

## Assembly of island ant communities

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Assembly of communities is studied using ants in the Tvärminne archipelago of the Baltic Sea as an example. It is suggested that community-level distributional data fit poorly into analyses of community assembly processes. Instead, autecologies should be studied for species-specific limitations to colonisation. Such deterministic ecological factors include (1) habitat requirements, (2) dependence on other ant species in colony foundation or during the whole colony cycle, (3) dispersal capacity, and (4) level of social organisation. The species can differ profoundly with respect to the above features, which strongly restrict the role of stochasticity in the assembly of insular ant communities.

Stochasticity, together with competition, may cause a priority effect. In other words, the first of a pair of ecologically similar species to settle on an island may keep out the second species or slow down its rate of colonisation.

Different levels of social organisation order ant species into a competition hierarchy. This causes locally expected ("accepted") vs. locally improbable ("forbidden") combinations of species.

As the same community structure may be reached by different mechanisms and their combinations, direct studies on the species' ecologies and relations between the species are needed to elucidate the assembly process.

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### 1. Introduction

A common practice in the study of island community assembly is to describe the structure of a community and then deduce the mechanisms operating during the assembly process (see Simberloff 1978). The traditional method of study is based on MacArthur's (1972) models and emphasises the role of interspecific interactions, in particular that of competition, in determining community structure. Diamond (1975) constructed a set of assembly rules for island bird communities, but as Connor & Simberloff (1979) argued, "at least one of the rules is untestable, three are tautological consequences of definition plus elementary laws of probability, and the remaining three describe situations which would for the most part be found even if species were randomly distributed on islands".

As an alternative to competition-centred assembly rules, stochastic processes have been suggested as a first-level explanation for community construction. The simplest stochastic null hypothesis (Simberloff 1970) assumes equiprobability of colonisation among all species of the species pool, but at present it is commonly

agreed that deterministic limitations (such as dispersal capacity and habitat) should be taken into account (Diamond 1975, Simberloff 1978). Nevertheless, failure in rejecting a null hypothesis does not mean that species are randomly distributed on islands, or that interspecific competition does not occur (Connor & Simberloff 1979). An inherent weakness of distributional data in shedding light upon the assembly process is that the result is affected by several underlying forces (Simberloff 1978) and that there are several routes and alternative sets of mechanisms leading to the same result. To paraphrase Grant & Abbott (1980), resorting to the community level of analysis runs the risk of throwing the baby out with the bath water, or to be more correct, drowning the baby by using too large and deep a tub.

Analytical difficulties may be mitigated through pairwise comparison of species, pinpointing pairs of species whose distributions are nonrandom (Wright & Biehl 1982). To detect the effect of competition, the analysis should be restricted to species which are potential competitors. Wright & Biehl (1982) make this point when criticising Simberloff's (1978) and Connor

& Simberloff's (1979) analyses of arbitrary taxonomic groups, without regard to species' autecologies.

The approach we are going to take here was suggested by Grant & Abbott (1980): "While refinement of stochastic models may help to resolve these complications", ... (caused by distributional data) "... we propose that detailed ecological studies hold out better hope, particularly if experimental and if directed towards specific questions of competition and dispersal."

## 2. Derivation of colonisation rules

We are not going to discuss the existence of competition between and within ant species. Instead, we shall try to estimate the role of competition and other interspecific relations relative to other factors in structuring ant communities by discussing the relevant limitations set by the ants and the environment. Experimental approaches to the study of competitive exclusion and co-existence are suggested.

We shall mainly use examples from our unpublished studies conducted in the Tvärminne archipelago, in the westernmost part of the Gulf of Finland, the Baltic Sea. Our data cover 45 islands and islets, mapped for their myrmecofauna over several years. The islands have been selected to cover the existing ranges for size (0.1–15 ha), stage of primary/secondary succession, habitat diversity, and isolation (20 m — 12 km from the mainland). The island species pool is 28 species, and the neighbouring mainland adds eight more species to the regional species pool (Table 1).

The Tvärminne archipelago belongs to the area of Fennoscandian land upheaval, which is rising at an average rate of 40 cm per hundred years. Measured on a geological time scale, this causes fairly rapid succession from small islets exclusively composed of bare basic rocks, to larger islands with a number of different habitats, including more or less mature forests.

### 2.1. Nesting behaviour restricts colonisation success to a limited number of habitats

The biology of most ant species severely limits their colonisation potential. To illustrate this point, we have selected four common species in the Tvärminne archipelago, viz. *Lasius niger*, *L. flavus*, *Camponotus ligniperda*, and *C. herculeanus*. All four species are known for their nuptial flights, which take place *en masse* over a wide area of the archipelago (see Sect. 2.3.). There is no doubt that considerable numbers of the species reach even

Table 1. The ant species collected in the Tvärminne archipelago. The symbols \*, \*\* and \*\*\* refer to increasing commonness and abundance and indicate weighting of each species over island size classes. The island size classes are: large ( $\geq 4$  ha), medium-sized (4 ha > 0.5 ha) and small ( $\leq 0.5$  ha). The nomenclature follows that of Kutter (1977).

	Occurrence on the islands		
	Large	Medium-sized	Small
<i>Myrmica laevinodis</i> Nylander	**	***	*
<i>M. ruginodis</i> Nylander	***	**	*
<i>M. scabrinodis</i> Nylander	**	***	*
<i>M. sabuleti</i> Meinert	*		
<i>M. lobicornis</i> Nylander	*		
<i>M. schencki</i> Emery	*		
<i>Anergates atratulus</i> (Schenck)	*		
<i>Leptothorax tuberum</i> (Fabricius)	*		
<i>L. acervorum</i> (Fabricius)	**	**	*
<i>L. muscorum</i> (Nylander)	*	*	*
<i>Formicoxenus nitidulus</i> (Nylander)	*		
<i>Harpagoxenus sublaevis</i> (Nylander)	*	*	
<i>Tetramorium caespitum</i> (Linné)	**	*	
<i>Camponotus herculeanus</i> (Linné)	**	*	
<i>C. ligniperda</i> (Latreille)	**	*	
<i>Lasius niger</i> (Linné)	**	**	***
<i>L. flavus</i> (Fabricius)	**	**	*
<i>L. umbratus</i> Nylander	*	*	
<i>L. fuliginosus</i> (Latreille)	*		
<i>Formica fusca</i> Linné	**	**	*
<i>L. truncorum</i> Fabricius	**		
<i>F. pratensis</i> Retzius	*		
<i>F. aquilonia</i> Yarrow	*	*	
<i>F. lugubris</i> Zetterstedt	*		
<i>F. rufa</i> Linné	*		
<i>F. polycletus</i> Förster	*		
<i>F. sanguinea</i> Latreille	*	*	
<i>F. exsecta</i> Nylander	**	*	

Additional species on the neighbouring mainland (at a maximum of about 10 km to the west on the coast, and 5 km to the north) are: *Myrmica jacobsoni* Kutter (*M. gallieni* Bondroit; Collingwood 1979), *M. hirsuta* Elmes (Pisarski & Vepsäläinen, unpubl.), *M. rugulosa* Nylander, *M. sulcinodis* Nylander, *F. picea* Nylander, *F. cinerea* Mayr, *F. rufibarbis* Fabricius, *F. urolensis* Ruzsky (our own collections).

the most remote islets: we have collected fundatrices from the outermost zone of the archipelago. However, *L. niger* is the only ant species found on the single-species islets (numbering seven in our study; goodness-of-fit  $\chi^2$  for equal distribution of *L. niger* vs. other species = 33.00,  $df = 1$ ,  $P < 0.001$ ).

More generally, the other three species do not live on any island in its earliest stage of primary succession, and thus lacking substantial areas of gravel, sand or soil layer (but *L. niger* is found on all the islands where any of the other species live). The *Camponotus* species are able to colonise an island only after it has produced substantial patches of coniferous forest (but all the 12 islands with *Camponotus* also have the two *Lasius* species).

The species distributions according to island size classes reflect the limitations set by the habitats: either or both of the *Camponotus* species nest on 12 of the 17 islands with forest, but on none of the 28 islands without forest. The probability of finding *L. flavus* increases with island size and

Table 2. Distribution among island habitat and size classes of four ant species with excellent dispersal abilities in the Tvärminne archipelago.

	Island size and habitat classes		
	Large and medium-sized with forest (n = 17)	Medium-sized without forest (n = 10)	Small (n = 18)
<i>Lasius niger</i>	17	10	18
<i>L. flavus</i>	16	5	4
<i>Camponotus ligniperda</i>	7	0	0
<i>C. herculeanus</i>	10	0	0
Either of the <i>Camponotus</i> spp.	12	0	0

stage of succession, but *L. niger* has been found on all the studied islands. Pairwise one-tailed  $\chi^2$  tests calculated on the basis of *a priori* knowledge of species-specific habitat limitations to distribution among island size and habitat classes are  $P < 0.05$  ( $\chi^2 = 5.32$ ,  $df = 2$ ) for *L. niger* vs. *L. flavus*,  $P = 0.00007$  for *L. niger* vs. *Camponotus* spp., and  $P = 0.017$  for *L. flavus* vs. *Camponotus* spp. ( $df = 1$  in the two latter comparisons) (Table 2).

A naturalist would expect the above result. The lifestyle of *L. flavus* is almost exclusively hypogoeic, i.e. it lives in the ground, feeding mostly on aphids on plant roots. Grasses such as *Deschampsia* spp., *Agrostis* spp. and *Rumex acetosella* (or Scots pine) are necessary for the aphids (Oinonen 1956). Both *Camponotus* species are dendrobionts, i.e. they are dependent on trees (e.g., Arnoldi 1968, Collingwood 1979). *C. herculeanus* constructs its nest exclusively in large, generally damaged trees (usually pines in the Tvärminne area), and *C. ligniperda* makes its nest either in large tree stumps or in the ground under stones. On the other hand, *L. niger* is able to nest even in minute rock crevices with minimal amounts of soil.

## 2.2. Dependence on other species restricts colonisation success

About 2% of the known ant species have evolved more or less strict dependence on other ant species (Czechowski 1975). The dependence ranges from founding a colony in other species' nests to being a workerless parasite species in the nest of the host species.

In Tvärminne archipelago a point in case is the species triplet *L. niger*, *L. umbratus*, and *L. fuliginosus*. For colony foundation the *umbratus* fundatrix has to invade a *niger* nest, and the *fuliginosus* fundatrix must find an *umbratus* nest (e.g., Collingwood 1979). But the colonisation success of the two latter species also depend on the minimal habitat requirements of the species.

Patches of deep soil are obligatory for *L. umbratus*, which is hypogoeic like *L. flavus* (e.g., Arnoldi 1968, Collingwood 1979). The species also seems to prefer root labyrinths of young birch trees as nesting places (own observations; cf. Collingwood 1979). This enables the colony foundation of *L. fuliginosus*, a dendrobiont constructing its nest in trees (e.g., Arnoldi 1968, Collingwood 1979).

The assembly rule mentioned here does not mean that *L. umbratus* should always exist on an island when *L. fuliginosus* does — after successful colony foundation the latter species is no longer dependent on its transient host species, which may become extinct. In our study area the two species are so rare (and it can be expected to be more difficult to find the hypogoeic one) that statistical tests are meaningless.

The primary colonisation of "red" ants of the genus *Formica* takes place through intrusion into the nest of "black" ants of the same genus (subgenus *Serviformica*) (e.g., Dlusskij 1967, Wilson 1971). The common black species in the Tvärminne area is *F. fusca*, which itself may be limited by its poor dispersal power (see Sect. 2.3.). The hill-building species of the *F. rufa* group are constrained to more mature (usually predictably and slowly changing) habitats with forest by several additional factors: i.e., the development of the large society and mound nests, and the production of sexuals, takes several years (Zakharov 1972). However, *F. sanguinea*, which constructs its nests under small stones in the ground, extends its relationship with *F. fusca* by raiding their nests after founding their own colony. Larvae and pupae are carried to the *F. sanguinea* nest and used as food for larvae, or allowed to develop into imagoes to be used as workers (Czechowski 1975, references in Dumpert 1981: 162). However, dulosis of this species is facultative (e.g., Wilson 1971).

More specialised parasites are exemplified by *Harpagoxenus sublaevis*, which lives in obligate dulotic association with *Leptothorax* species (three of which are known from the Tvärminne area). The host species are fairly good colonisers nesting in the ground, under stones, and in dead tree, mostly sticks (Collingwood 1979). It seems, however, that for the parasite to colonise an island — and to survive there by raiding neighbouring *Leptothorax* nests, the host species density must be high. In the Tvärminne archipelago this is true on islands in the later stages of succession, with abundant timber nests of the host species. *Harpagoxenus* has been collected on seven of the 17 large and medium-sized forested islands with *Leptothorax*, but on none of the remaining 11 islands with *Leptothorax* but without forests (Fisher's exact two-tailed test for the distribution

of the parasite between the forested islands and those without forest:  $P = 0.033$ ) (Pisarski & Vepsäläinen, unpubl.).

The most extremely parasitic species in the Tvärminne archipelago is *Anergates atratulus*, which lacks the worker caste, and lives in the nest of *Tetramorium caespitum* where only parasite broods are developed (Collingwood 1979). In our study area, the host is fairly common and abundant in habitats exposed to the sun, but the parasite has been found only once (Pisarski & Vepsäläinen, unpubl.). According to Dumpert (1981: 175), the adoption very probably succeeds only when an *Anergates* female comes across a *Tetramorium* colony without own female, and this cannot happen often.

The workers and the female of *Formicoxenus nitidulus* live freely in the nests of the *F. rufa* group species and are ignored by the host (Collingwood 1979). An island must have reached a late stage of succession to allow *Formicoxenus* to colonise — we know the species only from one island with old pine forest (Pisarski & Vepsäläinen, unpubl.).

To emphasise the point, *one third of the ant species of the Tvärminne archipelago are dependent on some other species during primary colonisation*. Colony foundation of many species always depends on a host species, and some species are dependent on their host to a lesser or greater extent throughout their colony cycle.

### 2.3. Species-specific differences in dispersal abilities are prominent

In Sect. 2.1. we indicated four species known to disperse *en masse* over the Tvärminne archipelago. No exact estimates are available, but in the case of *L. niger* and *L. flavus* the nuptial flight takes place simultaneously from a substantial proportion of the nests in the area — the suggestion that tens or hundreds of thousands of females are involved seems realistic in the study area of about 10 to 20 square kilometres. Mass flights take place during several days each year. The nest densities of the two *Camponotus* species (especially *C. herculeanus*) are lower than those of the two *Lasius* species, and smaller numbers of dispersants are released. Moreover the flights take place during a longer period and on many more days. The numbers of sexuals simultaneously in flight are considerable, however, as can be understood by observing the many species of birds, ranging in size up to the Great Black-Backed Gull (*Larus marinus*), which gather in flocks to catch taking-off *Camponotus* in the air space above the nest. After such days we have found pellets (presumably regurgitated by gulls) containing only chitin parts (mostly heads)

of *Camponotus* (unpubl.). The females may rise to heights of several tens of metres, and several thousand individuals can be seen to orientate out over the archipelago towards the outer islands.

The above four species show an extreme size difference between the female and the worker. The large size of the female (the fundatrix) increases the probability of success in colony foundation without any helpers or host species (cf. Sect. 2.2.). But as pointed out earlier, only *L. niger* is able to colonise islands during the earliest stages of succession, and the other three species are more or less in need of habitats that develop only later.

Judging from the habitat spectrum of *Formica fusca* on the mainland, and even on the islands where it occurs, it should — together with *L. niger* — be a real candidate as the first ant species on small islands with only early successional habitats. On the mainland, it is one of the most typical ants of the road-side/ditch-side gravel and turf banks. However, in the Tvärminne archipelago it occurs on 10 out of 24 small and medium-sized islands studied in the two zones closest to the mainland, but not on any of the 13 islands of the same size classes in the outer zones (Fisher's two-tailed exact test between the two zones:  $P = 0.012$ ).

It may of course be that the winter of the outer archipelago is too harsh to permit colonies of *F. fusca* to develop. One would then at least expect to find fundatrices, but the expectation was not borne out. Another explanation would be competition between *L. niger* and *F. fusca* (proposed on the basis of negative correlation between the densities in southern Finland by Oinonen 1956), but this does not explain the difference in the distribution of *F. fusca* between the inner and outer zones of the Tvärminne archipelago. The same is true for diffuse competition (see also Fig. 1). A more plausible explanation is poor dispersal ability: According to G. M. Dlusskij (Moscow, personal communication), the male flies close to the ground (as do the males of solitary wasps), the female runs on the ground and copulation takes place close to the nest, after

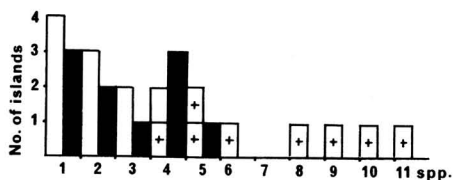


Fig. 1. The numbers of species (excluding *F. fusca*) on the studied small and medium-sized islands in the Tvärminne archipelago in the two zones closest to the mainland (white) and the two outer zones (black). Occurrence of *F. fusca* noted by a + sign.

which the female sheds her wings and begins to seek a nest place. However, to test the effect of the mating behaviour on colonisation, experimental transfers of numbers of fundatrices should be made to the small islands of the different archipelagic zones.

Most of the other species seem, if anything is known about them, to fall between the two extremes of dispersal ability described above. Without going into details, we conclude that differences in dispersal rates are large enough to be taken into account in the structuring of island ant communities, especially in explaining the community structure of islands in the early stages of succession. Thus, the species-specific dispersal potentials should be studied in more detail.

#### 2.4. Stochasticity plus competition may cause a priority effect

The social mode of life, and the susceptibility of fundatrix females to attacks by foraging worker ants, makes colonisation of an island a risky effort. The risk increases with increasing densities of ants present on the island. Generally, conspecific colonies of the immigrating female are no less harmful; in fact, the opposite is true — due to habitat selection of the fundatrix (see Brian et al. 1976, and also suggested by Boomsma & Leusink 1981), they may be the worst enemies. Such predation upon fundatrices is of course one aspect of competition, if the definition allows markedly one-sided negative effect.

Many ant species may also found new nests and disperse in another way, viz. by splitting off part of the workers and the females of the old nest to settle in a new nest in the vicinity. This leads to colonies with many nests (polycaly) and many females per nest (polygyny) — the other extreme is realised in monocaly and monogyny (a society of one nest with one female). The latter is usually the case during colonisation of an island by a new species (but primary pleometrosis, cooperation between two or more fundatrices, may take place in some species, e.g. in *L. niger*).

Because several ant species are able to transfer from monogyny to polygyny, and from monocaly to polycaly, the stage is set for a strong priority effect in community structuring. For example, even though the habitat spectra of *M. laevinodis*, *M. ruginodis* and *M. scabrinodis* differ, the species seem, as far as is known, to have fairly equal probabilities of colonising islands which have reached about 0.5 ha in size and a succession stage with *Juniperus* bushes and young trees in the bush layer, and perhaps occasional older trees. In such circumstances, chance may play a leading role in

determining which species will colonise and spread over the entire island, and keep out ecologically related species reaching the island later.

The material from the Tvärminne archipelago is anything but convincing proof of the priority effect, as the number of typical *Myrmica* islands (area about 0.5–1 ha) in the proper successional stage is too low. But the data are indicative. On one island we found 88 nests of *M. scabrinodis*, and on a second we counted 32 *M. laevinodis* nests — both species had spread densely over the suitable habitat and had apparently monopolised the “*Myrmica* niche space” on the islands. Application of Wright & Biehl’s (1982) shared island hypothesis did not, however, indicate deviation from random pairwise cooccurrence of the species, even when the largest islands with diverse habitat arrays were excluded. Similarly, negative correlations between the numbers of nests of the species found on the island level (without separation between habitats) were low and statistically insignificant.

Even if a priority effect seems a plausible explanation for single islands with dense colonies of *Myrmica* species, it is not likely to be revealed by statistical tests based on distributional data. However, it would be naive to expect a priority effect to be the factor assembling communities. Consequently, case studies on selected islands should be made. For example, efforts should be made to seek out possible differences between two island groups — those consisting of dense one-species colonies of *Myrmica*, and those of the same size class void of *Myrmica*. If no clear habitat and/or isolation differences can be found which might limit colonisation success on the latter islands, a priority effect need not be invoked. It then suffices to note that not all suitable islands are inhabited by *Myrmica*: the swarming behaviour of *Myrmica* (close to the nest and often close to the ground; own observations) indicates restricted dispersal potential.

#### 2.5. Differences in social organisation arrange species into competitive hierarchies

“The worst enemies of social insects are other social insects. Ants in particular are their chief predators” (Wilson 1971). Ants compete, often by fierce interference, both within and between species (e.g., Pontin 1981). However, some species are more prone to indulge in aggressive conflicts than others. By and large, success in direct interference is a function of colony size and organisation of the society (especially through communication and recruitment of nest mates; see Sect. 3).

Pisarski & Vepsäläinen (unpubl.; cf. Brian 1965, Dlusskij 1965, Czechowski 1977) have applied a simple competition hierarchy from top winners to bottom losers. The lowest level consists of species defending only their nest (e.g., *F. fusca* and the three Finnish *Leptothorax* species). The species of the next higher level also defend food resources (e.g., *L. niger*, *Tetramorium caespitum*, *C. herculeanus* and *C. ligniperda*). The top level is occupied by species also defending their foraging area (e.g., the *F. rufa* group species, *F. truncorum*, *F. sanguinea*, *F. exsecta*, and populous colonies of *L. niger*).

A corollary of the above hierarchy is that colonies belonging to the intermediate level tend to run into conflict with colonies of the same and the higher level, be they conspecifics or alien species. Thus species of the highest level replace those of the intermediate level in direct interference competition through higher numbers and/or more effectively organised recruitment of nest mates. Because the species of the lowest level defend only their nest, they may coexist with species of the higher levels. But we have also observed *F. polycytena* (a species of the *F. rufa* group) workers intrude into nests of *L. flavus*, *Myrmica* and *F. fusca* and carry out workers and offspring as prey. This impoverishes the ant fauna up to several tens of metres from the hills of the *F. rufa* group species. Likewise, the density of foragers, e.g., of *F. fusca*, is exceptionally low in the vicinity of *F. rufa*, *F. truncorum* and *F. exsecta* nests (Pisarski & Vepsäläinen, unpubl.).

Competitive relations between the species of the highest hierarchy level are demonstrated by the results collated in Table 3. The effect of stronger species upon weaker ones is great, but the competitive situation is highly skewed. The relations between two competing mature colonies of conspecifics may be more balanced, as is often the case in the so-called red wood ant wars. During food shortages, especially in spring when the colony activity is increasing rapidly, foraging areas of neighbouring colonies often overlap temporarily, and aggressive encounters occur between the workers. As concluded by Mabelis (1979) in his thorough study of such "wars" among *F. polycytena* colonies, they in no way differ from predatory behaviour insofar as motivation and behavioural details are concerned. When the history of the colonies is taken into account, priority effects (see Sect. 2.4) may emerge. Again, the situation is highly skewed, as lone fundatrices are killed and predated upon by workers of densely located mature nests.

The combined effect of priority effect, different habitat spectra and competition may explain why *F. rufibarbis*, a common species on the neigh-

Table 3. Areas of foraging territories without and with competing species of the same level of social organisation. The nests of each species are located in similar habitats on the 10 ha island Jöskär in Tvärminne. (Pisarski & Vepsäläinen unpubl.).

	Area (m <sup>2</sup> )	Forager population	Competing species
<i>Formica polycytena</i> (bicalic)	20,000	appr. 10 <sup>6</sup>	virtually none
<i>F. truncorum</i>	640	1850	virtually none
	84	1790	<i>F. polycytena</i>
<i>F. exsecta</i>	205	1220	conspecifics?
	4.3	1220	<i>F. truncorum</i>

bouring mainland in open dry pine forests, is not known from the archipelago. There is only one island in our area with a habitat suitable for the species, which is aggressive and has well organised societies. The only fundatrix in the archipelago has been collected on this suitable island, but it seems that another aggressive species, *F. sanguinea*, has monopolised the habitat with a dense network of nests. This is a species with a wider array of habitats, living on several islands, and thus being more probably the first of the two species in sun-exposed open pine forests. Oinonen (1956) suggested that the disappearance of *F. rufibarbis* with forest succession on southern Finnish rocks is speeded up by *F. sanguinea*.

### 3. Discussion

The ecologies of the species have been used above to study possible mechanisms of community structuring of island ants. The logic was that, even if there were strong and strict assembly rules for community structuring, the ecological limitations and thus the species-specific colonisation rules are expected to differ even profoundly. Statistical null hypotheses analysing the structure of the whole community tend to miss restrictions self-evident to a skilled myrmecologist. Of course such restrictions, e.g. differences in dispersal abilities and persistence, can be — and have been (e.g. Diamond 1975) — included into the statistical analyses. But the point is that they are only able to tell us something of the role of chance, after the relevant ecological facts have been included into the model.

In evaluating the role of competition in community assembly, we want to make the point that if competition and replacement are seen on one side of the coin, competition and coexistence reside on the other side. But exclusion from a community or coexistence may occur due to

reasons other than competition. As similar communities may be constructed in several different ways, descriptions of the structure are not expected to provide the best data for studies on the assembly process which has led to the observed structure. This seems to be a major reason for the apparent paradox that even large amounts of distributional data are inefficient in testing meaningful biological hypotheses. The value of community descriptions should rather be seen in pointing out specific questions for experimental studies on species' ecologies and interactions, and their role in community assembly. The most pertinent view on the assembly process of (desert) ant communities has been given by Dlusskij (1981) — the book includes a minimum amount of statistics but plenty of data on the species' ecologies and interactions.

The more we know about the autecology and relations among species, the more reliably can community descriptions be applied to reconstruct the assembly process. But simultaneously, the chances of pointing out possible assembly rules increase with our knowledge of the ecology of each species. Model communities can be built and tested — here stochasticity can and should be introduced on a more realistic basis.

In the following sections we try to indicate some possible ways to study competition by direct observation of the species, and by manipulating the environment. The logic behind this is that the instantaneous situation studied by a myrmecologist may be too close to stable relations among the species to allow any insight into competition. Changing the environment could set the stage alive, which would answer many of the questions otherwise needing long-term monitoring of the communities.

### 3.1. Competition may be observed by manipulating the environment

Interaction among and replacement of species have been studied by baiting (e.g., Czechowski 1979, Lynch et al. 1980, and Vepsäläinen et al. unpubl.). Radical improvement of the food resources (e.g. by placing syrup and/or fish baits in a grid with 1 m<sup>2</sup> squares) causes a succession of ant "communities" on the baits. Simultaneous mapping of the nest loci of each species improves the possibility of evaluating relations among the species on the baits. In addition to descriptions of the succession of the bait communities, direct observations can be made on the niche space usage (e.g. for food quality, daily activity, temperature) and behaviour during conflict situations. The results obtained (Vepsäläinen et

al., unpubl.) corroborate the picture arrived at in Sect. 2.5. on competitive relations among the species and on the role of social hierarchy.

Without going into details, poor competitors tend to find the bait first, but are later replaced by more aggressive species with better organised societies. For example, *F. fusca* may crowd in moderate numbers on the bait, but is easily replaced by the aggressive *L. niger*, which rapidly monopolises the bait. When the numbers of e.g. *F. exsecta* are low enough to permit access to the bait, *F. fusca* individuals may slip in and get their share, but sometimes such intruders are caught and carried to the nest.

Of course monopolisation of or replacement on baits are only indirectly related to fitness (ultimately measured by the production of sexuals by the female(s)). But it should be clear that improved food intake increases the size of the colony, and thus also its position in the social hierarchy. In extreme cases this may lead to monopolisation of the whole island by one species: e.g., in the Åland archipelago *F. lugubris* (a species of the late colonising *F. rufa* group) has spread densely over the whole island of Gålokobb (0.8 ha), and no other ants have been caught (unpubl.). It seems improbable that the production of the island could maintain such a dense and exclusive population, and it is presumably dependent on the high Chironomidae production in the Baltic Sea.

### 3.2. Differences in foraging strategies may allow coexistence

The division of ant species into three hierarchical groups by their defence of nest, food resources and foraging area (Sect. 2.5.) separated the species which are expected to coexist from those which are expected to be excluded by competitors. Here we discuss simple approaches to the study of foraging behaviour and niche separation of the species belonging to the different hierarchic levels.

Monitoring changes taking place in ant communities is certainly tedious, but also rewarding. In Sect. 2.5. we referred to the dependence of differences in species' foraging areas on neighbouring species. The situation described in Table 3 was for 1981, but the following year saw the evidence for competition — and its results in these specific cases — strengthened: the *F. truncorum* nest close to a *F. polyctena* foraging route was empty, and the *F. exsecta* nest close to *F. truncorum* had been invaded by the latter species and *F. exsecta* had disappeared. It seems that the competing *F. truncorum* colony had split into two

parts, the latter moving to the previous *F. exsecta* nest. In both cases, competitive exclusion is the simplest interpretation of the changes. In a similar way, changes in the ant fauna close to nests of the species on the highest level(s) of social hierarchy can be monitored to evaluate the effect of nest raids by aggressive species. Then communities in similar habitats without aggressive species should also be studied, i.e. to find out the effect of winter climate on colony extinction.

Direct observation of the behaviour of the species on the foraging ground and on baits also provides data on the problem of why some species are able to coexist and others are not. For example, *F. fusca* is not usually able to nest close to a mature colony of the *F. rufa* group species, but the *Leptothorax* species are. Observations on *F. fusca* penetrating the core area of a foraging territory of *F. rufa* show that it is either inefficient in gathering food and soon escapes after frequent confrontations with *F. rufa* workers, or then it is caught and killed. On the other hand, even when foraging *Leptothorax* workers are occasionally attacked by more aggressive and larger species (e.g. *F. rufa*, *F. exsecta*), they are usually not injured. An attacked individual presses itself close to the ground, and after a few unsuccessful attempts to grip the prey, the predator ant gives up (own observations). The food items gathered by *Leptothorax* are also considerably smaller than those manipulated by *Formica* species, which effectively separates the species along the food resource axis (unpubl.).

Baits can also be used to study the colonies' potential for expanding its foraging range when there is good-quality food farther away. While *F.*

*rufa* may defend aphids up to 200 metres from the nest, the potential to gather to the food and even monopolise it is restricted to less than one metre in *T. caespitum*. The species is, however, effective in mobilising nest mates over short distances by mass recruitment, and large numbers of workers gather themselves under the bait, where developing offspring may also be brought. Simultaneously, nest material is collected around the bait (own observations). Even though *T. caespitum* is one of the smallest Finnish ants, it is not likely that larger species from farther away are able to take over the bait.

Preferences for food quality and size of food items can be studied by baiting and by placing different-sized food items (e.g. seeds) randomly in the terrain (see Lynch et al. 1980). Simultaneously, data can be gathered on how easily different species find ephemeral, randomly located food. To improve the quality of the results, densities and foraging activities of the workers should be studied, e.g. by applying the method described by Järvinen et al. (1977).

To find out why *F. fusca* is the most effective discoverer of randomly emerging ephemeral food (Vepsäläinen, unpubl.), its foraging strategy must be studied. Clearly, the species forages individually by running rapidly over ground with little or no vegetation, but making frequent turns. Thus the probability of locating randomly placed food item should be higher than for most other species (cf. Lynch et al. 1980).

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