species, and the superscripts  $k' = 1, 2$  to numerate different species of plants (large-seeded and small-seeded, respectively). In general, both large and small ants can take and transport both kinds of seeds, but with different probabilities  $B_k^{k'}$ . This was previously shown experimentally for a series of plant species and a few ant species (Gorb 1998; Gorb and Gorb 1995, 1999b, 2000). The probabilities can strongly correlate with the presence or absence of ants of other species (Gorb and Gorb 1999b).

Large and small ants collect the seeds of different plant species having different sizes and dispose them either inside the rings near the borders of their territories (large ants) or inside small circles within the entire territory of the ant colony (small ants). The deposition of seeds close to the territory border is characteristic for large *Formica polyctena* ants (Gorb et al. 2000). Seed distribution over the entire ant colony territory results from a high dropping rate of small seeds during transport (Gorb and Gorb 1999a): collected seeds do not reach the nest and are dispersed along the foraging trails. In the model, it is accounted for in a different spatial structure of the “preference coefficients”:

$$z_1(x, y) = \sum_{k=1}^2 B_k^1 \sum_{j=1}^{N_1} \exp \left[ - \left( \frac{r - R_1}{R_2} \right)^2 \right];$$

$$z_2(x, y) = \sum_{k=1}^2 B_k^2 \sum_{j=1}^{N_1} \exp \left[ - \left( \frac{r}{R_2} \right)^2 \right]$$
(2)

where  $r = \sqrt{(x - x_{kj})^2 + (y - y_{kj})^2}$  is the distance from an arbitrary point in area  $L_x \times L_y$  to the position of the ant nest  $\{x_{jk}, y_{kj}\}$ . The values of the coefficients  $B_k^{k'}$  should be chosen to reflect experimentally observed preferences in the choice of different seeds by the different ant species (Gorb 1998; Gorb and Gorb 1995, 1999b, 2000) and were taken equal to  $B_1^1 = 4, B_1^2 = 0.1B_1^1, B_2^2 = 1, B_2^1 = 0.1B_2^2$ .

Space–time evolution of the seed densities  $f_{1,2}(x, y)$  is determined by the following equations:

$$\begin{cases} \frac{\partial f_1}{\partial t} = c_1 \Delta f_1 + f_1(G_1 - g + u z_1) \\ \frac{\partial f_2}{\partial t} = c_2 \Delta f_2 + f_2(G_2 - g + u z_2) \\ \frac{\partial u}{\partial t} = c_u \Delta u + u(G_u - f_1 - f_2) \end{cases}$$
(3)

The additional (last) equation in the system Eq. (3) describes time- and space-distributed resources (soil fertility, illumination, water supply), which are not directly

specified within the frames of this model, but integrally define necessary conditions for seed (plant) survival. As usual for all populations (including density  $u(x, y)$  of the resources), the evolutionary equations include “birth-rate” constant coefficients  $G_{1,2}$  and  $G_u$ , describing fertility of the particular species  $G_{1,2}$  or monotonous growth of the resources  $G_u$  in the absence of their consumption and ant activity. Activity- and resource-dependent impacts on the density evolution is incorporated into the model by the terms proportional to the products  $f_{1,2}u z_{1,2} \equiv f_{1,2}(x, y)u(x, y)z_{1,2}(x, y)$ . The biological meaning of these terms is as follows. Activity of the ants has an impact on local growth of the plants, which is proportional to the density  $f_{1,2}$  itself, the amount of the resources available in this territory and the “preference coefficients” defined according to Eq. 2. The products  $f_{1,2}u z_{1,2} \equiv f_{1,2}(x, y)u(x, y)z_{1,2}(x, y)$  in the equations are written in dimensionless form, and all conversion factors for the transformation of the resource  $u$  into the seed densities and vice versa are included in the coefficients connecting these values.

The system Eq. 3 also contains non-local terms with Laplacian operators

$$\Delta f(x, y) \equiv \frac{\partial^2 f}{\partial x^2} + \frac{\partial^2 f}{\partial y^2}$$
(4)

which describe spatial dispersion of the seeds and resources in each generation due to different physical factors (like wind or a random deposition, for example) that are independent on the activity of the ants. The coefficients  $c_1 = 0.1; c_2 = 0.3$  and  $c_u = 0.1$  near non-local terms of the system Eq. 3 regulate an intensity of the spatial dispersion  $f_{1,2}$  for both plants and resources, according to the biological meaning of each density. The death rate  $g = 0.1$  is taken to be equal for both of the plants. The particular values of the parameters  $c_1, c_2, c_u, g$  in the Eq. 3 define characteristic rates of the spatial dispersion, growth and death of the plants. These rates must correlate with other characteristic times of the problem. In particular, we have chosen mean time, during which the ant nest exists in one place, to be equal to 20 years and defined one year as a time unit in the corresponding function  $P_k(\delta t_j) = 1 / \left( \exp \frac{\delta t_j - \tau_k}{0.1 \tau_k^k} + 1 \right)$  (see Fig. 2). In these units, the rates of the spatial dispersion, growth and death of the plants must be faster. These values should be numerically adjusted to correspond to one year seasonal cycle. Numerical adjustment in the frame of the model gives the estimations used further in the Eq. 3:  $c_1 = 0.1; c_2 = 0.3; c_u = 0.1; g = 0.1$ .

As has already been commented above, initial conditions for solving the equations in Eq. 3 self-consistently with variable positions of the ant nests are unknown. But if the dynamics of the system described by these equations is

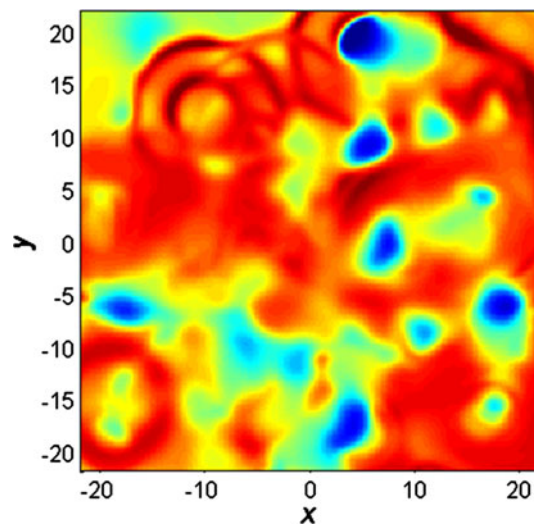


correct, it must be stable and stationary external conditions must tend at  $t \rightarrow \infty$  to some attracting scenario (some stationary, but generally non-static behaviour). In this case, we can “naturally” produce correct distribution starting from a quite arbitrary one. The quickest and one of the simplest ways to get it is to start from uniformly distributed random initial densities  $f_{1,2}$  and  $u$ . One can easily check that in a time scale of this particular problem, it takes around 40-60 years to reach almost stationary behaviour with deviations of the mean values smaller than 10 %. Below, we always used a period of 50 years as a transient run to create natural initial distributions from the random trial ones. Random initial conditions, together with the randomness in the motion of the ant nests during the process, including their possible appearance and disappearance in given positions, lead to different realizations of the stationary state. However, if the total number of the ant nests is fixed, the process is stable and leads to the same total plant populations  $F_{1,2} = \int_{Area} f_{1,2}(x,y) dx dy$  with deviations of the mean numbers of plant individuals smaller than 10 %.

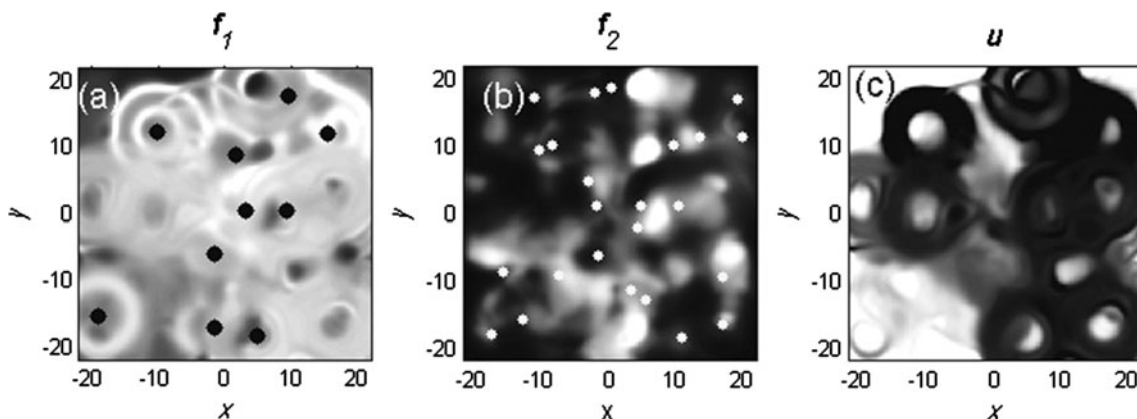
**Results**

Typical instant density distributions  $f_{1,2}$  and  $u$  obtained at  $N_1 = 10$  and  $N_1 = 50$  are shown in Fig. 3 by the grey-scale maps. Here, brighter regions correspond to higher densities. Two types of nests of larger and smaller ants are shown by circles of corresponding sizes. Mutual correlation between space distributions of two plant species is presented in Fig. 4 by the difference in the densities  $f_1 - f_2$ . Generally, each plant species avoids the places already occupied by another species. As a result, different regions are found to be occupied by different plant species. This can be visualized by the colour map, where red regions are occupied by  $f_1$  and blue ones belong to  $f_2$  densities, respectively.

The results of the numerical experiments with a decreasing number of ant nests are summarized in Figs. 5, 6, 7, 8, 9 and 10. During the first 50 years, we generated a stationary realization (new each time) of all the subsystems (ants and plants) with fixed numbers  $N_1 = 10$  and  $N_2 = 50$ , and then gradually decreased the total number of one type of the ant nests down to a given remaining value  $N_{1,2final}$ . Numerical procedure of changing the numbers  $N_1$  or  $N_2$  resembles one we used for the relocation of the nests from one place to another. For this purpose, we generate uniformly distributed random numbers  $\zeta_{kj}(t)$  and compare them with a preliminary specified threshold. If  $\zeta_{kj}(t)$  exceeds the threshold, the ant nest disappears. All continuous variables



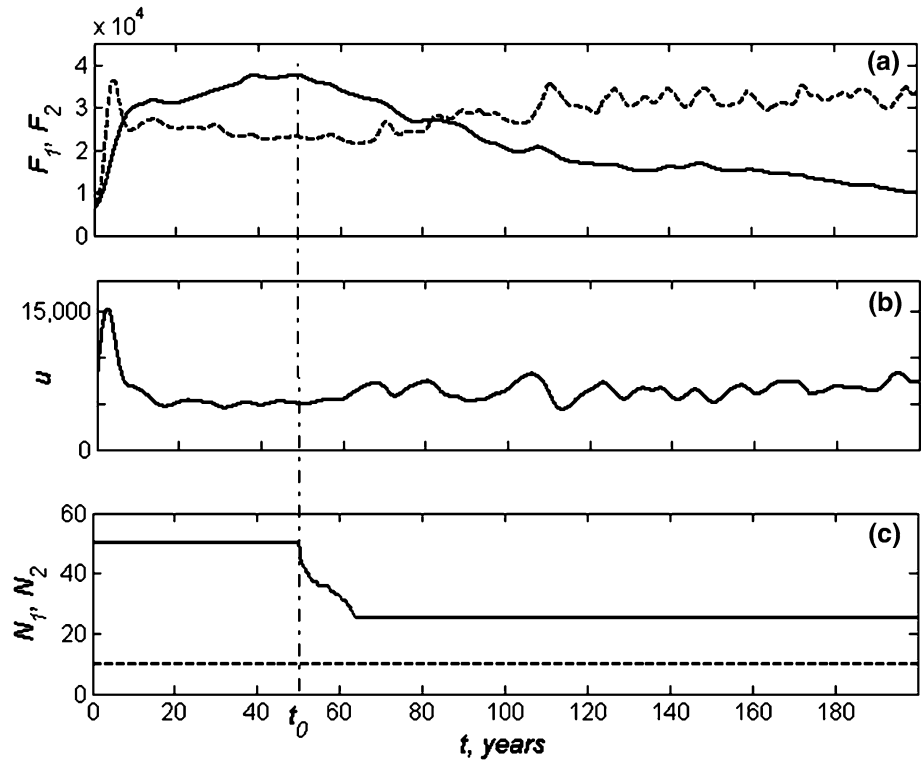
**Fig. 4** Spatial correlation of the instant distributions shown in Fig. 3. Each density distribution  $f_{1,2}$  avoids places occupied by other plant species. As a result, the regions occupied by different species are visualized here by a colour map for a difference  $f_1 - f_2$ , where bright regions correspond to higher density. Red and blue colours correspond to the densities  $f_1$  and  $f_2$ , respectively. (Color figure online)



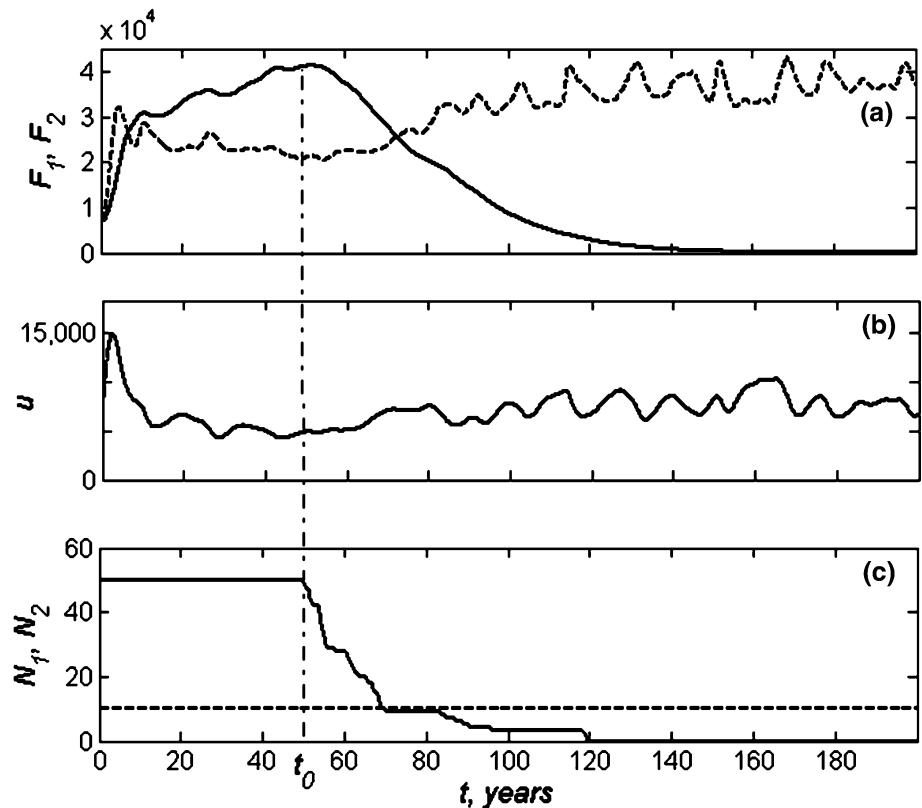
**Fig. 3** Typical instant configurations. Positions of the ant nests are shown by *large* and *small circles* in the subplots (a) and (b), respectively. Spatial configurations of the corresponding densities of

plants  $f_{1,2}$  are presented in the same subplots by the grey-scale maps. Distribution of the resources at the same moment in time is shown in the subplot (c)

**Fig. 5** Time-dependent total populations. The values  $F_{1,2} = \int_{Area} f_{1,2}(x, y) dx dy$  are shown in subplot (a) by *dashed* and *solid* lines, respectively. Subplot (b) presents corresponding time evolution of resources  $u$ . Time-dependent numbers of the ant nests  $N_1$  and  $N_2$  are shown by *dashed* and *solid* lines in the subplot (c), respectively. Vertical dash-dotted line marks a time moment, when number  $N_2$  begins to decrease from its trial value  $N_2 = 50$  to the final one  $N_2 = 30$



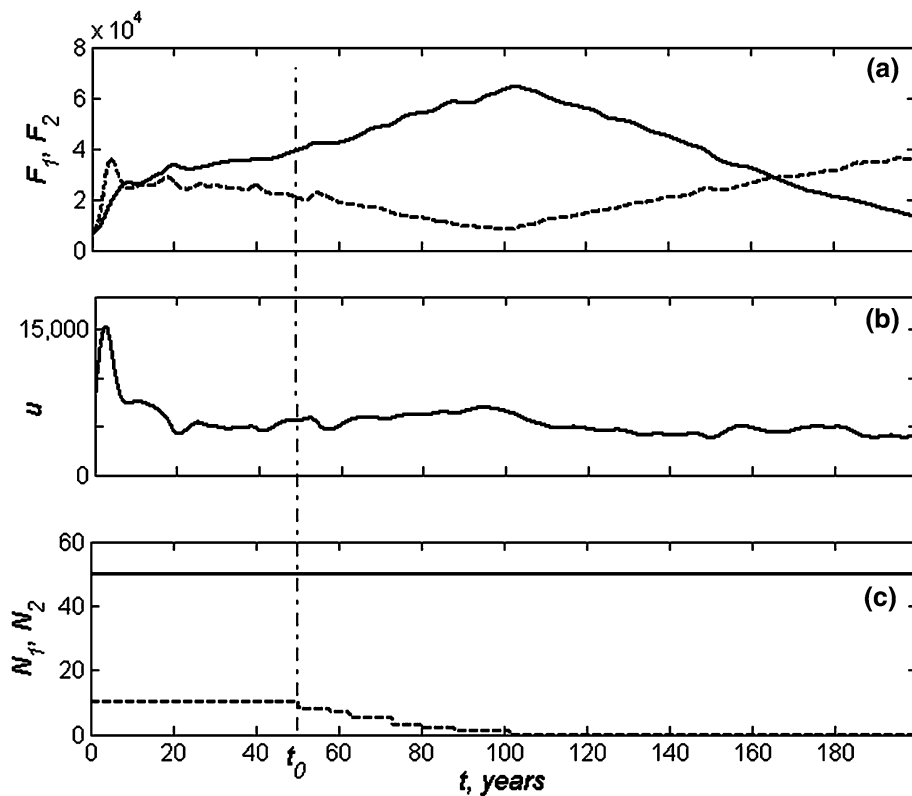
**Fig. 6** The same values as in Fig. 5 for the scenario, where value  $N_2$  varies from  $N_2 = 50$  to  $N_2 = 0$



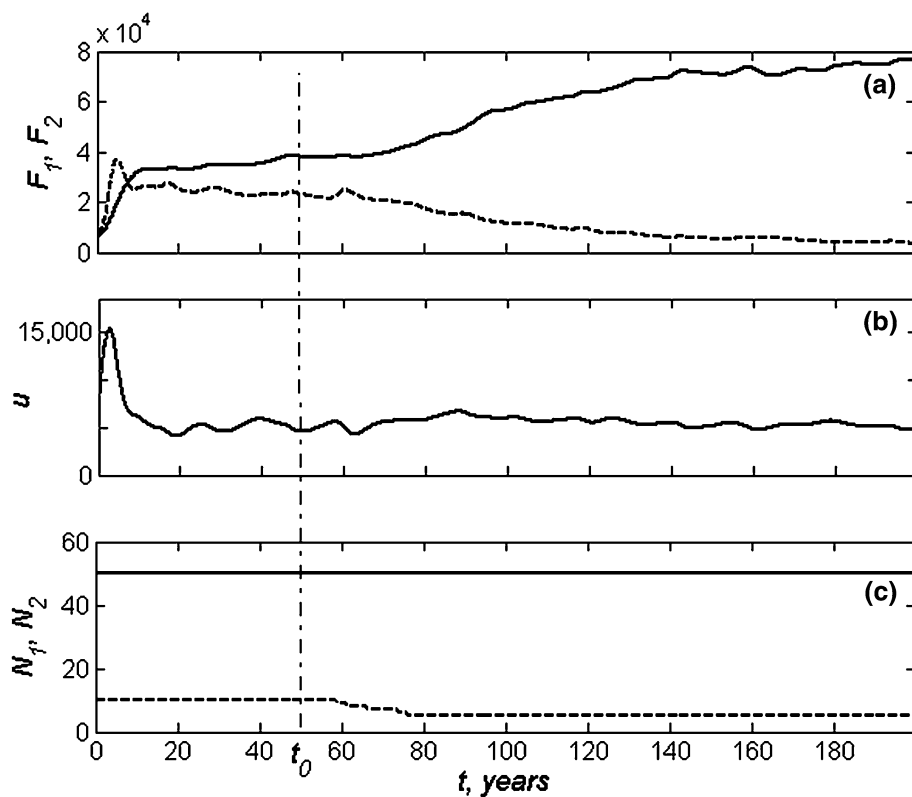
corresponding to the vanishing ant species become *sparse* arrays and corresponding numbers  $N_{1,2} = N_{1,2}(t)$  decrease as well. The process continues until  $N_{1,2} > N_{1,2final}$ . Both

plant species compete for the resources. A change in the numbers  $N_{1,2}$  modifies competition conditions and shifts the equilibrium between them.

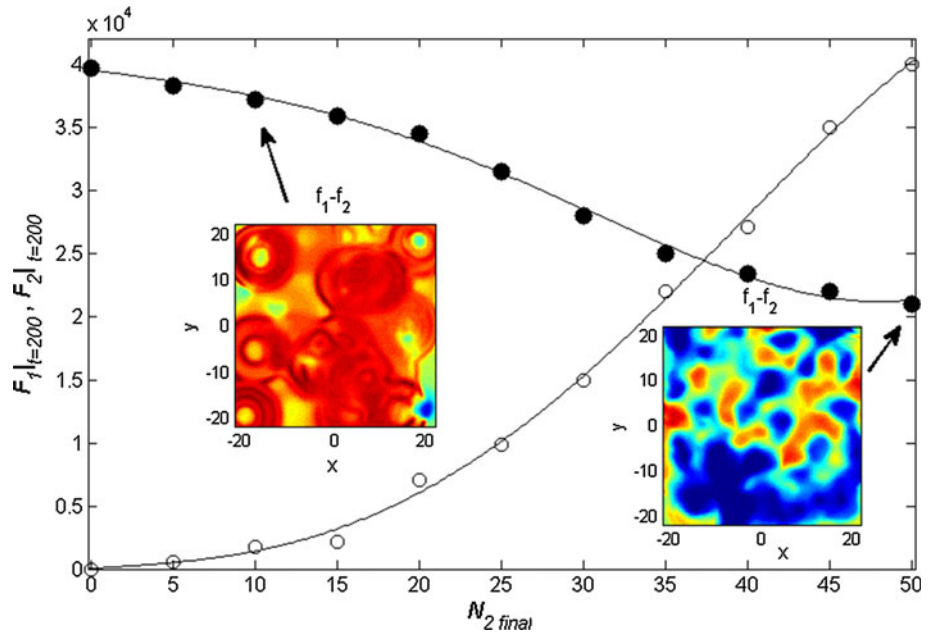
**Fig. 7** The same values as in Fig. 5 in the case, where  $N_1$  varies from  $N_1 = 10$  to  $N_1 = 0$



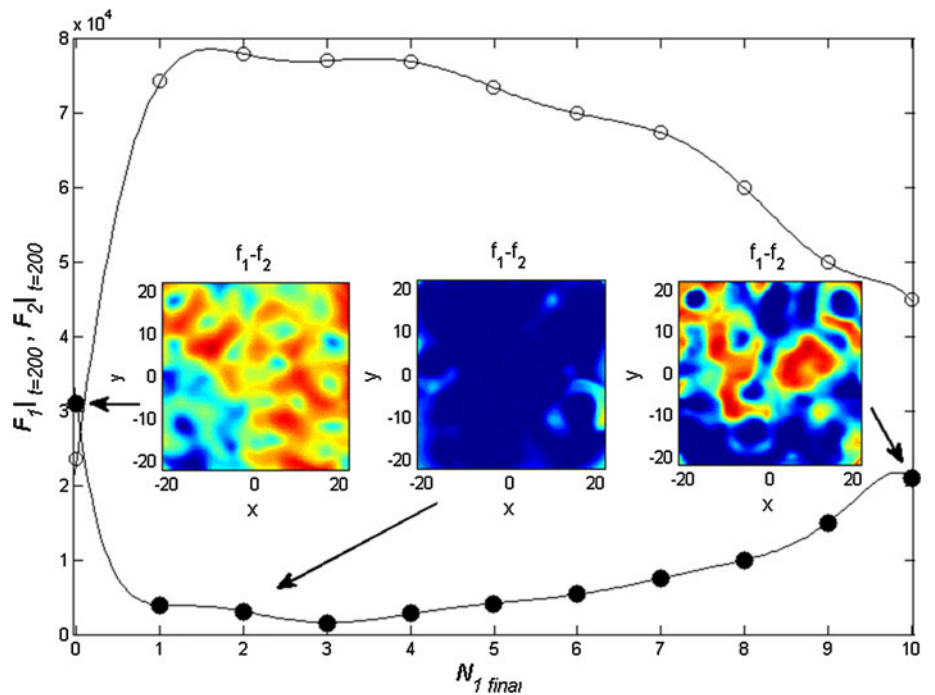
**Fig. 8** The same values as in Fig. 5 for the scenario, where the number  $N_1$  varies from  $N_1 = 10$  to half of its initial value ( $N_1 = 5$ )



**Fig. 9** Final total populations. The values  $F_{1,2}$  at  $t = 200$  years obtained for different  $N_{2\text{final}}$  are presented by *black* and *empty circles*, respectively. The curves connecting the circles are used as guides for the eyes only. Typical density maps of the difference  $f_1 - f_2$  at large  $N_{2\text{final}} = 50$  and small  $N_{2\text{final}} = 10$  values are shown in the inserts. The *arrows* mark total amounts  $F_1$ , to which these distributions are related. In the inserts, *red* and *blue colours* correspond to the densities  $f_1$  and  $f_2$ , respectively, and bright regions correspond to higher density. (Color figure online)



**Fig. 10** The same values as in Fig. 9 obtained when  $N_{1\text{final}}$  is varied. Typical density maps of the difference  $f_1 - f_2$  at large  $N_{1\text{final}} = 10$ , small  $N_{1\text{final}} = 2$  and zero  $N_{1\text{final}} = 0$  final numbers  $N_{1\text{final}}$  are shown in the inserts. The *arrows* mark total amounts  $F_1$ , to which these distributions are related. In the inserts, *red* and *blue colours* correspond to the densities  $f_1$  and  $f_2$ , respectively, and bright regions correspond to higher density. (Color figure online)



Figures 5 and 6 show how total populations  $F_{1,2}$  vary at two different final numbers of the ant nests  $N_{2\text{final}} = 25$  and  $N_{2\text{final}} = 0$  at fixed  $N_1 = 10$ . It is clearly demonstrated that a decrease in  $N_{2\text{final}}$  leads to a strong reduction in the corresponding plant species and can even cause its local extinction if  $N_{2\text{final}}$  is smaller than some threshold. On the contrary, when  $N_2$  is fixed and  $N_1$  goes down, this can lead to a wider variety of the scenarios. The main reason for such a complex behaviour comes from different preferences by the ants for the seeds of different plant species having different sizes. Experimental observations show that smaller ants also prefer larger seeds

(Gorb and Gorb 1999b). In the presence of large ants, they usually avoid confronting them and are not able to take the large seeds. However, when large ants are absent, small ants do take large seeds (Gorb and Gorb 1999b). One can account for such a possibility in the model by varying the coefficient  $B_2^1$ . Instead of a “naive” constant value  $B_2^1 = 0.1B_2^2$ , we suppose it to depend on a number  $N_1(t)$ :  $B_2^1(t) = \frac{2B_2^2}{1+1.9N_1(t)}$ . This value tends to the limit  $B_2^1 = 0.1B_2^2$  at  $N_1 = 10$  and goes to a new relation  $B_2^1 = 2B_2^2$  when  $N_1 \rightarrow 0$ , which corresponds to the above-mentioned preference  $B_2^1 > B_2^2$ .



Time-depending results of the simulations at  $N_{1\text{final}} = 0$  and  $N_{1\text{final}} = 5$  are shown in Figs. 7 and 8. A typical scenario of time evolution is presented in Supplementary videos 1–3. These movies present, in dynamics, a particular realization of the process shown as an example in Fig. 8. Supplementary video 1 corresponds to Fig. 1, Supplementary video 2 summarizes information presented in Figs. 2 and 8, and Supplementary video 3 reproduces configurations analogous to that shown in Fig. 4.

To get a general picture of the phenomenon, one can vary each final value  $N_{1\text{final}}$  or  $N_{2\text{final}}$  in the entire interval  $0 \leq N_{1\text{final}} \leq 10$  and  $0 \leq N_{2\text{final}} \leq 50$  and fix another one ( $N_1 = \text{const}$  for varied  $N_2$ , and vice versa). Corresponding results are summarized in Figs. 9 and 10, presenting final total plant populations  $F_{1,2}$  at  $t \rightarrow 200$  years for both cases. Some representative final configurations of the spatially distributed difference of the plant densities  $f_1 - f_2$  are shown in the inserts in the figures.

### Biological interpretation

Seed dispersal has an important effect on plant communities, it influences the dynamics and persistence of populations, the abundance and distribution of species, determines spatial structure of populations, and affects their adaptations to environmental changes and survival (Nathan and Muller-Landau 2000; Rico-Gray and Oliveira 2007). Our study demonstrates the dynamics of the spatial pattern of two myrmecochorous plant species varying in their dispersal strategies in the forest ecosystem with two ant species having different seed-related behaviours. We have found that in a stable ecosystem with a constant number of nests of two ant species, different plants tend to occupy different sites (Fig. 3a, b). Differences in distribution and population densities between the plant species (Fig. 4) result from different seed preferences by the ants, different deposition sites of seeds on the ant territories, and competition for resources (Fig. 3c).

The decrease in the nest number of one ant species (small ants) causes, with time, the gradual reduction in the total population of the small-seeded plant species, whereas the oscillating population of another (large-seeded) plant continuously grows and occupies more sites, profiting from decreased competition for resources (Fig. 5). These effects become more pronounced with the lessening of the number of surviving nests (Fig. 9). In the case of local extinction of these ant nests, the small-seeded plant species also disappear, and the entire territory will be occupied by a highly (up to twofold) increased population of the other plant species (Figs. 6 and 9 (at  $N_{2\text{final}} = 0$ )).

The reduction in the nest number of the other ant species (large ants) leads to various scenarios depending on the

number of remaining nests. For a given ant species complex, when the nest number of large ants decreases down to less than one-third of the initial number, a continuous strong reduction in the large-seeded plant population occurs simultaneously with an increase in the small-seeded plant population (Figs. 8 and 10 (at  $3 < N_{1\text{final}} < 10$ )). At a certain (critical) final nest number, almost local extinction of the large-seeded plant species occurs, while the small-seeded plant strongly dominates (Fig. 10 at  $N_{1\text{final}} = 3$ ). However, the situation changes cardinally, when only a very few nests of large ants remain or when these nests totally disappear. Since large seeds are attractive also to small ants, they readily collect these seeds when large ants are absent. Finally, small ants will prefer large seeds and refuse to disperse small seeds of the respective plants. This situation results in an extremely rapid growth of the large-seeded plant population, which will even exceed its initial condition, whereas the population and density of the small-seeded plant, initially associated with small ants, will drastically drop to a level lower compared to the initial one (Figs. 7 and 10 (at  $0 \leq N_{1\text{final}} \leq 2$ )).

This study shows that the abundance and spatial distribution of myrmecochorous plants strongly depends on both ant abundance and ant species composition in the ecosystem. The virtual long-term experiment revealed the importance of ant species diversity for maintaining myrmecochorous plant species diversity in the ecosystem. Competition for resources between the plant species is tuned by the ant community in such a way that it may lead to the reduction or even local extinction of a particular plant population, when one ant species disappears. The present model can be potentially extended to a higher number of ant and plant species and adapted to various seed-related behavioural features of different ant species.

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### References

- Alcántara JM, Rey PJ, Manzaneda AJ, Boulay R, Ramírez JM, Fedriani JM (2007) Geographic variation in the adaptive landscape for seed size at dispersal in the myrmecochorous *Helleborus foetidus*. *Evol Ecol* 21:411–430
- Beattie AJ (1983) Distribution of ant-dispersed plants. *Sonderbl Naturwiss Ver Hamburg* 7:249–270
- Beattie AJ (1985) The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge
- Beattie AJ, Culver DC (1981) The guild of myrmecochores in the herbaceous flora of West Virginia forests. *Ecology* 62:107–115
- Beattie A, Lyons N (1975) Seed dispersal in *Viola*: adaptations and strategies. *Am J Bot* 62:714–722
- Berg RY (1966) Seed dispersal of *Dendromecon*: its ecologic, evolutionary, and taxonomic significance. *Am J Bot* 53:61–73

- Bond WJ, Stock WD (1989) The costs of leaving home: ants disperse myrmecochorous seeds to low nutrient sites. *Oecologia* 81:412–417
- Bresinsky A (1963) Bau, Entwicklungsgeschichte und Inhaltsstoffe der Elaiosomen. *Studien zur myrmekochoren Verbreitung von Samen und Fruechten*. *Bibl Bot* 126:1–54
- Brian MV (1983) *Social insects: ecology and behavioural biology*. Chapman & Hall, London
- Buckley RC (1982) Ant-plant interactions: a world review. In: Buckley RC (ed) *Ant-plant interactions in Australia*. Dr. W. Junk, The Hague, pp 111–141
- Cuaute M, Rico-Grey V, Díaz-Castelazo C (2005) Effects of ant behaviour and extrafloral necteries presence on seed dispersal of the neotropical myrmecochore *Turnera ulmifolia* L. (Turneraceae), in a sand dune matorral. *Biol J Linn Soc* 86:67–77
- Culver D, Beattie A (1978) Myrmecochory in *Viola*: dynamics of seed-ant interactions in some West Virginia species. *J Ecol* 66: 53–72
- Culver D, Beattie A (1980) The fate of *Viola* seeds dispersed by ants. *Am J Bot* 67:710–714
- Davidson DW, Morton SR (1981a) Myrmecochory in some plants (F. Chenopodiaceae) of the Australian arid zone. *Oecologia* 50: 357–366
- Davidson DW, Morton SR (1981b) Competition for dispersal in ant-dispersed plants. *Science* 213:1259–1261
- Edwards W, Dunlop M, Rodgeron L (2006) The evolution of rewards: seed dispersal, seed size and elaiosome size. *J Ecol* 94: 687–694
- Fischer R, Richter A, Hadacek F, Mayer V (2008) Chemical differences between seeds and elaiosomes indicate an adaptation to nutritional needs of ants. *Oecologia* 155:539–547
- Garrido JL, Rey PJ, Cerda X, Herrera CM (2002) Geographical variation in diaspore traits of an ant-dispersed plant (*Helleborus foetidus*): are ant community composition and diaspore traits correlated? *J Ecol* 90:446–455
- Giladi I (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* 112:481–492
- Gómez C, Espadaler X (1998) Myrmecochorous dispersal distances: a world survey. *J Biogeogr* 25:573–580
- Gorb O (1998) Seed morphology and seed dispersal in two *Corydalis* species. *Ukrainian Bot J* 55:62–66
- Gorb SN, Gorb EV (1995) Removal rates of seeds of five myrmecochorous plants by the ant *Formica polyctena* (Hymenoptera: Formicidae). *Oikos* 73:367–374
- Gorb SN, Gorb EV (1999a) Dropping rates of elaiosome-bearing during transport by ants (*Formica polyctena* Foerst.): implications for distance dispersal. *Acta Oecol* 20:47–53
- Gorb SN, Gorb EV (1999b) Effects of ant species composition on seed removal in deciduous forest in Eastern Europe. *Oikos* 84:110–118
- Gorb E, Gorb S (2000) Effects of seed aggregation on the removal rates of elaiosome-bearing *Chelidonium majus* and *Viola odorata* seeds carried by *Formica polyctena* ants. *Ecol Res* 15:187–192
- Gorb E, Gorb S (2003) Seed dispersal by ants in a deciduous forest ecosystem. Kluwer, Dordrecht
- Gorb SN, Gorb EV, Puntilla P (2000) Effects of redispersal of seeds by ants on the vegetation pattern in a deciduous forest: a case study. *Acta Oecol* 21:293–301
- Handel SN, Fisch B, Schatz GE (1981) Ants disperse a majority of herbs in the mesic forest community in New York State. *Bull Torrey Bot Club* 108:430–437
- Higashi S, Tsuyuzaki S, Ohara M, Ito F (1989) Adaptive advantages of ant-dispersed seeds in the myrmecochorous plant *Trillium tschonoskii* (Liliaceae). *Oikos* 54:383–394
- Hölldobler B, Wilson EO (1990) *The ants*. Harvard University Press, Cambridge
- Horvitz CC, Schemske DW (1986) Seed dispersal of a neotropical myrmecochore: variation in removal rates and dispersal distance. *Biotropica* 18:319–323
- Hughes L, Westoby M (1990) Removal rates of seeds adapted for dispersal by ants. *Ecology* 71:138–148
- Hughes L, Westoby M (1992) Fate of seeds adapted for dispersal by ants in Australian sclerophyll vegetation. *Ecology* 73:1285–1299
- Keeler KH (1989) Ant-plant interactions. In: Abrahamson WG (ed) *Plant-animal interactions*. McGraw-Hill, New York, pp 207–242
- Kjellsson G (1985) Seed fate in a population of *Carex pilulifera* L. I. Seed dispersal and ant seed mutualism. *Oecologia* 67:416–423
- Lanza J, Schmitt MA, Awad AB (1992) Comparative chemistry of elaiosomes of 3 species of *Trillium*. *J Chem Ecol* 18:209–221
- Lengyel S, Gove AD, Latimer AM, Majer JD, Dunn RR (2009) Ants sow the seeds of global diversification in flowering plants. *PLoS ONE* 4(5):e5480
- Mark S, Olesen JM (1996) Importance of elaiosome size to removal of ant-dispersed seeds. *Oecologia* 107:95–101
- Mayer V, Ölzant S, Fischer RC (2005) Myrmecochorous seed dispersal in temperate regions. In: Forget P-M, Lambert JE, Hulme PE, Vander Wall SB (eds) *Seed fate: predation, dispersal and seedling establishment*. CABI Publishing, Wallingford, pp 176–195
- Nakanishi H (1994) Myrmecochorous adaptations of *Corydalis* species (Papaveraceae) in southern Japan. *Ecol Res* 9:1–8
- Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants, and consequences for recruitment. *Trends Ecol Evol* 15:278–285
- Ness JHJ, Bronstein L, Andersen AN, Holland JN (2004) Ant body size predicts the dispersal distance of ant-adapted seeds: implications of small-ant invasions. *Ecology* 85:1244–1250
- Ohkawara K, Higashi S (1994) Relative importance of ballistic and ant dispersal in two diplochorous *Viola* species (Violaceae). *Oecologia* 100:135–140
- Oostermeijer JGB (1989) Myrmecochory in *Polygala vulgaris* L., *Luzula campestris* (L.) DC and *Viola curtisii* Forster in a Dutch dune area. *Oecologia* 78:302–311
- Rico-Gray V, Oliveira PS (2007) *The ecology and evolution of ant-plant interactions*. University of Chicago Press, Chicago
- Sernander R (1906) *Entwurf einer Monographie der europäischen Myrmekochoren*. K Sven Vetenskapsacad Handl 41:1–410
- Smallwood J (1982) Nest relocation in ants. *Insect. Soc.* 29:138–147
- Soukup VG, Holman RT (1987) Fatty acids of seeds of North American pedicellate *Trillium* species. *Phytochemistry* 26:105–1018
- Thompson SN (1973) A review and comparative characterization of the fatty acid compositions of seven insect orders. *Comp Biochem Physiol* 45:467–482
- Ulbrich E (1928) *Biologie der Fruechte und Samen (Karpobiologie)*. Springer, Berlin