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Genetic population structure and dispersal patterns in *Formica* ants — a review

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Human impact on boreal forests has been extensive during a fairly short evolutionary time scale. Character species of boreal forests, such as *Formica* ants, may face loss of genetic diversity, increasing inbreeding, and decreasing gene flow among extant habitat fragments owing to habitat loss and fragmentation. Here we review the genetic data on old-world boreal species of the genus *Formica*. In *Formica* ants colonies can have one or several queens (mono- and polygyny respectively) and this trait is often assumed to be linked with dispersal propensity, such that monogyne species disperse well and polygyne species disperse less well. Our analysis of the available data reveals three important aspects of the social and dispersal biology of *Formica*. First, the traditional division in mono- and polygyne species is too simple and we propose a population-based division into highly polygyne, weakly or moderately polygyne, and monogyne populations. Second, there is indeed an association between colony kin structure and dispersal in the predicted direction, i.e. restricted dispersal in polygyne species. However, this only holds for between-population differentiation, not within population genetic viscosity. When genetic viscosity within populations was examined most species nevertheless showed a negative relationship between F_{IS} and relatedness, indicating that low relatedness (many queens) is associated with reduced dispersal also locally. Only one species (*F. exsecta*) showed a significant positive relationship. Finally, we predict that sex-biased dispersal may be a common trait in *Formica* species, although data on more species are needed to confirm this.

Introduction

The negative impact of human activities on the spatial distribution and extent of boreal forests has been extensive during a fairly short evolutionary time scale (Kilpeläinen *et al*. 2005 and references therein). Habitat loss and the fragmentation of forest habitats previously under a natural succession regime likely affect all organisms dependent on such habitats. When the extent of suitable habitat patches decreases and the isolation between them increases, population size of species dependent on those habitats tends to decline and the genetic composition of these populations may change (e.g. Gaggiotti 2003). In particular, habitat loss and fragmentation

may lead to loss of genetic diversity, increasing inbreeding, and decreasing gene flow among extant habitat fragments. Species adapted to continuous habitats may still be locally abundant and ecologically dominant, yet face problems persisting in fragmented habitats, because weak dispersal may prevent recolonization of the fragments that have gone extinct (Tilman *et al*. 1994, Hanski & Gilpin 1997).

In social insects, the division into single-queen (monogyne) and multi-queen (polygyne) societies entails a range of traits that have been collectively coined as the "polygyny syndrome" (Rosengren & Pamilo 1983, Keller 1993). The general view is that polygyny tends to be associated with short-range dispersal, whereas monogyny tends to be associated with long-range dispersal through nuptial flights (Hölldobler & Wilson 1977, 1990, Keller 1993, Rosengren *et al*. 1993, Sundström 1995a, 1995b). In its extreme, reduced dispersal in polygyny has led to the emergence of multi-nest colonies (polydomy) where new colonies are formed near the natal colony and exchange resources and workers with each other (Rosengren & Pamilo 1983). Evidence for this dichotomy in dispersal patterns between monogyne and polygyne species is based on studies of individual species (Pamilo *et al*. 1997, Chapuisat & Keller 1999, DeHeer *et al*. 1999, Rüppell *et al*. 1999, Liautard & Keller 2001, Seppä *et al*. 2005), whereas other studies have found curtailed dispersal and nuptial flights also in monogyne species (Sundström *et al*. 2003).

Red wood ants (*Formica s. str*.) are character species of the old world boreal zone. Typically they occur in mature forests with mixed tree stands of medium density, on bogs, or in open areas exposed to recent disturbance (Collingwood 1979, Seifert 1996, Czechowski *et al*. 2002). In forest areas disturbance would originally have been caused by forest fires, but more recently forest clear-cutting and other forms of human interference have produced similar effects. Indeed, clear-cut areas, road sides and meadows are suitable habitat for some mound-building red wood ants adapted to ephemeral habitats (Collingwood 1979, Seifert 1996, Czechowski *et al*. 2002). By contrast, the natural rate of successional change in bogs and mires is much slower than in forests, and the recent extensive ditching of bogs has had profound effects on ant communities in these areas (Vepsäläinen *et al*. 2000). Human interference is thus rapidly changing the ant communities within the boreal region (Punttila *et al*. 1994, 1996, Punttila 1996, Vepsäläinen *et al*. 2000). Of the ten mound-building *Formica* species discussed in this paper (*F. aquilonia*, *F. polyctena*, *F. rufa*, *F. lugubris*, *F. paralugubris*, *F. pratensis*, *F. exsecta*, *F. pressilabris*, *F. truncorum* and *F. sanguinea*), the first six are typical for sparse to medium dense mature forest stands or forest edges, whereas the last four are typical for ephemeral open patches that have arisen following disturbance (Collingwood 1979, Seifert 1996, Czechowski *et al*. 2002). An additional species — *F. uralensis*, not discussed here — inhabits bogs and wetland areas. In addition to the mound-building species, the genus *Formica* also includes ground-nesting species, such as *F. fusca*, *F. candida*, *F. cinerea*, and *F. selysi* and a range of less studied species (subgenus *Serviformica* Seifert, 1996). Of these, *F. fusca* is ubiquitous and occurs in a wide range of habitats, whereas the other three are more specialized and more patchily distributed. *F. cinerea* typically occurs in xerotermic habitats, *F. candida* (*syn. picea, transkaucasica*) on bogs and wetlands (Collingwood 1979, Seifert 1996, Czechowski *et al*. 2002), and *F. selysi* on frequently inundated wetlands (Seifert 1996). Whereas the mound-building *Formica* are usually territorial and ecologically dominant (i.e. tend to exclude each other from their territories), the *Serviformica* species tend to be less territorial and ecologically less dominant (Savolainen & Vepsäläinen 1988, Punttila 1996).

Formica species have been subject to many genetic studies (Crozier & Pamilo 1996, Pamilo *et al*. 1997). These have shown that colony kin structure and dispersal patterns differ among species, which makes the genus a good candidate for an overview of the links between kin structure and the genetic structure of populations. Based on both observations and genetic data, *Formica* species have traditionally been divided into monogyne and polygyne species. Here we use both published and unpublished genetic data on several *Formica* species and discuss (1) whether

the division into mono- and polygyne species is warranted, or whether a different division should be used, (2) whether dispersal generally differs depending on colony kin structure, especially queen number, and (3) to what extent sex-biased dispersal and limited colonization abilities may restrict the occurrence of *Formica* species.

The source of genetic structuring

Genetic differences among populations arise due to genetic drift. The rate of allele frequency change depends on the effective population size, so that genetic composition changes more rapidly in small populations (Wright 1931, 1951). Several factors decrease the effective population size as compared with the census size, and the one of particular interest here is living in social groups. The effective population size is determined by the number of reproductively active individuals, i.e. queens and males, whereas ant workers are usually sterile and do not contribute to the breeding population. In species with single-queen colonies, the effective population size matches the number of nests plus the number of colony fathers. In many ants, however, colonies have several reproducing queens, and the effective population size increases as a function of the number and relatedness of coexisting queens (Pamilo & Crozier 1997).

While mark-recapture studies can provide direct estimates of current dispersal, spatial genetic structuring of populations studied by using nuclear genetic markers (e.g. allozymes or DNA microsatellites) can provide a picture of the typical dispersal ranges of individuals, as well as footprints of past colonization events. The observed differentiation between populations is then a balance between drift and gene flow. Alternatively, the observed structuring can be a result of a founder effect rather than ongoing but restricted gene flow, i.e. provide footprints of historical colonization and other demographic events (Wright 1969, Hedrick 1999). Further details of gene flow can be obtained by using maternally inherited mitochondrial markers. They directly reveal the amount of female gene flow (Ennos 1994), and the parallel use of nuclear and mitochondrial markers allows us to estimate gene flow separately in the two sexes (Seppä *et al*. 2004).

Wright's (1931) island model for genetic differentiation assumes that dispersal occurs with equal probability among all subpopulations. However, the degree of genetic differentiation may differ between pairs of subpopulations, such that some pairs are genetically more similar and others differ to a greater extent. Such differences are expressed either as isolation by distance (IBD, Wright 1943) or genetic viscosity (GV, Hamilton 1964). Under IBD the genetic affinity in a system of discrete local populations decreases with distance, and arises when dispersing individuals can reach only their neighbouring populations. GV refers to the same phenomenon as IBD, but within populations. GV arises either when the dispersing individuals do not reach across a continuous population, or when nest proliferation in social insects occurs by budding. Thus, colony kin structure and the dispersal behaviour of reproductive individuals together determine the current average sizes of the breeding populations, connectivity of the populations, and genetic effects of past colonization events.

The sources of the data reviewed here are presented in the Appendix. We were particularly interested in three central measures of genetic population structure. First, genetic relatedness describes the genetic similarity of individuals within a group (Pamilo 1989). Relatedness is a central parameter in the evolution of sociality, because kin selection theory assumes that individuals involved in an altruistic interaction are related (Hamilton 1964). Here we used relatedness among worker nestmates to describe colony kin structure. Second, the fixation indices F_{IS} and F_{ST} describe how genetic variation is distributed in a subdivided population (Wright 1931, 1943, 1951, Weir & Cockerham 1984). F_{IS} is the inbreeding coefficient, which measures the departure from random mating within subpopulations, and can take values from strongly negative (total outbreeding) and 1 (total inbreeding). It results from the sampled population being genetically further subdivided (Wahlund effect, Wahlund 1928), or more rarely, from active mate choice favouring relatives. In our use here F_{IS} represents the combination of both genetic viscosity and mating between relatives as we

cannot, based on the available data, discriminate between the two. F_{ST} is a measure for genetic differentiation among subpopulations, and can take values from 0 to 1.

In addition we extracted information on the spatial scale of sampling to allow adjustments for different sampling scales. We estimated the sampling areas both within and across sampling sites (local and global scales, respectively), and included the relevant scale as a covariate in all analyses. In some studies the approximate area was reported and in some cases the sampling sites were checked from maps and the areas calculated based on the distribution of the sampled nests. Finally, sometimes the sampling was done along transects and here we assumed transects to be 20 m wide, and calculated the area based on it. Thus, the estimates of the sampling area are not precise, but should correctly reflect the orders of magnitude in sampling areas. The nuclear data comprise studies made by using both allozymes and DNA microsatellites as genetic markers (Appendix). As the estimates based on these two classes of markers may not be entirely comparable (Hedrick 1999) we included the marker type as a covariate in all analyses. Whenever a variable in the analyses did not conform to normality we used logarithm-transformed values ($\ln x + 1$), which led to fulfillment of the requirements of normality in all cases.

Patterns of intra-colony relatedness

Relatedness is a relative measure of similarity among group members. In principle, the correct reference population in the estimation procedure is the breeding population (Pamilo 1989, Queller & Goodnight 1989), but this is usually difficult to assess in the field, and for practical reasons the local sampling site is considered as the actual breeding population. In ants, colonies are family units, and relatedness among the brood directly reflects the breeding structure in the colonies i.e. the number of reproducing queens and males and the relatedness among them (Ross 1993), as well as the pattern of reproductive partitioning among these. However, the inbreeding coefficient often indicates some degree of non-random mating ($F > 0$), either due to disparity between the local sampling site and the actual breeding population (Wahlund effect, Wahlund 1928) or mating among relatives. In both cases the relatedness estimates are boosted as compared with those for the ideal random mating population and the number of breeders inferred from the relatedness values will be underestimated. Therefore, we adjusted all relatedness estimates used in the analyses for inbreeding (Pamilo 1985).

As noted previously by Pamilo *et al*. (1997), the average relatedness in *Formica* varies considerably both among and within species, and in none of the species indicates consistent monogyny (Table 1). In *F. aquilonia*, *F. polyctena* and *F. paralugubris* relatedness is invariably low indicating the obligate presence of many reproductively active queens. Indeed, excavations and calculations based on genetic data indicate that the queen number frequently rises to several hundreds (Rosengren *et al*. 1993 and references therein). Nevertheless, relatedness only rarely equals zero (but *see* Elias *et al*. 2005), suggesting some degree of relatedness structure despite high numbers of queens. Interestingly, *F. cinerea* (Goropashnaya *et al*. 2001), *F. lugubris* (Gyllenstrand & Seppä 2003), *F. exsecta* (Pamilo & Rosengren 1984, Seppä *et al*. 2004) and *F. truncorum* (Sundström 1993) are socially polymorphic, so that the average population-specific relatedness can vary from close to zero to 0.75, the expected value under monogyny/monandry. Finally, in several species the average relatedness across populations is intermediate. This indicates either the presence of a few queens and/or multiple mating by queens, or extensive within-population variation in relatedness so that some nests within a population have a single queen, while others are highly polygyne. In *F. selysi* colonies within the same population indeed are either monogyne or highly polygyne (Chapuisat *et al*. 2004).

Monogyny and polygyny refer to the state of a colony, and the above examples show that the division cannot always be extended easily to concern populations or species. Therefore a biologically more relevant division seems to be either "obligately" *vs*. "facultatively polygyne species", with the latter group including also socially polymorphic species, or "highly

polygyne", "weakly/moderately polygyne" and "monogyne" species/populations. The former classification goes along the species boundaries, whereas the latter emphasizes the prevailing status of each population and concedes the high degree of flexibility in queen numbers in the genus. In the highly polygyne group, we include the obligately polygyne species *F. aquilonia*, *F. polyctena* and *F. paralugubris*, as well as the polygyne populations ($r < 0.25$) of the socially polymorphic species *F. exsecta*, *F. truncorum*, *F. lugubris*, *F. selysi* and *F. cinerea*. The weakly/moderately polygyne group encompasses species with higher intracolony relatedness ($r > 0.25$), excluding the purely monogyne populations of socially polymorphic species ($r > 0.50$) (Table 1). Given the average degree of multiple mating by queens a relatedness of 0.50 can still be compatible with monogyny (Pamilo 1993, Sundström 1993, Boomsma & Ratnieks 1996, Hannonen *et al*. 2004). In our analysis below we have treated each population as an independent sample, and classified them as highly polygyne, weakly/moderately polygyne or monogyne. Our justification for this is that queen number is such a highly variable trait that different dispersal regimes may prevail within species as well as between species. When the entire data set was considered the average estimate of relatedness was $r = 0.28 \pm 0.26$ (mean ± SD) and $r = 0.22 \pm 0.24$, for allozyme and DNA-microsatellite data, respectively; $T = 1.26$, d.f. = 94, $p = 0.21$. When only those species were considered for which both allozyme and microsatellite data were available the corresponding values were: 0.22 ± 0.27, 0.23 ± 0.25, $T = -0.14$, d.f. = 65, $p = 0.89$. The mean pairwise difference between the markers within species was 0.026 ± 0.035, $T = 0.35$, d.f. = 6, $p = 0.71$.

Patterns of spatial genetic structuring

The general consensus has been that monogyny (high intra-colony relatedness) is associated with extensive dispersal and outbreeding, and polygyny (low intra-colony relatedness) is associated with restricted dispersal and inbreeding (Hölldobler & Wilson 1990). Restricted dispersal, especially by females, and observations of local matings on nest mounds indeed suggest that inbreeding could be more common in polygyne species (Hölldobler & Wilson 1990), although a

Table 1. Average inbreeding-corrected relatedness (r), inbreeding (F_{IS}), population differentiation (F_{ST}), isolation by distance (IBD) and genetic viscosity (GV) per species. The sample sizes (n) refer to the number of populations (F_{IS} and r) or sets comprising at least two populations (F_{ST}) that were used; standard deviations were calculated over populations (F_{IS} and r) or sets of populations (F_{ST}); for IBD and GV, the first value indicates the number of populations in which IBD or GV was found (either in nuclear and/or mitochondrial markers), and the second number indicates the number of populations studied.

	r			F_{IS}			F_{ST}			IBD	GV
	mean ± SD	*n*	min/max	mean ± SD	*n*	min/max	mean ± SD	*n*	min/max		
F. aquilonia	0.02 ± 0.08	19	–0.12/0.15	0.03 ± 0.05	19	–0.08/0.17	0.17 ± 0.07	3	0.09/0.24	1/1	0/1
F. candida	0.23	1	–	0.07 ± 0.10	1	–	–	–	–	–	0/1
F. cinerea	0.24 ± 0.31	15	–0.10/0.81	0.04 ± 0.07	15	–0.05/0.24	0.06 ± 0.03	5	0.03/0.10	0/1	1/8
F. exsecta	0.34 ± 0.25	21	–0.01/0.73	0.03 ± 0.10	21	–0.12/0.19	0.09 ± 0.05	4	0.05/0.15	0/4	6/10
F. fusca	0.48 ± 0.17	6	0.25/0.67	0.05 ± 0.08	6	–0.07/0.17	0.09	1	–	0/1	–
F. lugubris	0.21 ± 0.21	6	–0.02/0.54	0.03 ± 0.08	11	–0.11/0.17	0.07 ± 0.06	4	0.02/0.16	–	1/1
F. paralugubris	–0.03 ± 0.03	2	–0.05/–0.01	0.13 ± 0.04	2	0.10/0.16	–	–	–	–	1/1
F. polyctena	0.11 ± 0.05	6	0.01/0.16	0.17 ± 0.06	6	0.08/0.26	0.07 ± 0.06	2	0.02/0.11	–	0/1
F. pratensis	0.44 ± 0.26	4	0.15/0.66	–0.04	1	–	–			–	1/1
F. pressilabris	0.18 ± 0.16	2	0.07/0.29	–0.03 ± 0.03	2	–0.05/–0.01	0.09 ± 0.00	1	–	–	–
F. rufa	0.45 ± 0.12	9	0.27/0.59	0.09 ± 0.11	9	–0.06/0.27	0.04 ± 0.02	3	0.02/0.05	–	1*/2
F. sanguinea	0.44 ± 0.07	6	0.31/0.54	0.04 ± 0.10	6	–0.08/0.18	0.03	1	–	–	2/3
F. selysi	0.40 ± 0.44	2	0.09/0.71	0.04 ± 0.01	2	0.03/0.05	0.00 ± 0.00	2	0.00/0.01	–	0/1
F. truncorum	0.29 ± 0.27	11	–0.07/0.67	0.02 ± 0.10	11	–0.12/0.18	0.09 ± 0.08	4	0.03/0.19	–	0/1

* viscosity found only in resident colony queens.

high queen number in a nest means that intranidal mating does not necessarily occur between close relatives. Thus we would expect the estimate of inbreeding (F_{IS}), reflecting either within-population viscosity or mating among relatives, to be higher under polygyny than under monogyny. When the populations were classified as highly polygyne, weakly polygyne and monogyne, treating each population as an independent sample we found no significant effects of population type, marker type or species on inbreeding (F_{IS}) (Table 2). Only the scale of sampling had a significant effect, with the estimate of F_{IS} increasing with sampling area (Table 2). This lack of difference is largely due to the divergent pattern found in *F. exsecta*, where high estimates of inbreeding were obtained in several monogyne populations (Sundström *et al*. 2003, Seppä *et al*. 2004). When this species was omitted from the analysis the difference between population types was significant (GLM: $F_{2,74} = 5.2$, $p = 0.008$, species: $F_{12,74} = 1.01$, $p = 0.45$, marker type: $F_{1,74} = 0.17$, $p = 0.68$, scale: $F_{1,74} = 2.2$, $p = 0.14$). In this data set, the average degree of inbreeding decreased to 0.003 ± 0.07 for monogyne populations and remained unchanged for weakly and highly polygyne populations. The very high estimates of F_{IS} obtained in monogyne populations of *F. exsecta* may be due to the small number of colonies sampled (3–5 colonies in most cases; Seppä *et al*. 2004). Nevertheless, inbreeding was also high in a monogyne population where nearly 70 colonies had been sampled (Sundström *et al*. 2003).

We repeated this analysis but entered average relatedness instead of population type and added the interaction relatedness × species in our GLM model. As expected, based on the analysis above, relatedness had no significant effect on F_{IS}, but both the effect of species and scale as well as the interaction between relatedness and species were significant (GLM with stepwise backward elimination, species: $F_{12,85} = 2.2$, $p = 0.02$, scale: $F_{1,85} = 6.8$, $p = 0.01$, species × relatedness: $F_{13,85} = 2.6$, $p = 0.004$, the effects of marker and relatedness were eliminated under threshold criteria of $p > 0.15$) (Fig. 1a). This indicates that the degree of within-population viscosity as estimated by F_{IS} does not change in concert with queen number across species. Instead the species differ in their response such that the negative relationship holds in some species, but not in others (Fig. 2). Although the limited number of replicates in some species precludes more robust conclusions, several species show significant negative trends and one species (*F. exsecta*) shows a significant positive trend (Fig. 2). However, the pattern may change when more data becomes available.

Overall the average values of F_{IS} tended to be positive, but in many individual cases not statistically different from zero (Table 1 and Appendix). Some rather high values obtained with allozymes were not significant although similar and much lower values obtained with microsatellites were significant (Appendix). This highlights the problem of power in analyses based on few loci. We feel, however, justified in using all the

Table 2. Average degree of inbreeding (F_{IS}), population differentiation (F_{ST}) and nest mate relatedness (r) in highly polygyne, weakly polygyne and monogyne species/populations. Standard deviations calculated over the different studies. The lower half gives the results of a GLM with each of the three parameters as dependent variables.

	r			F_{IS}			F_{ST}		
	mean ± SD	n	min/max	mean ± SD	n	min/max	mean ± SD	n	min/max
Highly polygyne	0.05 ± 0.8	60	–0.12/0.23	0.05 ± 0.08	60	–0.12/0.26	0.10 ± 0.07	15	0.01/0.24
Weakly polygyne	0.39 ± 0.08	27	0.25/0.48	0.06 ± 0.10	26	–0.12/0.27	0.06 ± 0.03	7	0.02/0.09
Monogyne	0.62 ± 0.07	26	0.52/0.81	0.02 ± 0.08	26	–0.12/0.19	0.03 ± 0.02	8	0.00/0.05
GLM	F	d.f.	p	F	d.f.	p	F	d.f.	p
Population type	329.6	2,94	< 0.0001	0.96	2,94	0.38	4.15	2,16	0.03
Sampling scale	0.30	1,94	0.58	5.64	1,94	0.02	0.06	10,16	0.37
Species	1.75	13,94	0.06	0.80	13,94	0.66	1.46	1,16	0.24
Marker	0.47	1,94	0.49	0.08	1,94	0.78	0.11	1,16	0.74

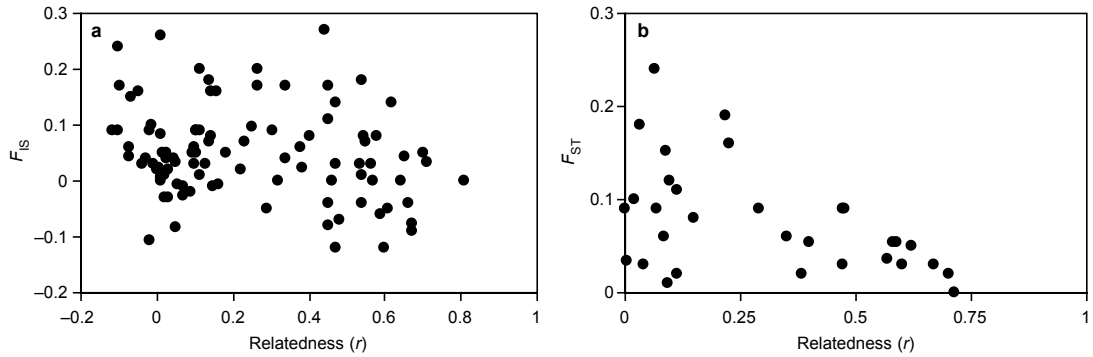

Fig. 1. The relationship between relatedness and F_{IS} (**a**) and F_{ST} (**b**) across all populations.

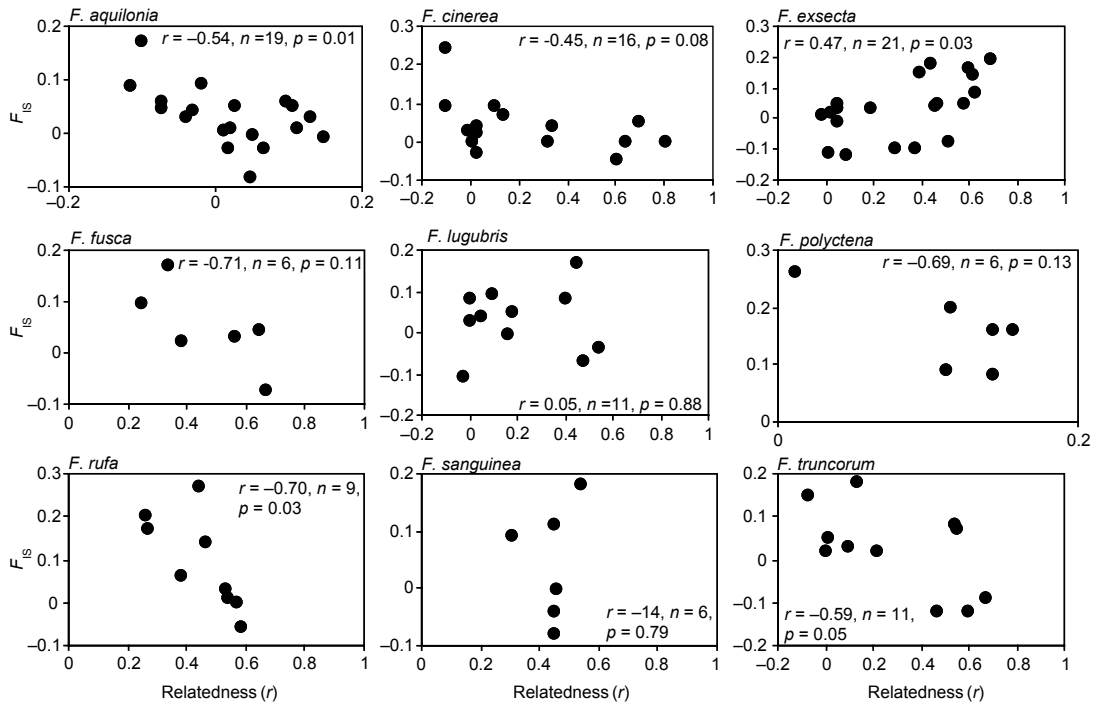

Fig. 2. The relationship between F_{IS} and relatedness for all species separately.

available values as they represent unbiased estimates of the actual degree of within population viscosity, albeit with wide confidence intervals. If no inbreeding were present, the average across 96 samples should indeed be zero, which it is not (mean = 0.05, SD = 0.08, t = 5.8, d.f. = 95, $p <$ 0.001). This indicates that some degree of genetic viscosity is present in *Formica* ants regardless of the number of queens, although viscosity may be absent or not detectable in individual populations. As the values obtained with allozymes were not consistently higher than those obtained with microsatellites and because the marker type was entered in all analyses it is unlikely that the marker type has influenced the conclusions. Nevertheless, in all highly polygyne species (*F. aquilonia*, *F. paralugubris* and *F. polyctena*) and several facultatively polygyne species (*F. rufa*, *F. lugubris*, *F. exsecta*, *F. fusca* and *F. cinerea*) a significant degree of inbreeding was found at least in some populations (Chapuisat & Keller 1999, Goropashnaya *et al.* 2001, Ranta 2002, Sundström *et al.* 2003, Hannonen *et al.* 2004, Gyllenstrand *et al.* 2005, Pamilo *et al.* 2005). The facultatively polygyne group also included monogyne populations. In the case of *F. rufa*

the spatial scale of sampling was relatively large (200 ha), but in the other monogyne populations the scale of sampling was usually less than 20 ha. The high degree of inbreeding in the monogyne population of *F. exsecta* at a very limited spatial scale (15 ha) (Sundström *et al*. 2003) shows that monogyny is not necessarily always associated with extensive dispersal. Interestingly, *F. exsecta* is the only species with dimorphic males, with male size apparently corresponding to their dispersal propensity (Fortelius *et al*. 1987).

Apart from mating between relatives, the coefficient of inbreeding (F_{IS}) may take positive values either because a population comprises several reproductively isolated sets of subpopulations or because colonies at greater distance differ more owing to colony reproduction by budding (GV). Genetic viscosity in nuclear markers has been studied in twelve species in a total of 28 populations. The distances between the nests in these studies ranged from a few meters to more than two kilometers. In twelve populations (43%), a significant degree of genetic viscosity (GV) was detected. This is most likely an underestimate, because GV cannot be detected if the sampling area is totally homogenous, e.g. if it comprises a single polydomous colony. This is entirely possible in some of the smaller sampling areas. In six cases the significant outcomes encompassed highly polygyne populations, whereas in six cases the populations were monogyne or weakly polygyne. Of the non-significant outcomes five cases encompassed monogyne populations and eleven cases polygyne populations (Fisher's exact test: $p = 0.31$). In cases where several populations had been tested (*F. cinerea*, *F. exsecta*, *F. rufa*, *F. sanguinea*), both significant and non-significant outcomes were found (Table 1). The smallest range at which isolation by distance was found was 100 m (*F. exsecta*) and five of the significant outcomes were found at scales of 500 m or less (*F. cinerea*, *F. lugubris*, and *F. pratensis* once, *F. exsecta* twice). Inbreeding, relatedness, and scale had no significant effect on the presence/absence of genetic viscosity (logistic regression: all p values greater than 0.59). Nevertheless, the results show that genetic viscosity can be found in more than one third of the populations, also at rather limited scales (a few hundred meters). Interestingly, mitochondrial markers indicated genetic viscosity in five of six cases (*F. exsecta*, four populations (Liautard & Keller 2001, Seppä *et al*. 2004); *F. lugubris*, one population (Gyllenstrand & Seppä 2003)). All these populations were highly polygyne, and the range of the populations was similar to that in the nuclear studies (< 500 m). This indicates that reduced female dispersal at local scales is common at least in polygyne species and highlights the need for corresponding studies in weakly or moderately polygyne species.

As with within-population differentiation we may also expect greater between-population differentiation in poly- than in monogyne populations, if the dispersal propensities of the two types differ. Indeed, the between-population differentiation estimate of F_{ST} was significantly lower in monogyne than in highly polygyne sets of populations (Table 2, Tukey post-hoc tests: $p = 0.01$, all other p values greater than 0.18). Similarly, F_{ST} decreased significantly with increasing relatedness (GLM with stepwise backward elimination, relatedness: $F_{1,29} = 8.4$, $p = 0.007$; the remaining factors, species, local scale or marker type were all eliminated with the threshold criterion for exclusion set at $p > 0.15$; Fig. 1b). Owing to the small number of population sets per species an analysis with the interaction species × relatedness was not considered appropriate. This shows that sets of populations with on average low relatedness also show higher between-population genetic differentiation, and the conclusion is that high queen numbers translate into reduced long-range dispersal. This is even more obvious when remembering the connection between genetic differentiation and effective population size: high queen numbers translate into greater effective population sizes, which should slow down the effects of genetic drift producing genetic differentiation. A more parsimonious scenario is, however, that most highly polygyne populations are not in drift-migration balance, but are founded through a bottleneck by only one or a few immigrants. This results in random representation of only a few alleles in each locus.

Between-population differentiation may follow either the infinite island model, or the stepping-stone model (Wright 1931, 1951). In the latter case more distant populations are predicted to differ more owing to isolation by distance.

Isolation by distance, decreasing genetic affinity of local populations with distance, has been studied only in seven populations of four species, and only one of them shows IBD (Table 1). In *F. aquilonia*, *F. exsecta* and *F. fusca*, the distances between local populations was between 0.2 and 50 km (Sundström *et al*. 2003, Helanterä 2004, Seppä *et al*. 2004, Pamilo *et al*. 2005), but in *F. cinerea* IBD was assessed in an area covering most of northern Europe (max distances > 1000 km, Goropashnaya *et al*. 2001). The studies also include one where genetic population structure was studied with mitochondrial markers (Liautard & Keller 2001).

The above estimates of genetic differentiation are based on nuclear markers, but these usually do not reveal the relative contributions of the two sexes to the observed genetic differentiation pattern (but *see* Sundström *et al*. 2003). Indeed, foundation of new populations may be severely constrained owing to restricted female dispersal, yet gene flow mediated exclusively by males may completely homogenize allele frequencies at nuclear markers, as for instance in polygyne populations of *Solenopsis invicta* (e.g. Ross & Shoemaker 1997). In the extreme, males may both mate in their natal colony and later disperse thereby effectively contributing to the homogenization of allele frequencies between populations. To date both nuclear and mitochondrial markers have been used to compare male and female gene flow in three *Formica* species. The most extensively studied species is *F. exsecta*. In one case the data allow comparisons of gene flow both within mono- and polygyne sets of populations as well as between sympatric monogyne and polygyne populations. The degree of isolation obtained with the maternally inherited marker was substantially higher than that obtained for the nuclear marker, and only the degree of differentiation among monogyne populations of *F. exsecta* was not significant for both classes of markers (Table 3; Seppä *et al*. 2004). This indicates that males disperse at a much higher rate than females. However, an additional study on a monogyne population of *F. exsecta* found sex-biased gene flow with reduced female dispersal at very small scales (300 m) (Sundström *et al*. 2003). This study was based on nuclear markers only, but detection of sex-biased gene flow was possible because post-dispersal genotypes of both parents in each nest could be inferred from worker genotypes. In a similar study on *F. rufa*, genetic viscosity was apparent in colony queens, but not in colony fathers (Ranta 2002). The effect was, however, weaker than in *F. exsecta* so no significant viscosity was detected in the offspring workers. In *F. truncorum* two adjacent monogyne and polygyne populations did not share any haplotypes in mitochondrial markers (N. Gyllenstrand *et al*. unpubl. data). This indicates a complete absence of female gene flow between the two population types, despite distances as short as a few hundred meters. Nuclear markers, on the other hand, showed moderate levels of differentiation between the population types, which must be due to male dispersal between the two populations. Finally, in a highly polygynous *F. lugubris* population female gene flow among subpopulations was also negligible, but nuclear

Table 3. Local differentiation when both nuclear (F_{ST}) and mitochondrial (Φ_{ST}) differentiation has been estimated from the same populations. #pops is the number of subpopulations in the study; type is the type of comparison in each case (M populations; P populations or all mixed); scale is the approximate distance between subpopulations in km. Asterisks mark estimates significantly greater than zero. The ratio F_{ST}/Φ_{ST} = 3 indicates equal gene flow among populations by both sexes (*see* Seppä *et al.* 2004), and ratios below and above three indicate an excess of male and female gene flow, respectively.

Species/population	#pops	Type	Scale km	F_{ST}	Φ_{ST}	Φ_{ST}/F_{ST}
F. exsecta/Uppsala	4	M-M	0.2–9	0.00	0.06	–
F. exsecta/Uppsala	6	P-P	0.2–9	0.10	0.46*	4.7
F. exsecta/Uppsala	10	M-P	0.2–9	0.06*	0.27*	4.3
F. exsecta/Åland	11	All	2–20	0.09*	0.13*	1.5
F. lugubris	5	P-P	1–3	0.03	0.53	15.6
F. truncorum	2	M-P	min 0.3	0.12	1.0	8.3

genetic structure was shallow due to extensive gene flow (Gyllenstrand & Seppä 2003).

In *F. exsecta*, the use of mitochondrial markers also revealed cases where multiple matrilines coexist in the same polygyne nest. In two different studies, eighteen (Liautard & Keller 2001) and sixteen (Seppä *et al*. 2004) percent of polygyne nests contained more than one mtDNA haplotype, which means that immigrating females have been accepted into existing polygyne nests at some point. Polygyne *Formica* colonies do readily accept alien queens (Fortelius *et al*. 1993, Brown *et al*. 2003), but whether these act as intraspecific parasites or become subordinate reproducers that only specialise in worker production is not known.

Finally, species adapted to ephemeral habitats are likely to be better dispersers than species adapted to continuous habitats. This should lead to lower degrees of between-population differentiation. However, colonization is often also associated with founder effects, which may counteract homogenization of allele frequencies across populations unless new immigrants continuously arrive to the area. We compared relatedness, inbreeding and population subdivision between species associated with ephemeral habitats and species associated with mature boreal forests. Although the F_{IS} was lower for species found in ephemeral habitats than forest dwellers, the difference between the two types of species was not significant (mean ± SD: 0.04 ± 0.08 and 0.06 ± 0.09, respectively; $t = 1.63$, $p = 0.11$, d.f. = 94). The average estimates of F_{ST} were of similar magnitude in both categories: 0.07 ± 0.05 and 0.08 ± 0.07, respectively; and did not differ significantly ($t = 0.4$, d.f. = 30, $p = 0.69$). However, the species associated with more ephemeral habitats have significantly higher average relatedness than the forest-dwelling ones (0.33 ± 0.26 and 0.16 ± 0.21; $t = 3.54$, d.f. = 94, $p = 0.0006$). Taken together, the type of habitat (fragmented *vs*. continuous) to which a species is adapted does not strongly affect population parameters.

Conclusions

Here we have quantified and statistically tested the general assumption that colony kin structure is associated with dispersal propensity. Although a wealth of studies address genetic population structure in conjunction with colony kin structure none have to our knowledge tested this basic prediction across species. Indeed our analyses verify that this assumption is valid and that polygyne populations or species also tend to have reduced long-range (between-population) dispersal. However, this association did not hold for short-range (within-population) dispersal across species. Instead the response varied among species with most of them showing a negative association between F_{IS} and relatedness. This genetic viscosity is most likely due to colony reproduction by budding. Interestingly, one species (*F. exsecta*) showed a significant positive trend which is mainly due to a high frequency of inbred monogyne populations (Sundström *et al*. 2003, Seppä *et al*. 2004). In this species sex-biased dispersal is pronounced, with strong female philopatry in polygyne populations (Seppä *et al*. 2004). Monogyne populations are often fairly small and it seems likely that the high inbreeding coefficients in these populations indeed are due to non-random mating. The fact that this species also has size-dimorphic males with different dispersal propensities raises new questions regarding its reproductive biology.

Our analysis also shows that the traditional division into monogyne and polygyne species is not well supported. Instead, populations of many species show the entire range of variation in dispersal and colony kin structure. None of the species is exclusively monogyne, although several species have largely monogyne populations. The trait (queen number) clearly is phylogenetically very flexible within this genus (for a more formal analysis *see* Helanterä 2004). Interestingly, only one species has so far been shown to have unicolonial populations with zero within-colony relatedness (*F. truncorum*; Elias *et al*. 2005), although several species have high numbers of queens (Rosengren *et al* 1993). Also in the case of *F. truncorum* unicoloniality is likely to be a matter of scale of sampling.

Most species show some degree of population viscosity or at least reduced dispersal also at very local scales. Given that polygyne species regularly have large effective population sizes the effects of genetic drift should be

less pronounced and therefore this result indicates strongly reduced gene flow. However, the alternative explanation that most populations of highly polygyne species result from single colonization events seems much more likely. Hence, these species may face severe colonization problems given the current rate of habitat fragmentation. This is further strengthened by the fact that many of the species studied so far appear to have some degree of sex-biased dispersal with females being more philopatric than males. Thus, colonization of new habitable areas may in fact be even more difficult than indicated by the observed overall degree of population viscosity in these ants.

Finally, the species adapted to more ephemeral habitats, such as *F. exsecta*, *F. truncorum*, *F. sanguinea*, and the *Serviformica* species do not show significantly lower estimates of F_{IS} or F_{ST} than the rest of the species associated with continuous forest habitat. Nevertheless, also these species can show extreme within-population genetic viscosity as evidenced by *F. exsecta*. Given that the ephemeral habitats also are highly fragmented founder effects in conjunction with low immigration rates and a reasonable persistence time of the habitat, could in fact also turn the balance in the opposite direction and lead to strong population subdivision in these species. When habitat persistence is very limited colonization rates necessarily must be high and no such differentiation is expected. One additional reason for the lack of a stronger substructuring in these species may be rapid population turnover, where populations frequently go extinct and new habitats are quickly colonized by immigrants. Conversely, large effective population sizes in conjunction with limited time span since habitat fragmentation may explain the as yet moderate degree of structuring in forest dwellers. Alternatively, some of these species are reasonably good colonizers, whereas others indeed have very limited colonization abilities. This is consistent with our result that at least the F_{ST} values differed significantly among species, with the highly polygyne species (low relatedness) having the highest degree of population subdivision. Within-population genetic viscosity was however of the same magnitude across all species. Taken together our analysis suggests some degree of population viscosity in many populations of *Formica* ants and this degree of viscosity can vary with kin structure both across populations within species and across species.

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Appendix. Data sources, sampling areas, sampling scales and average F_{ST}, F_{IS} and relatedness. The relatedness estimates are uncorrected for inbreeding. Asterisks indicate significant deviations from zero at least in some populations; marker: a = allozymes, m = DNA microsatellites, the number indicates the number of loci in each case; *N* = number of populations; *n* = number of nests; global and local sampling are the approximate sampling areas (in km^2 and ha, respectively);

	N	*n*	Marker	Area	Global sampling	Local sampling	Mean F_{ST}	Mean F_{IS}	Mean *r*	Reference
F. aquilonia	7	> 100	6a	Uusimaa, Finland	400	10	0.17*	0.05	0.13	Pamilo 1982, Pamilo *et al.* 2005
F. aquilonia	3	43	4m	Uusimaa, Finland	200	10	0.24*	0.04	0.14	Pamilo *et al.* 2005
F. aquilonia	9	76	12m	Moscow, Russia	4	2	0.09*	–0.001	0.04	Mäki-Petäys *et al.* 2005.
F. candida	1	55	1a	Vihti, Finland	n.a.	1	n.a.	0.07	0.23	Pamilo 1982
F. cinerea[1]	23	249	5m	Fennoscandia	100–200*	2	0.06*	0.01	0.36	Goropashnaya *et al.* 2001
F. cinerea	6	77	3m	Finland	n.a.	ca. 100	0.07*	0.08*	0.22	Zhu *et al.* 2003
F. cinerea	6	ca. 60	2a	Finland Europe	n.a.	2–20	n.a.	0.01	0.33	Lindström *et al.* 1996
F. exsecta M	4	17	6m	Uppsala, Sweden	50	50	0.004	0.08*	0.64	Seppä *et al.* 2004
F. exsecta P	6	63	6m	Uppsala, Sweden	50	50	0.15*	-0.02	0.09	Seppä *et al.* 2004
F. exsecta	11	103	3m	Åland, Finland	100	50	0.09*	0.03	0.50	Seppä *et al.* 2004
F. exsecta	3	70	2m+3a	Hanko, Finland	5	15	0.05	0.14*	0.71	Sundström *et al.* 2003
F. exsecta	2	71	1-2a	Uusimaa, Finland	n.a.	1.5	n.a.	0.03	0.08	Pamilo & Rosengren 1984
F. fusca	4	68	5m	Hanko, Finland	n.a.	3	0.07*	0.09*	0.56	Helanterä 2004
F. fusca	1	55	5m	Inkoo, Finland	130	15	n.a.	0.02	0.41	Helanterä 2004
F. fusca	1	34	4a	Hanko, Finland	n.a.	15	n.a.	0.03	0.59	Olsson 1999
F. lugubris	3	37	12m	Moscow, Russia	4	12	0.06*	0.005	0.14	Mäki-Petäys *et al.* 2005
F. lugubris	5	74	7m	Peak District National Park, U.K.	300	8	0.034*	0.03	0.05	Gyllenstrand & Seppä 2003
F. lugubris	2	59	8m	Swiss National Park, Switzerland	50	5	0.16*	0.08*/0.04	0.49/0.12	Bernasconi *et al.* 2005
F. lugubris	4	48	2-7a	Europe	n.a.	10–20	n.a.	0.04	0.47	Pamilo *et al.* 1992, Pamilo *et al.* 1994
F. paralugubris	1	46	6a	Jura B, Switzerland	n.a.	160 000	n.a.	0.16*	0.24	Pamilo *et al.* 1992
F. paralugubris	1	21	4m	Jura, Switzerland	n.a.	ca. 10	n.a.	0.10*	0.17	Chapuisat *et al.* 1997, Chapuisat & Keller 1999
F. polyctena	4	91	5m	Siuntio, Finland	4	2	0.11*	0.09*	0.23	Elias *et al.* pers. comm.
F. polyctena	4	59	8m	Uppsala, Sweden	400	200	0.02*	0.17*	0.37	Gyllenstrand *et al.* 2004
F. pratensis	2	> 10	4m	Öland, Sweden	n.a.	n.a.	n.a.	n.a.	0.14/0.51	Beye *et al.* 1998, Pirk *et al.* 2001
F. pratensis	1	35	2a	Hanko, Finland	n.a.	200	n.a.	–0.04	0.66	Pamilo *et al.* 1994
F. pressilabris	2	38	1-2a	Uusimaa, Finland	200	0.5	0.09	–0.01/–0.05	0.07/0.29	Pamilo & Rosengren 1984
F. rufa	2	49	5-6a	S-Finland	n.a.	ca. 1000	n.a.	0.16	0.63	Pamilo *et al.* 1994
F. rufa	4	26	4m	Siuntio, Finland	15	1200	0.05*	–0.06	0.59	Ranta 2002
F. rufa	8	65	4m	Inkoo, Finland	15	100	0.04*	< –0.01	0.57	W.T. Tay, pers. comm.
F. rufa	5	??	8m	Uppsala, Sweden	400	200	0.02*	0.12*	0.52	Gyllenstrand *et al.* 2004

F. sanguinea	4	114	1-4a	S-Finland	n.a.	200–1200	n.a.	0.04	0.44	Pamilo 1981, Pamilo & Seppä 1994
F. sanguinea	4	79	4a	Hyytiälä, Finland	36	15	0.03	0.04	0.47	Seppä *et al.* 1995, P. Seppä unpubl. data
F. selysi[2]	1	112	9m	Valais, Switzerland	2	75	0.005	0.03/0.05	0.73/0.18	Chapuisat *et al.* 2004
F. truncorum	3	89	3a	Inkoo, Finland	15	10	0.19*	0.02	0.25	Sundström 1993
F. truncorum	6	85	3a	S-Finland	n.a.	10–15	n.a.	0.07	0.40	Sundström 1989, 1993, Seppä *et al.* 1995
F. truncorum	1	15	5m	Inkoo, Finland	n.a.	3	n.a.	0.02	0.04	Elias *et al.* 2005
F. truncorum	5	30	3-4a	Hanko, Finland	4	15	0.03	–0.09*	0.67	Sundström 1993
F. truncorum	5	91	3a	Mols, Denmark	100	15	0.03	–0.12*	0.60	Sundström 1993
F. truncorum	1	19	5m	Hanko, Finland	n.a.	2	n.a.	0.0	0.01	Gyllenstrand *et al.* 2005
F. truncorum	2	13	4a	Forssa	4	1	0.12*	0.03	0.15	Seppä *et al.* 1995, L. Sundström unpubl. data

[1] the global scale as well as the average F_{ST} calculated for subsets of the entire sample.
[2] the population comprised monogyne and highly polygyne colonies, with very few intermediates.