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# Dynamics of species coexistence: maintenance of a plant-ant competitive metacommunity

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The metacommunity approach is an adequate framework to study coexistence between interacting species at different spatial scales. However, empirical evidence from natural metacommunities necessary to evaluate the predictive power of theoretical models of species coexistence remains sparse. We use two African ant species, *Cataglyphis mckeyi* and *Petalomyrmex phylax*, symbiotically associated with the myrmecophyte *Leonardoxa africana africana*, to examine spatio-temporal dynamics of species coexistence and to investigate which environmental and life-history parameters may contribute to the maintenance of species diversity in this guild of symbiotic ants. Using environmental niche partitioning as a conceptual framework, we combined data on habitat variation, social structure of colonies, and population genetics with data from a colonisation experiment and from observation of temporal dynamics. We propose that the dynamics of ant species colonisation and replacement at local and regional scales can be explained by a set of life history traits for which the two ants exhibit hierarchies, coupled with strong environmental differences between the different patches in the level of environmental disturbances. The role of the competition–colonisation tradeoff is discussed and we propose that interspecific tradeoffs for traits related to dispersal and to reproduction are also determinant for species coexistence. We therefore suggest that species-sorting mechanisms are predominant in the dynamics of this metacommunity, but we also emphasise that there may be many ways for two symbionts in competition for the same host to coexist. The results speak in favour of a more complete integration of the various metacommunity models in a single theoretical framework.

How do species coexist? How is cooperation maintained in the face of cheating? These two questions have long occupied distinct intellectual traditions in ecology, but recently have begun to merge in the field of interspecies interactions, in which, for instance, mutualists (cooperators) and parasites (cheaters) may compete to exploit the same resources. The motivating idea is that for interspecific interactions involving cheater and cooperator species, the persistence of cooperation is tantamount to the persistence of the cooperator species, despite competition with cheater species (Yu 2001, Ferdy et al. 2002, Hoeksema and Kummel 2003). As a result, species coexistence theory (Chesson 2000) provides a useful way to examine the maintenance of mutualism, with the added twist being that the 'resource' being competed for is itself one of the mutualistic partners (typically, the 'host'), which allows the host to evolve mechanisms to skew competition in favour of the cooperator (Kiers et al. 2003, Edwards et al. 2006).

Diverse theories attempt to explain species coexistence (i.e. the patterns of distribution, abundance and interaction of competing species) at both local and regional scales (Chesson 2000, Amarasekare et al. 2004, Holyoak et al.

2005). The precursor work of Skellam (1951) provided the basis for competition–colonisation (CC) and source–sink (SS) hypotheses. But there was rapid separation between studies that considered spatially homogeneous and heterogeneous competitive environments, and for decades this artificial dichotomy has clouded some issues. It has resulted, for example, in CC tradeoffs and SS dynamics being viewed as mutually exclusive mechanisms of coexistence, when they should rather be studied in a common framework relevant to metacommunity ecology (Amarasekare et al. 2004). Building on the inputs of the metapopulation approach (Levins 1969), but still anchored in the dichotomy between CC and SS hypotheses, four major classes of models exist to date to explain species coexistence at the metacommunity level – a metacommunity being defined as a set of local communities that are linked by the dispersal of multiple interacting species. They are referred to as the 'neutral', 'mass-effect' (a multi-species version of SS dynamics), 'patch dynamic' (a multi-sites version of the CC tradeoff) and 'species-sorting' (a filtering of species based on variability in the environment and in species traits) paradigms (Leibold et al. 2004). These models differ in

the assumptions made about the nature of differences among local sites, or about the ecological traits of species in the metacommunity.

Several attempts have been made to combine different models of species coexistence within a single coherent metacommunity framework and the idea of environmental niche partitioning is one of them (Chesson and Huntly 1997, Pacala and Rees 1998, Bolker and Pacala 1999, Yu and Wilson 2001, Levine and Rees 2002). This approach expands upon the 'species-sorting' paradigm and incorporates both source-sink dynamics and pre-emptive competition. Environmental niche partitioning hypothesizes coexistence as a result of tradeoffs between life history traits of competing species and of at least one source of environmental heterogeneity, potentially being an axis of the ecological niches of the species. A key point here is that niche partitioning is not a prerequisite to coexistence but rather the ecological outcome of species confrontation, i.e. the niche partitioning is not the process that determines coexistence but the result of that coexistence. Few empirical studies have so far supported this model (Yu et al. 2004, Gilbert et al. 2008, Questad and Foster 2008).

Some of the mutualisms that have been most usefully examined under the species coexistence framework are symbioses between plants and ants (Stanton et al. 2002, Yu et al. 2001, 2004, Feldhaar et al. 2003, Fonseca and Benson 2003, Palmer et al. 2003). In the tropics, symbiotic ant-plant mutualisms involve species of over 100 genera of angiosperms and 40 genera of ants (Davidson and McKey 1993). Generally, plants involved in these interactions – myrmecophytes, or ant-plants – develop myrmecodomatia, structures that are inhabited by symbiotic plant-ants. The ant colony exploits resources from its host-plant in the form of housing and sometimes food provided by the plant, e.g. extrafloral nectar (Heil and McKey 2003). These plant-ants often protect the plant against herbivores. These mutualistic interactions are frequently parasitized by other species which exploit resources provided by the plant partner, and are competitors of mutualistic ants. Ant-plant mutualisms parasitized by other ant species are particularly convenient models to study the coexistence of species competing for the same resource. Coexistence of different ants restricted to the same host species has so far been studied only in two plant-ant systems in which the parasitic ants protect but 'castrate' their plant hosts, destroying flowers so that plant resources are redirected to growth, and thus to housing and food for the ants. Parasitic plant-ants coexist with mutualistic ants, the latter being presumably responsible for the maintenance of myrmecophytic traits in host-plant populations. The first of these systems is the interaction between the Neotropical plant *Cordia nodosa* and its ant associates. Yu et al. (2001, 2004) proposed that mutualistic ants of the genus *Azteca* were able to coexist with the parasite *Allomerus* within a replacement model through lottery processes. Variation in plant density may favour spatial coexistence through a competition-colonisation tradeoff and a between-species hierarchy in dispersal capacity (Yu et al. 2001, 2004). The other system is a guild of East African acacia ants, inhabiting the hollow spines of *Acacia drepanolobium* (Young et al. 1997, Palmer et al. 2000, 2002, 2003). This system is somewhat different insofar as the four protective host-specific ant species

mutually exclude each other, and all occur at high frequency. There is ecological succession of ant species according to tree size and occupant turn-over may occur through a competition-colonisation tradeoff corresponding to a displacement lottery model, though other mechanisms also play a role in the maintenance of species diversity in this system (Palmer 2003, Palmer et al. 2003).

The objective of the present study is to apply a metacommunity approach to a third ant-plant system, this time including a parasitic, non-protecting but non-castrating ant symbiont to examine which mechanisms are likely to contribute to species coexistence. In this study we use environmental niche partitioning as a conceptual framework. We first looked for environmental factors that showed sufficient variation, either at the intra- or at the interpopulation scale, to have explanatory power. We then focused on a set of life history traits of the two ants, in order to identify those for which the two species showed marked differences. Life history traits indeed condition species' responses to environmental heterogeneity and are thus key components in the spatio-temporal niche differentiation that is required for coexistence under this framework (Shea et al. 2004). While using previously published information as background on the system, this paper is based on original and multidisciplinary data collected from 1995 to 2002.

## Methods

### Study system

The system is the protection mutualism between the African ant-plant *Leonardoxa africana* ssp. *africana* (Leguminosae: Caesalpinioideae) and the ant *Petalomyrmex phylax* (Formicinae), an interaction parasitized by the ant *Cataulacus mckeyi* (Myrmicinae). *Leonardoxa a. africana* (hereafter referred to as *Leonardoxa*) is a highly specialized myrmecophytic understorey treelet restricted to a narrow band of coastal lowland forest in Cameroon, Central Africa (McKey 2000). *Leonardoxa* individuals occur in dense, well-defined and patchily distributed stands, each patch often comprising between 100 and 500 trees. This myrmecophyte provides nest sites and food for ants, in the form of hollow stem chambers and nectar produced by foliar nectaries, respectively. It is associated with two host-specific symbiotic plant-ants. Workers of the mutualistic species, *Petalomyrmex phylax* (hereafter referred to as *Petalomyrmex*), actively patrol leaves and significantly deter herbivory (McKey 1984, Gaume et al. 1997). Workers of the parasite of the mutualism, *Cataulacus mckeyi* (hereafter referred to as *Cataulacus*), do not patrol leaves, and trees occupied by this ant suffer high levels of herbivory (Gaume and McKey 1999, Debout et al. 2005). Each tree is most often occupied by a single colony of only one of the two ant species.

Each mature colony of *Petalomyrmex* is restricted to a single tree (McKey 1984). Occupation of a tree always implies foundation of a new colony that is initiated by a single winged female (called alate) after dispersing from her natal tree and mating. Then the new queen, confined within a domatium, rears the first brood in isolation by claustral founding. Once established, the resident colony usually prevents the effective establishment of new founding

individuals on the same plant. However, in most populations, some *Petalomyrmex* females never leave their natal colonies and mate locally with related males, resulting in secondary polygyny and a slight inbreeding at the population scale (Dalecky et al. 2005, 2007). The single patch for which within-population genetic structure has been studied showed a more pronounced pattern of genetic isolation by distance (IBD) among *Petalomyrmex* colonies than that found for *Cataulacus* (Debout et al. unpubl.). These data suggest that dispersal of *Petalomyrmex* is more restricted than that of *Cataulacus* at the scale of a host-plant patch. The distribution of *Petalomyrmex* is restricted to the area occupied by *Leonardoxa*, but within this area it is absent from the northernmost populations of the plant (McKey 2000, Brouat et al. 2004).

*Cataulacus* is present over the entire range of *Leonardoxa*. Colony size is smaller than that of *Petalomyrmex*, and workers do not display the stereotyped patrolling behaviour of *Petalomyrmex* (Gaume and McKey 1999, Debout et al. 2005). Workers of *Cataulacus* have no measurable protective effect against herbivores of the host's young leaves (Gaume and McKey 1999). Trees they occupy are thus usually unhealthy and very slow-growing. Genetic analysis has shown that colonies of *Cataulacus* are mono- or oligogynous with usually singly-mated queens and that the mating system is panmictic at the population scale. This fact, together with the absence of genetic isolation by distance among colonies within a population, suggests longer-distance alate dispersal than in the mutualist *Petalomyrmex* at the scale of a host-plant patch (Debout et al. 2003, Debout et al. unpubl.). *Cataulacus* commonly has a polydomous colonial structure, in that one colony may occupy two or more neighbouring trees. Workers colonise these neighbouring trees and transport brood into their domatia. Genetic data indicate that polydomy in *Cataulacus* is unrelated to queen-worker conflict and instead confers an advantage by providing a mechanism of short-distance dispersal initiated by workers (Debout et al. 2003). This mechanism is absent from the mutualist *Petalomyrmex*, in which occupancy of a tree always implies the riskier strategy of independent claustral foundation.

This guild of symbiotic plant-ants appears to be ideally suited to study species coexistence. The strict host-specificity of the two ant species and the restriction of their diet to resources provided by their host-plant simplify characterisation of their ecological niches. Furthermore, colonies can be easily collected whole, allowing reliable measures of allocation to growth and reproduction. Finally, species frequencies in different parts of the range can be easily measured by censusing the host-plants, i.e. the obligatory ant nest sites, and scoring the resident ant species. In this paper we use the term 'microsite' (or nest site) to denote a single individual plant, capable of holding the nest of one ant colony, and the term 'patch' to denote a locality (a discrete area of habitat) holding a stand of host plants and consequently a local community of their associated ants. A metacommunity is defined as a set of local communities that are linked by dispersal of multiple potentially interacting species (Gilpin and Hanski 1991, Wilson 1992). Despite the difficulty of applying theoretical definitions of metacommunities to real empirical situations (Leibold et al. 2004), we are confident that our system approximates quite well to the theoretical

concept since it is an assemblage of discrete, permanent habitat patches.

## Metacommunity structure and description of the patches

### Study sites

We limited our study to the southern third of the known range of the ants' host-plant, as the forest habitat within the remaining part of its range has been largely destroyed by clearing for plantations. Experiments and surveys were carried out in 25 patches along an 85 km transect, with endpoints at two intensively studied patches of *Leonardoxa*, Ebodjé (termed EBO, 02°34'N, 09°51'E), Southern Province, and N'kolobondé (termed BOU, 03°13'N, 10°15'E), Littoral Province, Cameroon (Fig. 1). This corresponds to the southern half of the known historical distribution of *Petalomyrmex* and to the southern third of the known historical distribution of *Cataulacus*.

### Environmental parameters

Three sources of environmental heterogeneity were investigated. (1) Nest site density may affect the cost of dispersal, as local scattering of nest sites may be a constraint for dispersing queens. Within seven patches of plants, nest site density was measured as the mean number of *Leonardoxa* individuals in a grid of adjacent 5 × 5 m quadrats (from 19 to 76 quadrats in each patch). Independently, we assigned for 24 patches (including the previous seven) a semi-quantitative index of relative nest site density (from 1 to 4). (2) Tree height was measured for 1034 trees across seven patches (62 to 261 trees per patch) in order to estimate the distribution of tree size and examine whether identity of the ant inhabitant varied with tree height. (3) Local disturbance, caused by selective logging or by natural branch- or tree-fall gaps, is a major extrinsic factor of colony extinction and subsequent nest site release. *Leonardoxa* trees are frequently sufficiently damaged so that resident colonies die, particularly when the trunk is broken. A few months after such a disturbance, *Leonardoxa* individuals usually produce new branches by regrowth, creating opportunities for colonisation by founding females (Gaume and McKey 1999, Dalecky et al. 2005). Disturbance therefore increases both the mortality rate of adult colonies and the frequency of vacant microsites available for colonisation. We scored disturbance in 13 host-plant patches as the proportion of *Leonardoxa* exhibiting signs of major injury and regrowth on the trunk. This estimate integrates disturbance over a few decades (Dalecky et al. 2005).

### Ant species distribution at the regional level

The frequency of colonies was investigated for each ant species in 25 patches by scoring host-plants for ant occupancy by opening a few domatia per plant. In 16 patches we also scored instantaneous nest site availability defined as the percentage of vacant host plants within a patch. We counted trees sheltering only founding females as vacant and excluded young seedlings (<15 cm height) as they had not yet produced habitable domatia. Before attempting to interpret species coexistence in the context

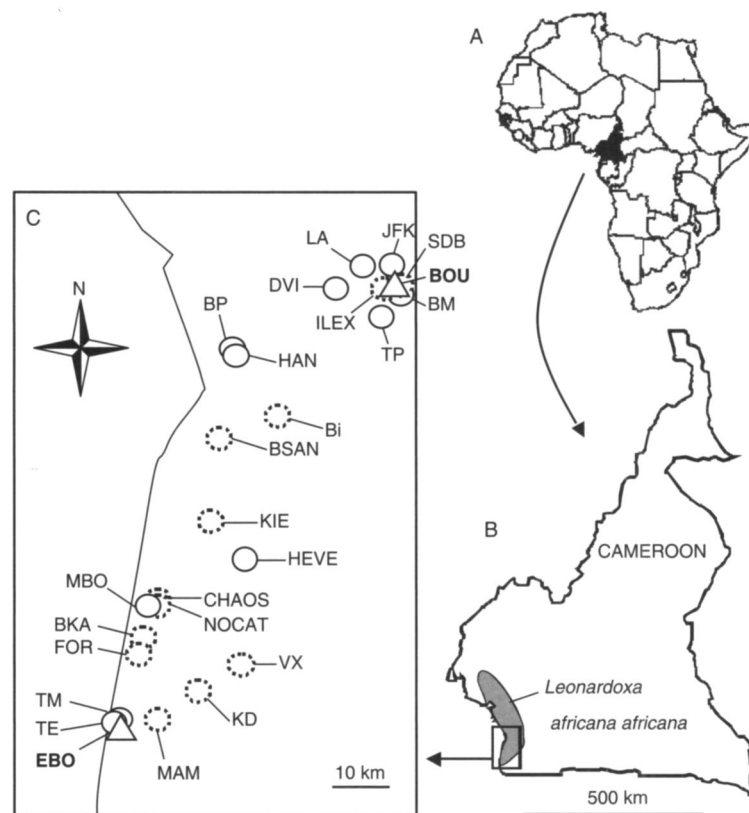


Figure 1. Spatial distribution of the 25 study sites. The two long-term study sites EBO and BOU are represented by triangles. For these populations data are available on all parameters studied. Plain circles indicate populations for which data on disturbance and occupation frequencies are available, and dotted circles indicate populations for which only occupation frequencies were measured.

of environmental niche partitioning, we considered whether species distribution pattern differed from null expectations under the neutrality hypothesis. In the context of neutral communities, in which all individuals are equivalent with regard to their prospects of reproduction, competition and death, but with limited dispersal, a decrease of community similarity with geographic distance is expected (Hubbell 2001). Similarity of ant communities between patches was evaluated using the abundance-based Bray–Curtis index computed using the software EstimateS ver. 8.0 (Colwell 2006). To test for a correlation between matrices of geographic distances (log-transformed) and Bray–Curtis indices we use the sub-program ISOLDE (from the software GENEPOP ver. 3.3, Raymond and Rousset 1995) to compute Mantel's tests (10 000 permutations).

### Life history traits of the ants

With the aim to determine candidate tradeoffs facilitating coexistence, we investigated whether there was interspecific variation in five life history traits: colony maximum fecundity, rate of growth to reproductive maturity, mortality rate of incipient colonies, dispersal distance and longevity of nest site occupation.

### Colony fecundity and rate of growth to reproductive maturity

The social structure of colonies for the two ant species was examined by collecting and counting pupae and adults from

all castes for 75 colonies of *Cataulacus* and 90 colonies of *Petalomyrmex*, collected whole from 10 and 14 patches respectively. Colony dissections allowed us to obtain precise snapshot measures of both colony size (number of adult workers, i.e. the basis of ant benefits to plants) and colony fecundity (total number of male and female alates).

### Recolonisation experiment: dynamics of nest site colonisation

In the EBO study site, we monitored the live stumps of 25 experimentally-defaunated trees, after they had been cut for colony dissection, within a patch where non-manipulated trees were used as controls. Because all domatia had been removed on manipulated trees, de novo colonisation was dependent on the growth of new shoots. Ant occupancy of manipulated and control trees was scored first one year after the original cutting, and then a further three months after that. Average frequencies of the two species in the community were computed using a mean of 157 non-manipulated trees over three years, two before and one after the experiment.

### Genetic estimates of dispersal

Using microsatellite markers, the genotype of one diploid individual (worker or queen) per colony was determined in *Petalomyrmex*, for 12 polymorphic loci (detailed genetic results in Dalecky et al. 2007) for 427 colonies from 21 populations (on average  $20 \pm 1$  colonies per population) and in *Cataulacus*, for 10 polymorphic loci (Debout et al.

2002) for 218 colonies from 18 populations (average over 16 populations  $10 \pm 2$  colonies per population; and a further two populations with 2 and 62 colonies respectively). Between-population genetic differentiation and isolation by distance (IBD) were investigated using GENEPOP ver. 3.3 (Raymond and Rousset 1995) by regressing multilocus pairwise estimates of  $F_{ST}/(1 - F_{ST})$  on pairwise ln-geographical distances (Rousset 1997), and tested with the Spearman rank correlation coefficient using Mantel's tests based on 10 000 permutations of locations. Confidence intervals for the slopes of IBD were implemented using the IBD Web Service ver. 3.11 (Jensen et al. 2005) with 10 000 randomisations. As for genetic distances we used population pairwise  $\theta_{ST}$  (an analogue of  $F_{ST}$ ) previously calculated in GENEPOP. Geographical distances between sample locations were measured as linear distance in meters. Estimators of the relative per-generation among-patch average dispersal distance of the two ants can be estimated from the genetic pattern of IBD, once the relative abundance of each ant is taken into account. The value of the slope of this regression calculated in GENEPOP is approximately equivalent to the quantity  $1/(4 \pi D \sigma^2)$  (Leblois et al. 2003), where  $\sigma^2$  is an estimator of the average dispersal distance, and  $D$  is the density of reproductive individuals (here approximated as colonies). Confidence intervals for  $\sigma^2$  were estimated by jackknifing over populations when calculating the slope of IBD in GENEPOP.

#### Temporal dynamics of microsite occupation

The temporal dynamics of occupation of nest sites were investigated by monitoring a total of 1215 permanently tagged trees in seven patches (62 to 442 trees per patch) over two to seven years. We applied mark-recapture models to estimate annual probabilities of transition,  $\psi$ , between

the different occupancy states (unoccupied, occupied by *Petalomyrmex*, by *Cataulacus* or by both species), and average longevity of nest site occupation for each of the two species. To describe patch-level dynamics of the different occupancy states, we used an information matrix derived from recapture histories of nesting sites and the multi-state option in the software MARK (G. C. White, <<http://www.warnercnr.colostate.edu/~gwhite/mark/mark.htm>>) that generates the maximum-likelihood estimates of survival and transition probabilities for occupancy states.

Unless specified otherwise, all statistical analyses were performed using SYSTAT ver. 9, SPSS 12.0.2 or SAS/STAT, p-values are two-tailed and mean  $\pm$  SE are given. We also present confidence intervals (CI) at 95% level following Colegrave and Ruxton (2003).

## Results

### Distribution and frequencies of the two ants at the regional level

The relative abundances of the two ant species were highly variable among patches (Table 1). The mutualist ant *Petalomyrmex* was present in all studied patches and was always more abundant than the parasite *Cataulacus*, occupying a mean of  $77 \pm 4\%$  of the trees (range: 37–100%). The parasite *Cataulacus*, although found throughout the transect, was absent from 36% of the sampled patches. The relative abundance of this species was quite low ( $7 \pm 2\%$ ) and varied considerably among patches, ranging from 0 to 31%. The remaining trees ( $15 \pm 3\%$ ) were unoccupied, but were most likely unfavourable nest sites, being they were either too small or unhealthy host-plants. No relationship was found between the geographic

Table 1. Occupation data of *L. a. africana* in all studied populations. Percentages are of the total number of trees.

Site	Total number of trees	<i>P. phylax</i>	%	<i>C. mckeyi</i>	%	Empty trees	%	Unknown	%	Sampled area (m <sup>2</sup> )	Density index
EBO	277	211	76	15	5	47	17	4	1	2500	3
TE	82	69	84	2	2	11	13	0	0	800	4
TM	94	66	70	14	15	13	14	1	1	800	3
MAM	71	53	75	11	15	5	7	2	3	2500	1
KD	34	34	100	0	0	0	0	0	0	.	2
VX	153	133	87	2	1	18	12	0	0	.	3
FOR	27	10	37	2	7	15	56	0	0	~600	1
BKA	13	9	69	0	0	4	31	0	0	~900	0.5
MBO	88	85	97	0	0	3	3	0	0	~1500	3
CHAOS	62	54	87	0	0	8	13	0	0	~900	3
NOCAT	50	50	100	0	0	0	0	0	0	~900	3
HEVE	137	61	45	43	31	32	23	1	1	800	4
KIEN	55	40	73	5	9	10	18	0	0	~500	2
BSAN	29	15	52	4	14	10	34	0	0	~800	3
Bi	36	17	47	4	11	15	42	0	0	~400	2
HAN	100	91	91	4	4	5	5	0	0	.	3
BP	113	110	97	1	1	2	2	0	0	~900	3
TP	45	40	89	1	2	4	9	0	0	.	3
DVI	110	106	96	0	0	4	4	0	0	~900	3
BM	146	124	85	17	12	1	1	4	3	~1500	3
BOU	277	188	68	40	14	44	16	5	2	2500	3
ILEX	30	19	63	5	17	6	20	0	0	~400	2
SDB	11	8	73	0	0	3	27	0	0	.	.
JFK	32	28	88	3	9	1	3	0	0	~800	3
LA	35	25	71	5	14	3	9	2	6	~500	2

distance and the Bray–Curtis index of similarity of ant communities between patches ( $p_{\text{(one-sided)}} = 0.861$ ).

## Sources of environmental heterogeneity

### Tree height

The distributions of the two species varied significantly across tree height (Kolmogorov–Smirnov  $D = 0.1791$ ,  $p < 0.001$ ). The parasite *Cataulacus* was present in all height classes, though rare below 0.5 m and above 7 m ( $n = 1$  and 2 respectively; Fig. 2). In contrast, the mutualist *Petalomyrmex* was present in all height classes, and always in high proportion ( $> 55\%$ ). Despite the statistical difference in the distribution of the two ant species, the data showed no clear niche separation by tree height (Fig. 2), suggesting that coexistence does not occur via succession. However, very young trees appeared more likely to be occupied by *Petalomyrmex* during their establishment stage: for trees below and above 1 m proportions of occupation were significantly different from the expected proportions over all patches ( $\chi^2_1 = 5.94$ ,  $p = 0.015$ ). Beyond this extremely low frequency of occurrence of *Cataulacus* in very young trees, there was no temporal niche partitioning. Once present, *Cataulacus* could be replaced. Foundation attempts by *Petalomyrmex* queens on *Cataulacus*-occupied trees and transition of occupation from *Cataulacus* to *Petalomyrmex* were relatively common.

### Local tree density

At the regional scale, the relative abundance of *Cataulacus* in a patch was not correlated with the host-plant density, whatever the measure of local density we considered: quantitative measure ( $n = 7$  patches, Spearman's  $\rho = -0.04$ ,  $p = 0.94$ ) or semi-quantitative index ( $n = 24$ , Spearman's  $\rho = -0.05$ ,  $p = 0.81$ ). On the other hand, at the within-patch scale, very local aggregations of *Leonardoxa* allowed some *Cataulacus* colonies to be polydomous (Debout et al. 2003).

### Local disturbance

Disturbance level, as gauged by tree injury rate, varied considerably among patches, with 15 to 86% of trees bearing evidence of breakage of the trunk and regrowth. The frequency of the parasite *Cataulacus* was positively correlated with this estimate of disturbance level (Fig. 3). The distributions of four variables (disturbance level, frequencies of the two species and of empty trees) were all normal (all; Kolmogorov–Smirnov's  $Z > 0.65$ ,  $p > 0.51$ ). Patches with higher disturbance had a higher frequency of empty trees (Pearson's  $r = 0.743$ ,  $p = 0.004$ ), a higher

frequency of *Cataulacus* ( $r = 0.655$ ,  $p = 0.011$ ), and a lower frequency of *Petalomyrmex* ( $r = -0.756$ ,  $p = 0.003$ ).

## Life history traits

### Genetic estimates of dispersal

At a regional scale, both species exhibited high genetic diversity. The multilocus  $F_{ST}$  value computed over all populations was 0.171 for *Cataulacus* and 0.126 for *Petalomyrmex*. The difference between the two species was not significant (Mann–Whitney test;  $Z = -0.75$ ,  $p = 0.45$ ). We then tested for genetic isolation by distance among pairs of patches for the two ant species using microsatellite markers. For both species, the slope of the relationship between the logarithms of inferred levels of gene flow [ $M_{hat} = (1/F_{ST} - 1)/4$ ] and geographic distance was equal to  $-0.50$ , i.e. differentiation between populations followed a two-dimensional model (Slatkin 1993). Consequently, geographic distances were log-transformed for the analyses and we used  $F_{ST}/(1 - F_{ST})$  as the measure of genetic differentiation (Rousset 1997). A significant genetic pattern of IBD, with a positive slope, was observed for both species (*Cataulacus*:  $p < 10^{-5}$ , slope = 0.096,  $r^2 = 0.44$ ; *Petalomyrmex*:  $p < 10^{-4}$ , slope = 0.033,  $r^2 = 0.31$ ), suggesting spatially limited dispersal (Fig. 4). IBD Web Service results were qualitatively comparable (*Cataulacus*:  $p < 10^{-4}$ , slope = 0.13 ( $\pm 0.01$ ),  $r^2 = 0.44$ ; *Petalomyrmex*:  $p < 10^{-4}$ , slope = 0.10 ( $\pm 0.01$ ),  $r^2 = 0.32$ ) and gave slightly overlapping 95% CI around the slopes that equalled respectively [0.108, 0.157] and [0.089, 0.126]. Although we did not detect a significant difference for the genetic pattern of IBD between the two species at  $\alpha = 0.05$ , in both analyses this pattern seemed more pronounced, with a higher slope, in *Cataulacus* than in *Petalomyrmex*. The mean pairwise  $F_{ST}$  were 0.152 ( $\pm 0.007$ ) for *Cataulacus* and 0.116 ( $\pm 0.004$ ) for *Petalomyrmex*, with non-overlapping 95% CI of [0.139, 0.166] and [0.108, 0.123] respectively. It shows that, on average, the genetic pairwise differentiation at this regional scale was higher in *Cataulacus* than in *Petalomyrmex*.

If we take into account the relative abundance of each ant species, we can compute a relative estimate of  $\sigma^2$ , the average dispersal distance. Considering typical plant patch size to be of the order of 500 individuals, and using observed mean colony frequencies of each species in the communities, we estimated mean relative values of population size  $N$  of colonies for the two ant species ( $N_{\text{Petal}} = 388$  [ $\pm 85$ ] and  $N_{\text{Catau}} = 44$  [ $\pm 42$ ]). We then obtained mean relative values for  $\sigma^2$  of 0.0054 (95% CI = [0.0053, 0.0055]) for *Petalomyrmex* and 0.0189 (95% CI = [0.0185, 0.0193]) for *Cataulacus*. The bootstrap distributions of the two specific  $\sigma^2$  have non overlapping 95% CI

Table 2. Hierarchies between life history traits for both species.

Life history traits		<i>C. mckeyi</i>	<i>P. phylax</i>
Fecundity	of alates at local scale	low (~10 sexuals)	high (>60 sexuals)
Dispersal		high	low
		high (polydomy)	low (monodomy)
Competitiveness at incipient colony stage		low	high
Growth		fast (~30 workers)	slow (~1000 workers)
Adult survivorship		low (2–4 years)	mean (8–10 years)

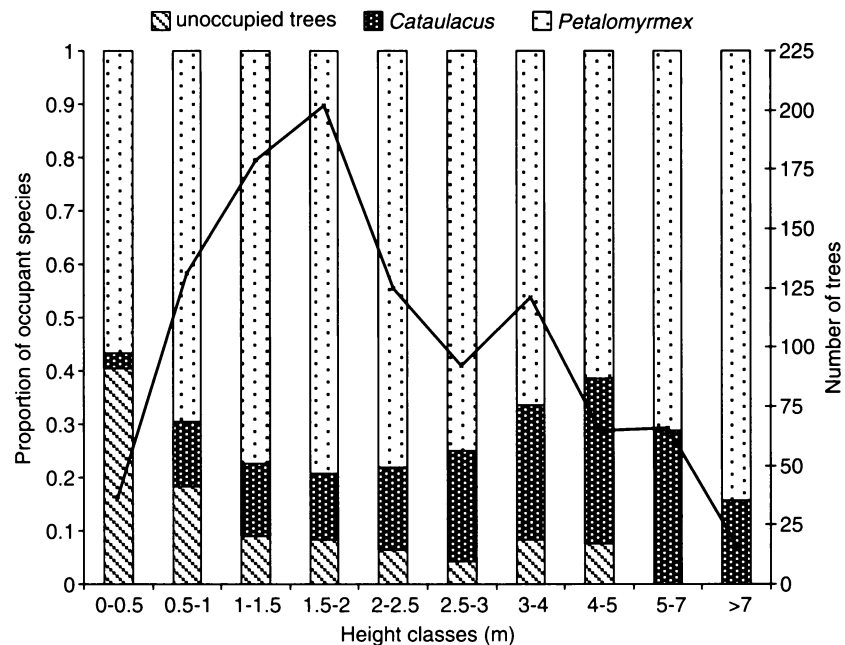


Figure 2. Proportion of occupant ant species as a function of the size (height) of trees. Black line: number of trees. Dashed bars: empty trees; black bars: trees occupied by *Cataulacus*; dotted bars: trees occupied by *Petalomyrmex*.

and so are significantly different at the  $p < 0.05$  level. Among-patch dispersal distance was thus estimated to be about four times higher for the parasite *Cataulacus* than for the mutualist *Petalomyrmex*, despite a similar or slightly more pronounced genetic pattern of IBD for the former.

Debout et al. (2003) showed that colonies of *Cataulacus* are facultatively polydomous, i.e. each colony may occupy one to several *Leonardoxa* trees. As a mechanism of short-distance dispersal initiated by workers, polydomy may further confer on *Cataulacus* the ability to pre-empt resources at a local scale.

#### Recolonisation experiment: dynamics of nest site colonisation

The average frequencies found for control trees in this local community were 71% for *Petalomyrmex* and 19% for

*Cataulacus*. One year after having been experimentally defaunated, all 25 manipulated trees showed new shoots that bore habitable domatia. All but two of these trees had been already recolonised and were occupied by incipient colonies with 52% of *Petalomyrmex* and 40% of *Cataulacus*. These frequencies were significantly different from the average frequencies of control trees found in this local community (Fisher's exact test,  $p = 0.003$ ). A further three months later, frequencies had changed, and 72% of manipulated trees were inhabited by *Petalomyrmex*, whereas only 12% were occupied by *Cataulacus*. The remaining trees were empty. Occupation frequencies of manipulated trees 15 months after cutting were significantly different from those of those trees 12 months after cutting ( $p < 0.001$ ), but converged towards the average frequencies of control trees in the same patch ( $p = 0.253$ ).

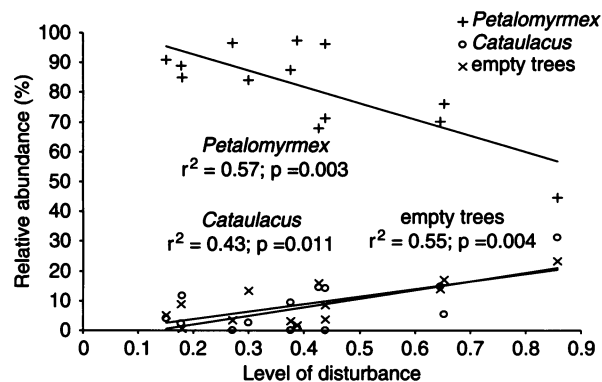


Figure 3. Relative abundance of the different occupancy states of the host-plant as a function of the level of disturbance, for 13 populations. ○: *Cataulacus*-occupied trees; +: *Petalomyrmex*-occupied trees; ×: empty trees.

#### Colony fecundity and rate of growth to reproductive maturity

Mean colony sizes were  $248 \pm 25$  for *Cataulacus* ( $n = 75$ ) and  $2978 \pm 260$  for *Petalomyrmex* ( $n = 90$ ; Mann-Whitney test:  $p < 0.0001$ ). The mean number of alate sexuals found while dissecting colonies was  $18 \pm 3$  for *Cataulacus* and  $69 \pm 12$  in *Petalomyrmex* (Mann-Whitney test:  $p < 0.001$ ). *Cataulacus* exhibited a smaller colony size (20 to 300 workers per colony) but colonies produced sexuals early in development (about 20 workers). In contrast, *Petalomyrmex* had larger colonies (up to 10 000 workers), but colonies only began to reproduce at a size of around 1000 workers (Fig. 5). As a result, slopes of the regression line between number of workers and number of sexuals were significantly different for *Cataulacus* and *Petalomyrmex* ( $t_{161} = 3.3$ ,  $p < 0.001$ ), revealing a growth-fecundity tradeoff between the two species.



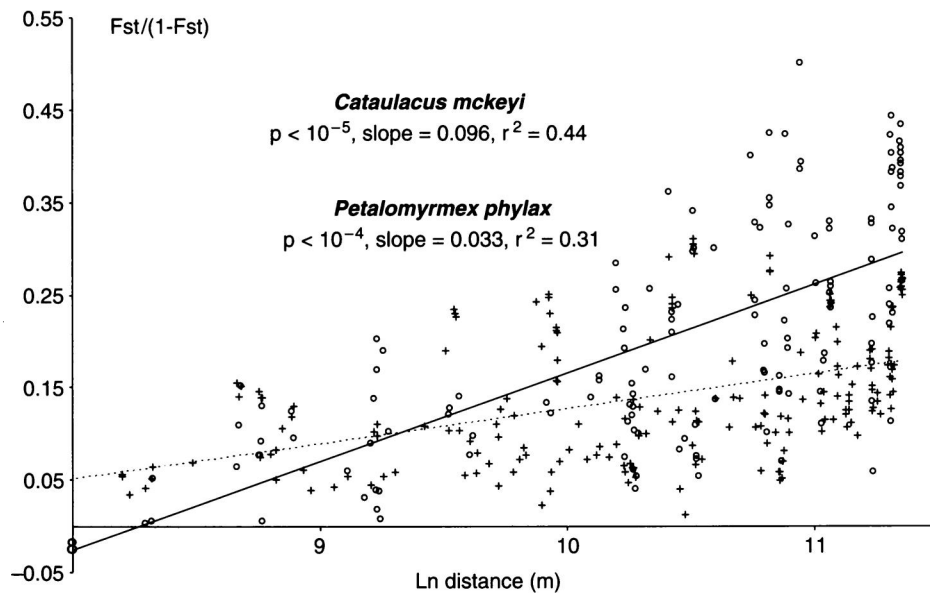


Figure 4. Regional-level of spatial genetic structure at microsatellite markers between pairs of populations for both species. Circles: *Cataulacus*, crosses: *Petalomyrmex*.

#### Temporal dynamics of microsite occupation

Mark-recapture data allowed us to estimate the within-population temporal dynamics of nest site occupation in seven patches. The mutualist species *Petalomyrmex* is a relatively perennial inhabitant of the plant: the survival probability of occupancy by *Petalomyrmex* on its host-tree was high ( $\psi_{\text{maintenance}} = 0.89$ ; 95% CI = [0.83; 0.93]), and significantly higher ( $p < 0.05$ ) than that of *Cataulacus* ( $\psi_{\text{maintenance}} = 0.63$ ; 95% CI = [0.51; 0.73]). From these probabilities, the estimated longevity of nest site occupation is about two to three times higher for *Petalomyrmex* than for *Cataulacus*. Moreover, among-site variability of the probabilities of transition was high for *Cataulacus* but low for *Petalomyrmex*. There were some cases of mixed occupation ( $\leq 1\%$  of the trees). However, this state was unstable (whatever the patch,  $\psi_{\text{maintenance}} < 0.5$ ) and generally

a mixed tree ended up being occupied solely by *Petalomyrmex* (in studied patches in which  $n_{\text{mixed trees}} > 1$ ,  $\psi_{\text{mixed} \rightarrow \text{Petal}} = 1$ ).

#### Discussion

We propose here an ecological and evolutionary scenario explaining coexistence of the two African ant species *Cataulacus mckeyi* and *Petalomyrmex phylax*, host-specific symbionts of the myrmecophyte *Leonardoxa a. africana*. We think it illustrates how an environmental niche partitioning approach can help analyse multidisciplinary datasets to explore in greater depth the dynamics of a metacommunity. At the regional scale, ant species distribution pattern did not conform to the expectations of a neutral model under

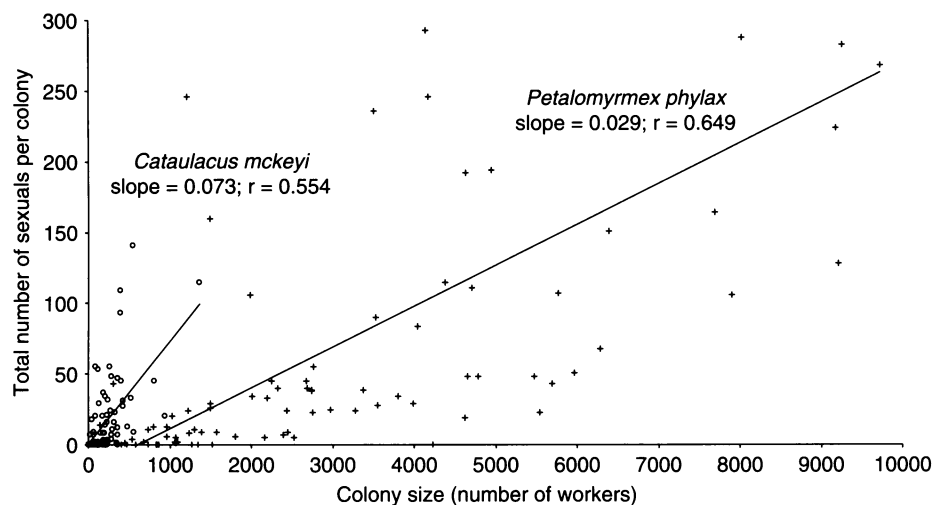


Figure 5. Growth-fecundity tradeoff. ○: *Cataulacus* colonies, +: *Petalomyrmex* colonies.

dispersal–assembly rules. This justifies investigating environmental and life history determinants of observed patterns of species diversity.

We have ample evidence that the guild of two symbiotic ants inhabiting *Leonardoxa* is competitively structured. First, food and nest sites are provided exclusively by the host-plant. Second, the frequency of unoccupied trees is typically low (about 15%), and field observations suggest that these are mostly too low quality sites to be successfully colonised by ant colonies. The instantaneous proportion of host plants available for founding was thus low in most patches, suggesting that nest site limitation was generally high. This conclusion is further sustained by results of the recolonisation experiment where within a year after cutting most of the trees (92%) had already been colonised by a new ant colony. Third, most ( $\geq 99\%$ ) of the occupied trees are inhabited only by a single colony of only one of the two ant species, and the rare ( $\leq 1\%$ ) cases where incipient colonies of both species could be found are extremely transient.

### What about a classic competition–colonisation tradeoff?

Theoretical models predict (Pacala and Rees 1998, Amarasekare and Nisbet 2001, Wang et al. 2002) and empirical data for plant–ants suggest (Yu and Wilson 2001, Stanton et al. 2002), that competition–colonisation tradeoffs may promote species coexistence in competitively structured communities. Multidisciplinary data helped us to decipher components of competition and colonisation for the two ant species of our system. Population genetic data, the recolonisation experiment and the social structure of colonies show that *Cataulacus* has a higher ability than *Petalomyrmex* for colonisation at local and regional scales, conferred by its earlier reproductive maturity, the ability of its foundresses to disperse further, the ability of its workers to colonise nearby plants (Debout et al. 2003), or by all three traits. In contrast, *Cataulacus* is a poor competitor at the incipient stage, unable to maintain viable colonies on many plants it colonises, presumably partly because *Petalomyrmex* has the ability to rapidly produce a large number of small patrolling workers. These results underline the fact that a dominant feature of dynamics is likely competition between foundresses or incipient colonies to occupy empty trees, i.e. to replace adult colonies that die at a density-independent rate.

A process of replacement means that competition is mainly expressed in a race towards the acquisition of resources that have recently become available, for instance a new tree or a tree that has lost its colony. In contrast, a process of displacement implies the death of a colony following the invasion of its tree by a new colony of the other species, for instance through aggressive interactions aiming at tapping the resources acquired by the competitor. The hypothesis of replacement competition agrees with the facts that in this system (1) direct interactions between adult colonies of both species are very rare (aggressive interactions between adult colonies likely occur in our system, but appear restricted to the rare and transitory cases of mixed occupations); (2) adult colonies, in particular those of

*Petalomyrmex*, resist displacement by incipient colonies (A. Dalecky, G. Debout, L. Gaume, D. McKey, unpubl.); and (3) distinctive morphological and behavioural traits of both species make displacement difficult (McKey 1984, Gaume and McKey 1999). For both species, foundation opportunities are thus mainly restricted to seedlings or to unoccupied trees. Nevertheless, since biological systems rarely fit perfectly to only one theoretical model, there may also exist here elements of competition through displacement, e.g. killing of foundresses by workers of a resident colony and occasional invasion of *Cataulacus*-occupied trees by *Petalomyrmex*.

In summary, these data strongly suggest that in the potential competition–colonisation tradeoff between these two species, it is competition between juvenile colonies that is decisive. Dynamics thus correspond much more closely to a replacement model through lottery processes, than to a strict competition–colonisation tradeoff through displacement. Lottery models are among the simplest to explain the effects of a variable environment on ecological processes (Chesson and Warner 1981). However, if adult colonies are impervious to displacement by propagules, and if propagules compete to replace adults that die for reasons independent of the outcome of juvenile competition (a lottery system), a competition–colonisation tradeoff alone may not be able to produce coexistence (Yu and Wilson 2001, but see Calcagno et al. 2006).

### A set of tradeoffs may promote species coexistence in the *Leonardoxa* system

Interspecific variation in life history traits suggests that, beyond the competition–colonisation tradeoff, other candidate tradeoffs could partition environmental heterogeneity and may thus promote species coexistence in this system. If one considers the life history traits that directly contribute to the fitness of colonies, five different principal hierarchies between the two species (i.e. a trait for which the species show strong differences) can be proposed (Table 2). (1) the winged individuals of *Cataulacus* disperse relatively further than those of *Petalomyrmex* (hereafter referred to as ‘dispersal’); (2) the colonies of *Cataulacus* reach reproductive maturity at a smaller colony size than those of *Petalomyrmex* (‘growth’); *Petalomyrmex* is characterized by (3) greater fecundity (‘fecundity’), (4) higher survival rate of adult colonies (‘adult survival’), and (5) a competitive advantage through more rapid production of workers in incipient colonies (‘competitive ability’). One factor that could contribute to higher survival rate of *Petalomyrmex* colonies is strong philopatry: in most of the patches studied, sexual females mate inside their natal nest and remain in it, leading to secondary polygyny (Dalecky et al. 2005), a space-perennial strategy that could delay *Petalomyrmex*-occupied trees from re-entering the competitive lottery. Considering dispersal and growth to reproductive maturity as central traits, we postulate the existence of six between-species tradeoffs (each linking two life history traits) that allow sources of environmental heterogeneity to function as niche axes, thereby facilitating coexistence between *Cataulacus* and *Petalomyrmex*. The global diagram (Fig. 6) integrates information on all of these. These six between-species potential tradeoffs are:

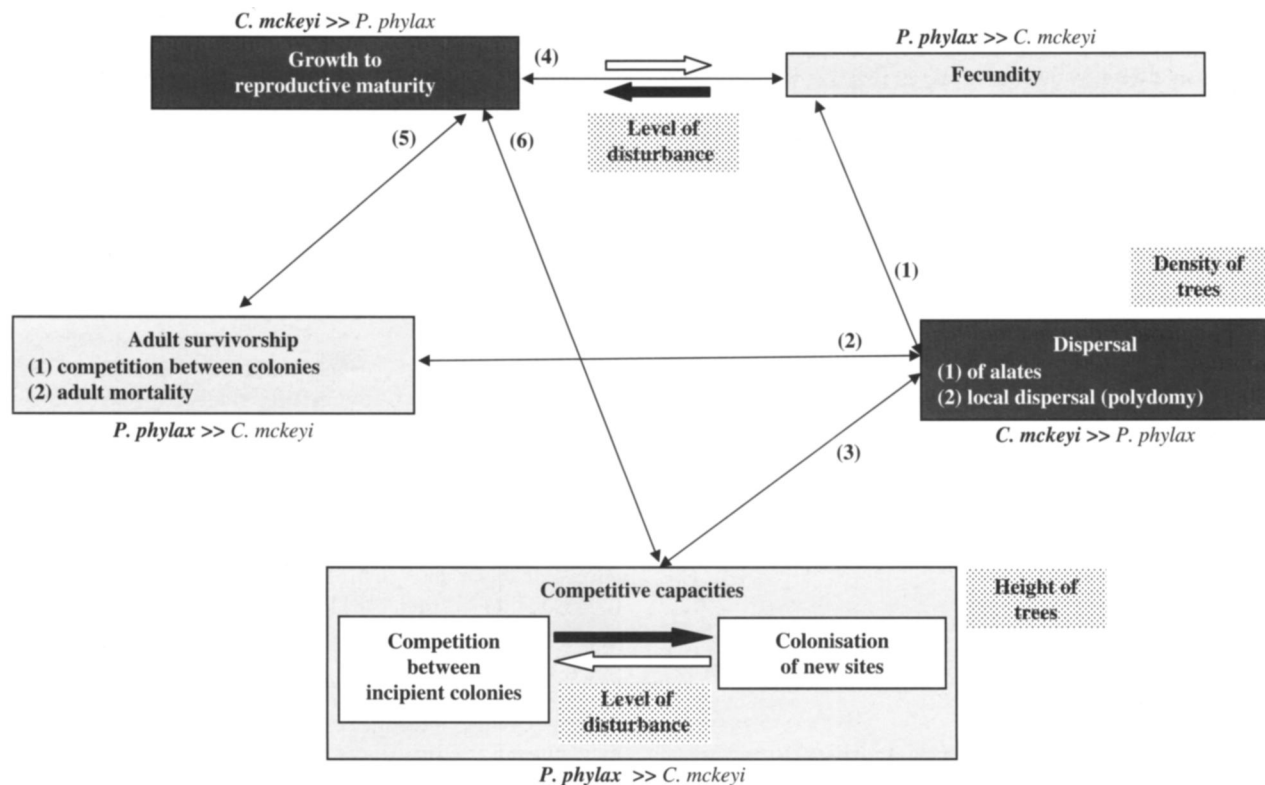


Figure 6. Dynamics of coexistence in the *L. a. africana* system. The five life history traits for which between-species hierarchies were identified appear in grey boxes. For each of these five hierarchies, the species in bold type is the one enjoying a relative advantage for the parameter in question. The arrows symbolize the between-species tradeoffs between one of the two central traits (dark grey boxes) and the other three traits (light grey boxes). Placement of the sources of environmental heterogeneity (in dot-matrix boxes) represents their actions as niche axes.

(1) dispersal–fecundity, (2) dispersal–adult survival, (3) dispersal–competitive ability, (4) growth–fecundity, (5) growth–adult survival, and (6) growth–competitive ability. The identified major sources of environmental heterogeneity are tree size, tree density and local disturbance rate, and one particularly – local disturbance – explains a large proportion of variance in ant species frequency among patches. High disturbance rates indeed reduce colony lifespan, thereby favouring species with precocious reproduction such as *Cataulacus*.

### Environmental heterogeneity is a potential axis of ecological niches of the species

Three major sources of environmental heterogeneity were investigated. First, though subtle differences in the distributions of the two species according to tree height were detected, particularly resulting from a higher frequency of *Petalomyrmex* colonies in small trees, variation of tree height was not related to a strong temporal niche partitioning. This suggests that coexistence does not occur via succession, contrarily to what has been observed in other plant–ant guilds (Young et al. 1997, Fonseca and Benson 2003). Second, variation of host-plant density did not explain variation in frequency of the two ant species at the regional scale, contrarily to the *Allomerus/Azteca* plant–ant guild associated with *Cordia nodosa* (Yu et al. 2001). In contrast, we note that aggregation of host plants at the local scale may

facilitate coexistence, as it allows *Cataulacus* colonies to occupy several neighbouring nests (Debout et al. 2003), whereas a *Petalomyrmex* colony is always restricted to its single host tree. The *Petalomyrmex* colony thus maximizes the resources it obtains from the tree by ensuring its future production of nectar and domatia through the protection of young leaves by a large number of patrolling workers (Gaume et al. 1997). Third, local disturbance explained a large proportion of variance in ant species frequency among patches. This suggests that this extrinsic factor of colony extinction and subsequent nest site release plays here a major role in the dynamics of species coexistence.

Our study moreover provides empirical evidence at a regional scale for theoretical models of coexistence in a heterogeneous environment. Snyder and Chesson (2003) have shown that local dispersal in an ecologically heterogeneous environment could lead to concentration of the low-density (at a metacommunity scale) species in areas where the conditions are most favourable for it. In these areas, the low-density species will escape inter-specific competition (because these areas are not suitable for its competitor) and also to some extent intra-specific competition (because of its low density). This model applies only if the environmental differences are long-lasting, relative to the generation renewal time. Local dispersal can thus facilitate coexistence if species in competition respond differently to spatial heterogeneity of the environment, i.e. when suitable habitats for each species are differently

distributed over the whole area occupied by the two competitors. In our case, spatial heterogeneity of the disturbance rate is the main factor that allows the maintenance of this community at a regional scale. Because dispersal in both species is mostly local (i.e. foundresses have a higher probability of coming from the natal population than from a neighbouring one), spatial variation of mortality and fecundity rates allow coexistence through covariance between environment and competition. Where dispersal is regional, only variation in mortality rate comes into play (Muko and Isawa 2003). In populations in which colonial perenniality is favoured (little-disturbed environments) opportunities for foundresses are rare and between-species competition is strong, favouring less dispersive species such as the usually secondarily polygynous *Petalomyrmex*.

Coexistence in the system we have studied is characterised by spatio-temporal differentiation in how two species use a single resource (niche partitioning: Levins and Culver 1971, Tilman 1994). We have shown the likely validity of the hypothesis that environmental niche partitioning can explain coexistence in this ant-plant symbiosis, this partitioning being executed through several tradeoffs which all play a role in promoting coexistence, but of which none may explain alone species coexistence. Environmental niche partitioning in our system better matches the assumptions of mass-effect/species-sorting models than those of patch-dynamic models. Our study offers new insights into mechanisms of coexistence of plant-ants using the same host-plant species. Compared to the *Cordia* system (Yu et al. 2001, 2004), our study further suggests the complementary roles that various between-species tradeoffs play in structuring populations and maintaining the diversity of the host-plant users. The *Leonardoxa* system clearly highlights that coexistence of species sharing the same resource may be the result of several tradeoffs acting at different spatial scales and of abilities of each species in using each particular environmental feature. Following Palmer et al. (2003) and Palmer (2004), we emphasize that the likely presence of one mechanism does not exclude that other mechanisms may also be at work in this natural system. Future studies should address to what extent each of the different mechanisms we propose plays a role in maintaining diversity in the symbiotic plant-ants associated with *Leonardoxa*.

Our study highlights that there are many ways for a parasite to persist within a mutualism. Coupling different approaches – behavioural, ecological, and evolutionary dynamics – allowed a more comprehensive investigation of the possible mechanisms explaining competitive coexistence of a mutualist and a parasite. These data provide a new argument in favour of a more complete integration of the various species coexistence models in a single theoretical framework within a metacommunity in spatially heterogeneous ecological environments (Amarasekare 2003, Holoak et al. 2005).

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