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Report

Convergent Genetic Architecture Underlies Social Organization in Ants

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Summary

Complex adaptive polymorphisms are common in nature, but what mechanisms maintain the underlying favorable allelic combinations [1–4]? The convergent evolution of polymorphic social organization in two independent ant species provides a great opportunity to investigate how genomes evolved under parallel selection. Here, we demonstrate that a large, nonrecombining "social chromosome" is associated with social organization in the Alpine silver ant, *Formica selysi*. This social chromosome shares architectural characteristics with that of the fire ant *Solenopsis invicta* [2], but the two show no detectable similarity in gene content. The discovery of convergence at two levels—the phenotype and the genetic architecture associated with alternative social forms—points at general genetic mechanisms underlying transitions in social organization. More broadly, our findings are consistent with recent theoretical studies suggesting that suppression of recombination plays a key role in facilitating coordinated shifts in coadapted traits [5, 6].

Results and Discussion

The convergent evolution of similar traits in distantly related species demonstrates the power of natural selection [7]. But when complex sets of behavioral and morphological traits arise repeatedly, are they controlled by similar genetic mechanisms? Comparing the genetic architecture underlying convergent adaptations can lead to key insights into how genomic evolution shapes phenotypic innovations.

Many ant species exhibit strikingly convergent behavioral syndromes depending upon the number of queens reproducing in the colony. In general, colonies with multiple queens (polygynous) produce smaller queens and workers than colonies with a single queen (monogynous), and the two forms differ in key behavioral traits such as tolerance of conspecifics and mode of dispersal [8, 9]. A recent study in the fire ant *Solenopsis invicta* identified a large, nonrecombining "social chromosome" that is associated with alternative social organizations in that species [2]. Here, we investigated the genomic architecture underlying social organization in the Alpine silver ant, *Formica selysi*, which is polymorphic in queen number and exhibits a similar suite of behavioral and morphological traits associated with each form.

Populations of *F. selysi* contain a mix of monogynous and polygynous colonies [10, 11], with rare oligogynous colonies headed by two closely related queens (see Table S1 available online; [12]). In our study population in the Swiss Alps, we have monitored the social organization of 121 colonies over the past 14 years [10, 11]. We have identified differences between the two common social forms in body size of workers and queens [12, 13], colony lifespan [13], colony size [13], allocation to reproductive offspring [14], and brood development time [15]. The social forms are not differentiated at eight polymorphic microsatellite loci but instead form a single, apparently genetically homogeneous population [10, 11]. Taken together, these characteristics make this species an ideal system for the investigation of the genetic basis of social organization.

Here, we performed a genome-wide association study to search for genetic markers exhibiting significant allele frequency differences between the two social forms. Through genotyping-by-sequencing [16, 17] of haploid males from monogynous and polygynous colonies within the focal population, we identified 18,199 SNPs (see Experimental Procedures). At a genome-wide false discovery rate of 0.01 (per-SNP $\alpha = 0.0003$), 643 of these markers were significantly associated with social organization in our mixed-effects model (Table S2).

To identify the position of these markers in the genome, we constructed a linkage map (see Experimental Procedures). This map contained 27 main linkage groups, consistent with the haploid chromosome number of members of the *Serviformica* subgenus (Figure 1A; [18]). A total of 2,409 markers, located on 1,763 genome scaffolds, were heterozygous in the focal queen. These scaffolds contained 36.7% of the SNPs from the population data set. Strikingly, of the 136 SNP markers associated with social organization that could be placed on the linkage map, 134 were located on a single linkage group (Figure 1A). Only two markers did not map to this linkage group, a number consistent with the number of false positives expected given the false discovery rate we used. These two markers each mapped to a different linkage group. The linkage group (LG3) containing highly differentiated SNPs between males of monogynous and polygynous origin is hereafter called the "social chromosome." The differentiated SNPs occurred across most of the linkage group (183 of 244 cM), with short sections of low differentiation characterizing each end (Figure 1B).

We identified two major haplotypes at the social chromosome: the sequence found in males of monogynous origin is designated as the "Sm" haplotype, and the sequence associated with males of polygynous origin is called the "Sp" haplotype. How are these allelic differences maintained over such a large region of the genome? We expected that this pattern could result from suppression of recombination between the two haplotypes, and we investigated this possibility by constructing a linkage map of markers on the social chromosome from offspring of four Sm/Sp heterozygous queens. As predicted, the linkage map showed perfect cosegregation of the Sm versus Sp variants of markers from 36.6 to 195.1 cM along the Sm/Sm linkage map (Figure 2A; see Experimental Procedures). This pattern shows that recombination is suppressed between the two haplotypes in these four families.

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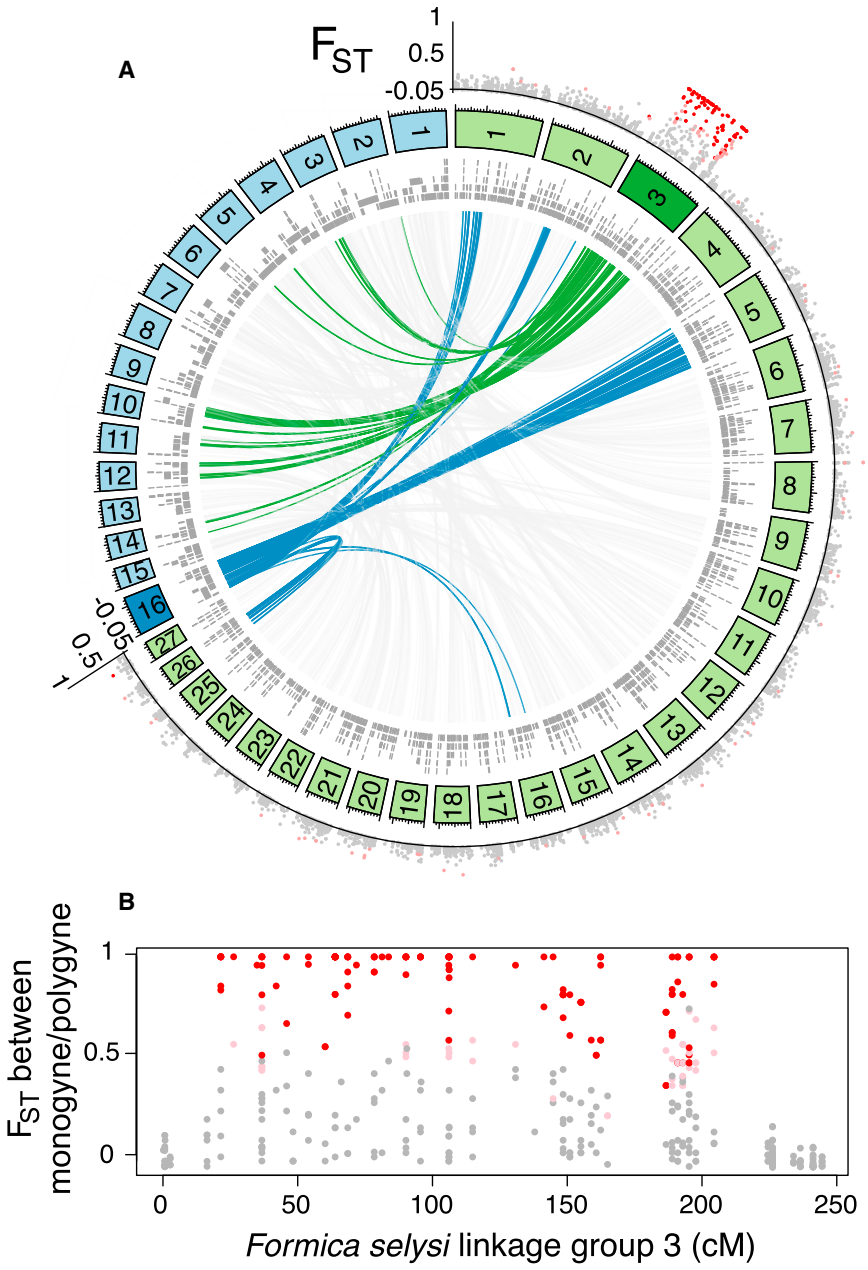

Figure 1. The Social Chromosomes of *F. selysi* and *S. invicta* Are Not Homologous

Markers with a high degree of differentiation between monogynous and polygynous males were localized on one *F. selysi* linkage group not homologous to the fire ant social chromosome. The circle in (A) shows linkage groups of *F. selysi* (green panels) and *S. invicta* (blue panels), with scaffolds from respective genomes aligning to loci in each linkage group (gray bars, inner circle). The interior lines show synteny between the two genomes for the *F. selysi* social chromosome (green), the *S. invicta* social chromosome (blue), and scaffolds on other linkage groups (light gray). The F_{ST} value between monogyne and polygyne males at each SNP placed on the linkage map is shown in the outer circle, with colors indicating no significant differentiation between the two forms (gray dots), significant differentiation at $\alpha = 0.01$ (light red dots), and significant differentiation at $\alpha = 0.0003$ (dark red dots). In (B), a zoomed view of the F_{ST} value between monogyne and polygyne males on the *F. selysi* social chromosome shows the lack of divergence at each end of the chromosome.

This genomic region is characterized by high linkage disequilibrium and differentiation between Sm and Sp haplotypes, suggesting a long history of suppressed recombination, beyond the single generation demonstrated with the linkage map (Figures 1, 2, and S1).

Identifying genomic regions associated with colony social organization raises immediate questions about the distribution of the two social haplotypes in diploid individuals within and across field colonies. Assessing the genotypic structure of 42 monogynous, 44 polygynous, and 5 oligogynous colonies, we found that monogynous and oligogynous colonies contained only Sm/Sm queens and workers, and Sm males (Table 1). Polygynous colonies contained a combination of Sm/Sp heterozygous and Sp/Sp homozygous queens and workers, as well as Sp males. We never found Sm/Sm queens or workers, or Sm males, in polygynous colonies. Individuals with the Sm/Sm genotype were significantly larger than individuals with a Sp haplotype; there was no difference in size between Sm/Sp and Sp/Sp workers or queens (Table S1; see also [12, 19]).

The absence of Sm/Sm females and Sm males from polygynous colonies is surprising, since the Sm/Sp queens are expected to produce Sm and Sp male offspring and, when mated with Sm males, heterozygous and Sm/Sm females. The causes of the absence of Sm or Sm/Sm individuals in polygynous colonies deserve further investigation. Possible mechanisms that might generate this unusual genotype distribution include assortative mating (e.g., [20]), meiotic drive (e.g., [21]), differential mortality (e.g., [22]), or brood elimination by workers [23]. More generally, studies on mate choice, brood development, and ecological success will be needed to explain the maintenance of the genetic polymorphism at the social chromosome in this system.

The genotypic system underlying social organization in *F. selysi* colonies resembles that of fire ants (Table 2). Fire ants exhibit two haplotypes associated with colony queen number: SB and Sb. In both species, monogynous colonies have similar homozygous genotypic compositions at the social chromosome: *F. selysi* colonies contain only Sm/Sm females mated with Sm males (Table 1), and *S. invicta* colonies contain only SB/SB females mated with SB males [23]. There are, however, at least two major differences between the two systems. First, polygynous *S. invicta* colonies contain a mix of SB/SB, SB/Sb, and rare Sb/Sb workers, while all reproductive queens are SB/Sb [24]. In contrast, we found a mix of Sp/Sp and Sm/Sp queens and workers, and no Sm/Sm females or Sm males, in polygynous *F. selysi* colonies. Second, *S. invicta* Sb/Sb workers are rare because Sb is

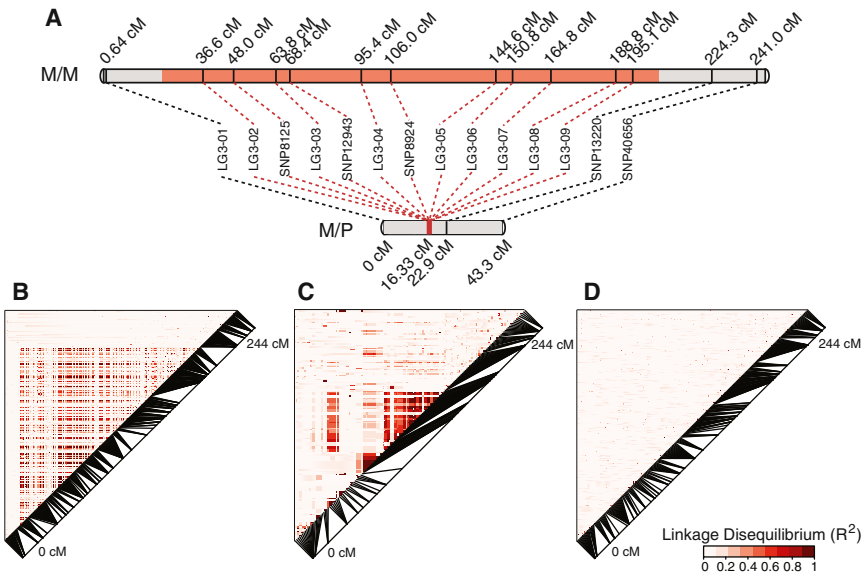

Figure 2. Recombination Is Suppressed over the Central Region of the Social Chromosome

(A) Linkage maps of the social chromosome show suppressed recombination in 80 worker offspring of four Sm/Sp queens relative to 59 male offspring of one Sm/Sm queen; no recombination was observed in offspring of Sm/Sp queens (i.e., map length 0 cM) for markers in the region that is divergent between the Sm and Sp chromosomes, which spans 183 cM in the Sm/Sm linkage map. The region with significantly different Sm and Sp haplotypes is shown in orange, while regions with little differentiation between monogynous and polygynous individuals are shown in gray.

(B–D) Linkage disequilibrium (LD; R^2) between markers along linkage group 3 (the social chromosome) is shown between Sm and Sp (B; n = 79 males), within Sp (C; n = 30 males), and within Sm (D; n = 49 males). Between social forms, the area of suppressed recombination shows a higher degree of LD compared to the recombining edges of the linkage group (B). Within Sp (C), the high degree of LD between nonadjacent markers (on the monogyne linkage map) suggests some degree of chromosomal rearrangement and suppression of recombination. No evidence of suppressed recombination is visible in Sm (D).

generally a recessive lethal allele in females [2, 23]. The *F. selysi* Sp allele is not lethal in homozygous individuals, as Sp/Sp queens and workers were present in many polygynous colonies (Table 1).

The social chromosome of *F. selysi* shows structural similarities with that of *S. invicta* (Figure 1A). In both species, a large nonrecombining region is associated with variation in colony social organization, which includes having one or more queens, as well as multiple correlated morphological and behavioral traits (Table 2). Each nonrecombining region is flanked by genomic regions that recombine between the two haplotypes. Hence, the lineages in which the two species originated, which separated from their common ancestor roughly 130 million years ago [25] and represent distinct origins of polygyny, independently evolved a similar genomic architecture associated with social organization.

Although the two species exhibit similarities in the genetic architecture associated with convergent, multitrait phenotypes, we detected no homology between the social chromosomes of *F. selysi* and of *S. invicta*. The scaffolds in the *F. selysi* social chromosome align to *S. invicta* scaffolds in seven linkage groups, not including the *S. invicta* social chromosome, while the *F. selysi* scaffolds aligning to the *S. invicta* social chromosome occur in five non-social linkage groups (Figure 1A). Overall, we found no evidence that the social chromosomes of the two species harbor the same set of genes. Despite this general absence of homology, it is still possible that a few genes that were not present on our linkage map are shared between the social chromosomes of *F. selysi* and *S. invicta*. Moreover, different transcription factors or other *trans*-acting elements in each social chromosome may trigger a similar downstream regulatory cascade in the two species. More work is needed to pinpoint the causative mutations and developmental pathways leading to alternative social organization in both species.

The convergence of the genetic architecture underlying *F. selysi* and *S. invicta* social organization sheds light on the genomic evolution underlying coordinated shifts in multiple traits. Nonrecombining regions associated with such evolutionary shifts are widely acknowledged to play a central role in speciation and local adaptation (e.g., [26–28]). The ant social chromosomes show that this genetic architecture is also important for maintaining sympatric polymorphisms. Nonrecombining regions are likely shaped by similar selection pressures, which have been explored in models of coadapted gene complexes, also called supergenes (e.g., [5, 6, 29, 30]). Dobzhansky [29] proposed that zones of suppressed recombination in the genome maintain beneficial combinations of alleles. These diverging allele combinations can be positively selected either in alternative external environments, as in locally adapted populations, or in alternative phenotypes (i.e., when genes harbor alleles with different fitness effects in males and females, or in monogynous and polygynous colonies; e.g., 31]). Suppressed recombination between such genes often involves chromosomal inversions, gene translocations, insertions, or deletions [29] but can also occur in the absence of chromosomal rearrangements (e.g., [32, 33]).

Supergenes underlie very diverse coadapted phenotypes, from the maintenance of two sexes through nonrecombining sex chromosomes [31] to the control of wing coloration and mimicry in *Heliconius* butterflies [4] and the maintenance of alternative behavioral syndromes in mice and white-throated sparrows [20, 34–36]. A key difference between the *F. selysi* social chromosome and many previously studied supergenes indicates that the *F. selysi* social chromosome follows a distinct evolutionary trajectory. In *F. selysi*, both social chromosome haplotypes occur in homozygotes. In contrast, in many other systems, one haplotype occurs only in heterozygotes. For example, mice and sparrows strongly prefer to mate with individuals exhibiting the opposite behavioral syndrome [20, 34–36], and one haplotype tends to be a recessive lethal in both fire ants and mice [2, 35]. Consequently, one haplotype is restricted to heterozygotes, recombination ceases for this haplotype, deleterious mutations accumulate through Muller's ratchet, and this haplotype tends to degenerate [31] (e.g., the Sb haplotype in fire ants has a higher frequency of repetitive elements and larger introns than the

Table 1. Genotype and Allele Frequencies of Individuals from Monogynous, Oligogynous, and Polygynous Field Colonies

	Genotype Frequencies Observed			Allele Frequencies Observed	
	MM	MP	PP	M	P
Males					
Monogyne (N = 22; n = 60)	–	–	–	1	0
Oligogyne (N = 3; n = 13)	–	–	–	1	0
Polygyne (N = 7; n = 58)	–	–	–	0	1
Nonreproductive queens					
Monogyne (N = 8; n = 19)	1	0	0	1	0
Oligogyne (N = 2; n = 11)	1	0	0	1	0
Polygyne (N = 5; n = 40)	0	0.2	0.8	0.1	0.9
Reproductive queens					
Polygyne (N = 23)	0	0.35	0.65	0.17	0.83
Workers					
Monogyne (N = 35; n = 273)	1	0	0	1	0
Oligogyne (N = 5; n = 40)	1	0	0	1	0
Polygyne (N = 31; n = 237)	0	0.68	0.32	0.34	0.66

N refers to the number of colonies used; n refers to the total sample of individuals.

Table 2. Comparison of the Social Organization of *F. selysi* and *S. invicta*

	Formica selysi		*Solenopsis invicta*	
	Monogynous (Oligogynous)	Polygynous	Monogynous	Polygynous
Phenotypic traits				
Number of reproductive queens per nest [9, 11]	1 (2)	2 to 15[a]	1	2 to 200
Relative gyne body size [9, 19]	large	small	large	small
Relative worker body size [9, 12]	large	small	large	small
Relative nest density [9, 13]	low	high	low	high
Relative investment in sexual offspring [9, 14]	high	low	high	low
Genetic basis (this article, [2])				
Queen genotypes	Sm/Sm	Sm/Sp, Sp/Sp	SB/SB	SB/Sb
Worker genotypes	Sm/Sm	Sm/Sp, Sp/Sp	SB/SB	SB/SB, SB/Sb
Alate male genotypes	Sm	Sp	SB	SB, Sb

In *F. selysi*, Sm and Sp refer to the social chromosome haplotypes found in monogynous males and polygynous males, respectively. In *S. invicta*, the corresponding haplotypes are denoted SB and Sb [2].
[a]We have observed up to 15 queens in colonies, but it is likely that there are more queens present in highly polygynous colonies, since queens spend most of their time in the subterranean nest chambers, and we only survey the top layer of the nest.

SB haplotype [2]). In *F. selysi*, viable Sm/Sm and Sp/Sp homozygotes are common, so degeneration of one haplotype is not expected despite the suppression of recombination between Sm and Sp (Figure 2A). We do, however, observe reduced polymorphism in the Sp haplotype compared to the Sm, and further research is required to determine the implications of this pattern (Figure S2). Comparing systems that differ in assortative mating tendencies and haplotype degeneration will provide insights into the factors that initiate chromosomal degeneration in autosomal nonrecombining regions.

Overall, the convergence in genetic architecture and phenotype of two independent socially polymorphic ant species demonstrates that the formation of nonrecombining regions is a key genetic mechanism underlying transitions in social organization in ants. The parallel evolution of nonrecombining regions underlying variation in social systems strongly supports recent theoretical claims that chromosomal rearrangements and the formation of supergenes are important for the evolution of novel phenotypes [5, 6, 37]. Blocks of suppressed recombination would facilitate coordinated shifts in coadapted traits, which may lead to speciation and/or adaptive shifts, or allow for the maintenance of complex phenotypic polymorphisms [3, 4, 38, 39]. The lack of homology between the social chromosomes of two independent ant species further suggests that the genetic systems underlying the convergent evolution of complex phenotypes are not strongly constrained at the level of individual genes. At a larger scale, the similar architecture and independent evolution of social chromosomes and other supergenes point to common principles governing the suppression of recombination in large genomic regions controlling complex coadapted polymorphisms.

Experimental Procedures

A genotyping-by-sequencing approach [16, 17] was used to test the association of markers throughout the genome with social structure and to construct a linkage map for *F. selysi*. For the association study, the genomes of 79 haploid males from a total of 23 field colonies from a single locality were scanned (2–5 individuals from each of 18 monogynous colonies and 5–6 individuals from each of 5 polygynous colonies). Social structure of all colonies was independently assessed through microsatellite parentage analysis [10, 11]. A linear mixed-effects model was used to test for association between each SNP marker and the social organization of the colony. From 59 male offspring of a single monogynous queen, a linkage map was generated. In complement, a draft genome was produced from a single monogynous male. This genome assembly was used to investigate synteny between *F. selysi* and *S. invicta*. Across the social chromosome, nine microsatellite and five SNP markers were developed from the genome, and these were used to prepare a linkage map for 80 worker offspring of four heterozygous queens. Three SNPs that were diagnostic for social organization were further used to assess the genotypic structure of males, queens, and workers from additional *F. selysi* colonies. Additional males (n = 52), unmated queens (n = 70), reproductive queens (n = 23), and workers (n = 550) from 91 field colonies belonging to the same population were tested with this method.

Detailed methods are provided in the Supplemental Experimental Procedures.

Accession Numbers

Genetic sequences reported herein have been deposited at the NCBI Sequence Read Archive with the accession numbers PRJNA260443 (genome), PRJNA260459 (association study), and PRJNA260462 (linkage map).

Supplemental Information

Supplemental Information includes two figures, three tables, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2014.09.071.

Author Contributions

J.P., A.B., and M.C. designed the study and contributed to all aspects of the project. J.P. and A.B. carried out genetic data collection and bioinformatics analyses. Y.W. provided advice on genetic methods and bioinformatics approaches. N.P. clarified and developed the analogy with models of supergene evolution. J.P., A.B., and M.C. wrote the manuscript with editorial input from all authors.

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