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CHROMOSOMAL REARRANGEMENTS DO NOT SEEM TO AFFECT THE GENE FLOW IN HYBRID ZONES BETWEEN KARYOTYPIC RACES OF THE COMMON SHREW (*SOREX ARANEUS*)

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Chromosomal rearrangements are proposed to promote genetic differentiation between chromosomally differentiated taxa and therefore promote speciation. Due to their remarkable karyotypic polymorphism, the shrews of the *Sorex araneus* group were used to investigate the impact of chromosomal rearrangements on gene flow. Five intraspecific chromosomal hybrid zones characterized by different levels of karyotypic complexity were studied using 16 microsatellites markers. We observed low levels of genetic differentiation even in the hybrid zones with the highest karyotypic complexity. No evidence of restricted gene flow between differently rearranged chromosomes was observed. Contrary to what was observed at the interspecific level, the effect of chromosomal rearrangements on gene flow was undetectable within the *S. araneus* species.

KEY WORDS: **Genetic structure, microsatellites, Robertsonian rearrangements, *Sorex araneus*, speciation.**

The role of chromosomal rearrangements (such as Robertsonian [Rb] fusions and fissions, translocations, and inversions) in speciation is much debated (e.g., White 1978; Coyne and Orr 2004). Two main categories of models were developed to explain how rearrangements may promote genetic differentiation and therefore facilitate speciation (Ayala and Coluzzi 2005). First, the "hybrid dysfunction" models suggest that changes in the karyotype (i.e., chromosome number, chromosomal morphology) can cause meiotic problems when heterozygous that will reduce the fertility and the reproductive fitness of heterozygous hybrids (White 1978; King 1993). Second, the "recombination suppression" models propose that recombination is reduced or suppressed in the vicinity of the rearrangement (Noor et al. 2001; Rieseberg 2001; Navarro and Barton 2003a,b). This reduction could favor speciation by reducing gene exchange in the region of the rearrangement, whereas gene flow in the rest of the genome is unrestricted. Although recombination models were mainly developed thinking about inversions, they can also be applied to other categories of rearrangements such as Rb fusions, which are known to reduce or suppress recombination in heterozygous Rb chromosome pairs (Davisson and Akeson 1993; Haigis and Dove 2003). Although chromosomal speciation models have been addressed in a variety of taxa (see for reviews Ayala and Coluzzi 2005; Hoffman and Rieseberg 2008), the conclusions of these studies are often questionable (Noor and Bennet 2009; Faria and Navarro 2010).

The shrews of the *Sorex araneus* group constitute a fascinating model to study the impact of chromosomal rearrangements on gene flow. This group is characterized by extensive variation in the autosomal karyotype, mainly attributed to Rb fusions, and the chromosome arms are labeled from *a* to *v* according to a nomenclature defined by Searle et al. (1991). In particular, almost 70 chromosomal races have been described in *S. araneus* sensu stricto (Wójcik et al. 2003). These races share three pairs of metacentrics (*af*, *bc,* and *tu*) and a sex chromosome trivalent (X,Y1,Y2) whereas the remaining chromosome arms can be differently rearranged among races. Thus, when comparing races, chromosomes can be similarly arranged, or rearranged differently into distinct metacentrics and acrocentrics (later designated "common" or "rearranged" chromosomes, respectively see Fig. 1).

Several hybrid zones between species or races have been described within the *S. araneus* group (Searle and Wójcik 1998). The karyotypic complexity encountered in hybrids is expected to vary according to the level of differences between the two species or races involved. For example, the hybrids produced in some zones will carry only trivalents (i.e., simple heterozygotes) whereas hybrids in others will carry long chain of up to 11 chromosomes (i.e., complex heterozygotes). In such situations, according to chromosomal speciation models, gene flow should be lower in situations with the highest chromosomal complexity and lower in the proximity of rearranged regions (Basset et al. 2006a; Yannic et al. 2009). Using microsatellite markers mapped at the chromosome level, these predictions were empirically confirmed in two hybrid zones between *S. araneus* and *S. antinorii* (Basset et al. 2006a; Yannic et al. 2009) and in pairwise comparisons between karyotypically distinct taxa with different levels of evolutionary divergence (Basset et al. 2008). Yet no study has compared the impact of chromosomal rearrangements on the gene flow in multiple intraspecific hybrid zones of *S. araneus*. Such comparisons would be of primary importance to further estimate the role of the rearrangements in the genetic diversification of the *S. araneus* group.

In this study, we investigated the impact of chromosomal rearrangements on gene flow in five hybrid zones with increasing levels of karyotypic complexity due to different combinations of rearrangements. The impact of rearranged chromosomes might change according to the chromosome. Moreover, the position within chromosomes is likely an important factor because the recombination rate varies along chromosomes (Borodin et al. 2008). Nevertheless, although both of these factors could add noise to our analyses and similarly to previous shrew studies (Basset et al. 2006a, 2008), we considered the rearranged chromosomes as a group. Our general predictions were thus, that if chromosomal rearrangements affect genetic isolation: (1) gene flow should be lower in the zones that present the most complex heterozygous karyotypes and (2) gene flow between rearranged chromosomes should be reduced compared to common chromosomes.

Material and Methods

SAMPLING AND HYBRID ZONES IDENTIFICATION

Five European intraspecific hybrid zones of *S. araneus* were analyzed in this study, for a total of 876 samples genotyped. Hybrid zones were named according to the two different races involved (Table 1). Samples were collected in the last decade and karyotypes were obtained for all shrews (except some individuals from England). Each population was described as containing one or two races.

Hybrid zones were characterized according to the meiotic configurations expected in the hybrids (see Fig. 1). The most simple hybrid zone was that with heterozygous individuals that showed only meiotic "trivalent" configurations (formed when the arms of three chromosomes pair during meiosis). The level of complexity increased when configurations involved a higher number of chromosomes (e.g., meiotic chain of five to 11 chromosomes in hybrids; see Fig. 1).

DNA EXTRACTION AND MICROSATELLITE ANALYSIS

DNA was acquired from previous samplings or was newly extracted using the DNeasy Tissue Kit (Qiagen, Valencia, CA),

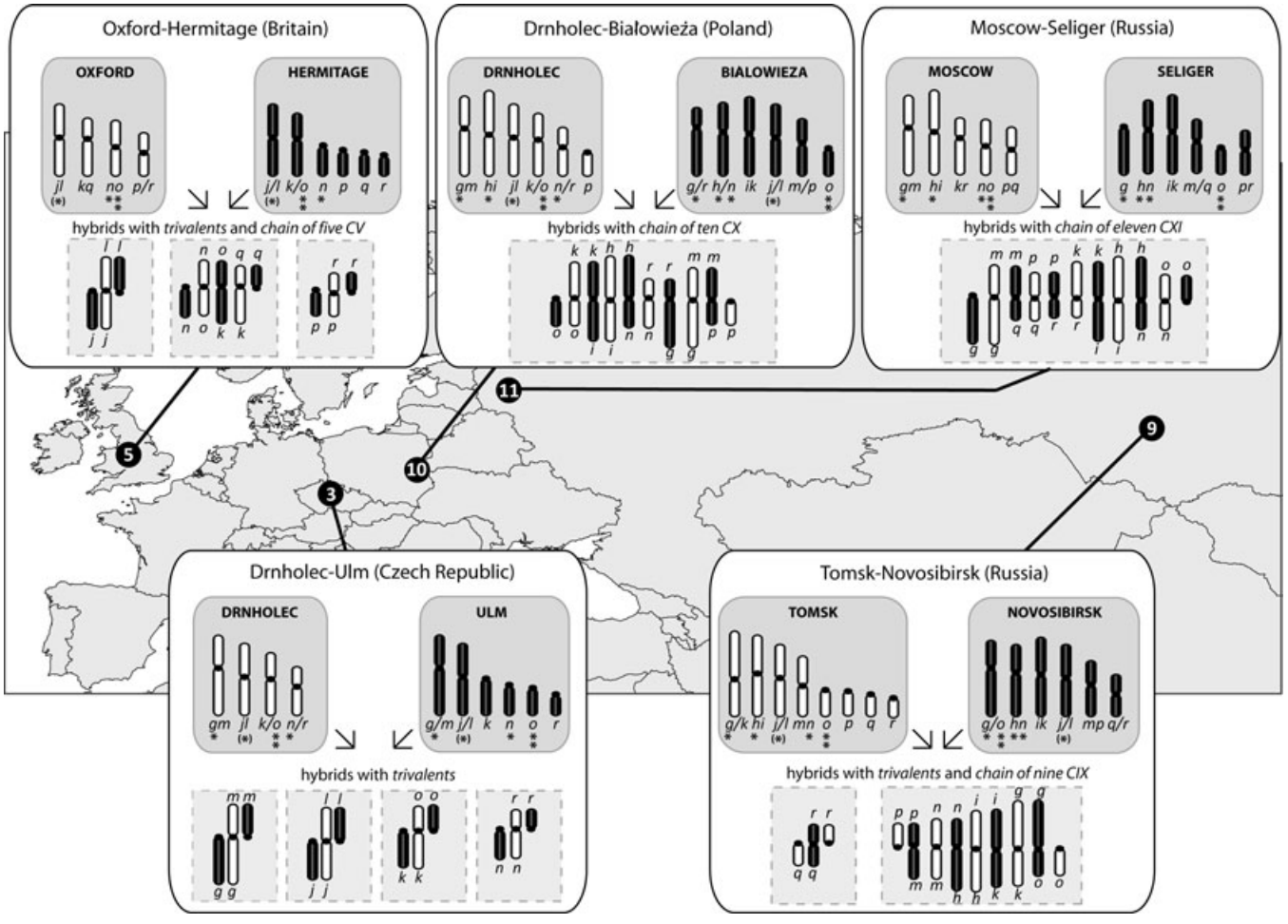

Figure 1. Location of the five European hybrid zones of the *Sorex araneus* group used in the study and rearranged chromosomes of each parental races and corresponding F1 hybrids. The most complex heterozygote configuration of F1 hybrids is indicated within each rectangle. The chromosome arm localization of the markers of the rearranged chromosomes is indicated by asterisks. The position of locus D24 is ambiguous (*j* or *l* chromosome arms) and therefore indicated in brackets.

following the manufacturer's protocol. Sixteen microsatellite loci were chosen among those unambiguously mapped at the chromosome level by Basset et al. (2006c), the letter in parentheses indicating their chromosome localization: L69(*f*), B3(*f*), D107(*a*), D112(*a*), L9(*c*), L68(*b*), C117(*b*), L13(*de*), C171(*de*), L57(*de*), L62(*g*), D24(*jl*), D106(*h*), L99(*n*), B30(*o*), D109(*o*). No information was available regarding the exact localization of the loci within a chromosome. Each locus was part of either the common or rearranged group depending on its chromosome localization and the hybrid zone under study (Table 1; Fig. 1). When the same metacentric was present in both races but polymorphic in at least one race, the corresponding loci were classified as rearranged.

DNA was amplified according to protocols described in Wyttenbach et al. (1997); Balloux et al. (1998); Lugon-Moulin et al. (2000); and Basset et al. (2006a,b) in a final volume of 20 μl. One primer of each pair was labeled with a fluorescent dye on the 5′ end. The amplified products were detected on an ABI 3100 automatic sequencer (Applied Biosystems, Foster City, CA) and allele sizes were analyzed using GeneMapper (Applied BioSystems) followed by manual proofreading.

STATISTICAL ANALYSIS

The following analyses were performed for each hybrid zone independently.

Genetic variability

Allele frequencies, allele numbers, observed heterozygosities (H_O), expected heterozygosities within (H_S), and between (H_T) samples following Nei (1987) were calculated for each hybrid zone using FSTAT version 2.9.4 (updated from Goudet 1995). Heterozygote deficit within populations ($F_{IS} > 0$) was tested using a permutation procedure (10,000 randomizations) to infer random mating. The exact *G*-test (Goudet et al. 1996), as implemented in FSTAT 2.9.4, was used to assess the significance of genetic differentiation. Comparison of number of alleles located on common or rearranged chromosomes in each hybrid zone was performed

Table 1. List of the five hybrid zones with their corresponding level of complexity. The number of populations in each hybrid zones "Npop" and the number of individuals per taxon "*N*" are indicated. "Rearranged markers" correspond to the loci that are located on rearranged chromosomes for each zone.

Hybrid zone					
Code name	Complexity	Taxon	Npop	*N*	Rearranged markers
Dn–Ul	3	Drnholec	14	35	L62, D24, L99, D109, B30
		Ulm		48	
		Hybrids		14	
Ox–He	5	Oxford	46	52	D24, L99, D109, B30
		Hermitage		97	
		Hybrids		92	
To–No	9	Tomsk	24	61	L62, D106, D24, L99, D109, B30
		Novosibirsk		113	
		Hybrids		20	
Dn–Bi	10	Drnholec	9	49	L62, D106, D24, L99, D109, B30
		Białowieża		60	
		Hybrids		31	
Mo–Sl	11	Moscow	13	54	L62, D106, L99, D109, B30
		Seliger		92	
		Hybrids		29	

with Shapiro–Wilk to test for normality and then by Student's *t*-tests with R software (R Development Core Team 2010).

GENETIC STRUCTURE OVER EACH HYBRID ZONE

We analyzed genetic structure using estimates derived from *F*-statistics according to Weir and Cockerham (1984), using FSTAT version 2.9.4. Populations were then separated into single races according to their karyotype (i.e., populations sharing individuals from the two races were divided into two populations of a single race and hybrids or individuals with unknown karyotypes were removed from the dataset) to assess structure within and between the different taxa. Differentiation of populations within taxa (intraracial, F_{SC}) and between populations of the two taxa (interracial, F_{CT}; Weir 1996) was obtained using the software package ARLEQUIN version 3.1 (Excoffier et al. 2005).

Estimates of F_{ST} and hierarchical F_{SC} and F_{CT} were measured across all loci but also across common and rearranged chromosomes using FSTAT and ARLEQUIN, respectively. Differences of genetic structure between common and rearranged chromosomes were tested by a permutation test. A distribution of difference between the two groups of chromosomes was generated by carrying out of 10,000 permutations of microsatellite loci between the two groups and the observed difference was compared to this distribution.

To test whether the interracial structure F_{CT} was influenced by the degree of hybrid zone complexity CX or the type of chromosomes CHR (i.e., common or rearranged), we compared several mixed models as follows: a null model (Model 1), with no effect of CHR and CX on F_{CT}; the Model 2 tested the effect of CHR on F_{CT}; the Model 3, the effects of CHR and CX on F_{CT}; the Model 4, the effects of CHR in interaction with CX on F_{CT}; and finally the Model 5 tested the effect of CX on F_{CT}. Mixed models were performed using the nlme package in R (Pinheiro et al. 2011) and the five models were compared using a model selection procedure based on corrected Akaike information criterion (AICc) as implemented in the AICcmodavg package in R (Mazerolle 2011). Analyses of variances were also used with R software to assess whether the effects tested by each model were significant.

Results

GENETIC VARIABILITY

Basic population parameters for each hybrid zones are detailed in Table S1.

GENETIC STRUCTURE OVER EACH HYBRID ZONE

Low but highly significant F_{ST} values were obtained in each hybrid zones (Table 2), suggesting a weak genetic structure. When estimating hierarchical *F*-statistics (F_{SC} and F_{CT}), we found significant F_{SC} values that ranged from 0.013 to 0.036 (Table 2). Genetic structure between races (F_{CT}) was weak and nonsignificant in most hybrid zones (Table 2; Fig. 2). The detailed results of hierarchical F statistics are shown on Table S2.

Values of F_{ST} estimated across rearranged or common chromosomes were highly significant (Table 2; $P < 0.001$). In some hybrid zones, the genetic structure estimated over rearranged and common chromosomes gave contrasting results but differences were never significant (Table 2). When measuring hierarchical

Table 2. Values of F_{ST}, F_{SC}, and F_{CT} per locus across common, rearranged, and all loci for each hybrid zone. The level of chromosomal complexity of each hybrid zone is indicated in brackets.

Hybrid zone	Locus	F_{ST}		Diff.	F_{SC}		Diff.	F_{CT}		Diff.
Dn–Ul (3)	Common	0.030	***	0.242	0.031	***	0.370	0.003	NS	0.693
	Rearranged	0.029	***		0.040	***		0.012	NS	
	Overall	0.030	***		0.032	***		0.002	NS	
Ox–He (5)	Common	0.033	***	0.136	0.022	***	0.830	0.003	*	0.816
	Rearranged	0.065	***		0.041	***		0.020	**	
	Overall	0.040	***		0.026	***		0.007	**	
To–No (9)	Common	0.035	***	0.849	0.038	***	0.784	0.005	NS	0.123
	Rearranged	0.014	***		0.013	*		−0.002	NS	
	Overall	0.027	***		0.029	***		0.003	NS	
Dn–Bi (10)	Common	0.033	***	0.804	0.033	***	0.737	0.009	*	0.867
	Rearranged	0.037	***		0.044	***		0.009	NS	
	Overall	0.035	***		0.036	***		0.009	*	
Mo–Sl (11)	Common	0.012	***	0.701	0.016	***	0.614	−0.001	NS	0.090
	Rearranged	0.006	*		0.003	NS		0.011	**	
	Overall	0.011	***		0.013	***		0.002	NS	

Diff = difference between common and rearranged.

Asterisks indicate significant values for the estimators: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$; NS, not significant.

F-statistics over common and rearranged chromosomes, we found no significant differences for values of population differentiation within races F_{SC} and between races F_{CT} (Table 2; Fig. 2).

COMPARISONS BETWEEN HYBRID ZONES

Neither the level of complexity nor the type of chromosomes had an effect on the genetic differentiation between races. Our analysis detected the null model (model 1, with no effect of the chromosomes or the level of complexity) as best fitting (minimized AICc = −396.42, Table S3). The ΔAICc for model 1 versus model 5 was < 2, but there was no effect of the level of complexity on F_{CT} ($F_{1,3} = 0.269$, $P = 0.64$). There was also no effect of the types of chromosomes ($F_{1,70} = 0.020$, $P = 0.89$).

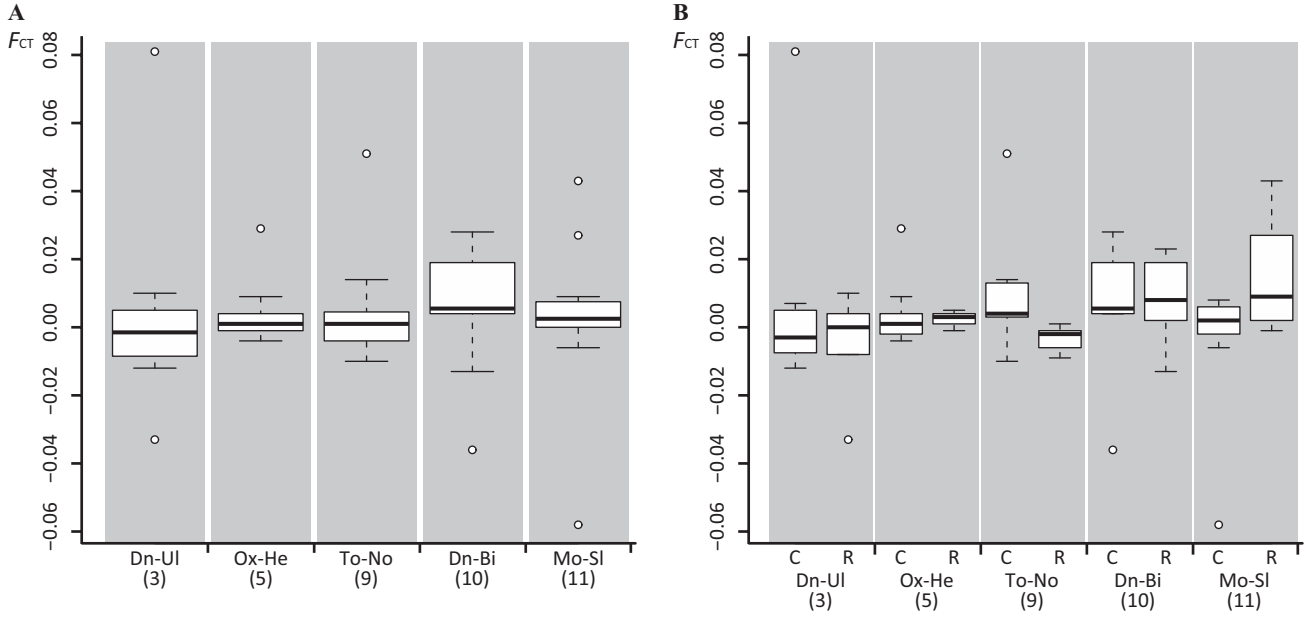

Figure 2. Box plot of interracial indices of differentiation F_{CT} obtained in the five hybrid zones in relation with the level of karyotypic complexity (indicated in brackets). (A) Indices of differentiation estimated with the 16 microsatellite markers (overall F_{CT}). (B) Indices of differentiation measured over common "C" and rearranged chromosomes "R."

Discussion

Our study of five karyotypic *S. araneus* hybrid zones exhibiting increasing levels of karyotypic complexity showed that these zones exhibit similarly low levels of gene flow even in the zones with the highest level of complexity. Moreover, no difference between common and rearranged chromosomes could be detected in any of the zones. These results suggest that chromosomal rearrangements do not have a strong impact on the structure of these zones and contrast with previous observations in the same group of shrews (Basset et al. 2006a; Yannic et al. 2009) and in various taxa such as sunflowers, flies, or house mice (e.g., Rieseberg et al. 1999; Machado et al. 2002; Franchini et al. 2010). Several nonexclusive factors could explain the differences between our results and theoretical expectations.

First, although several studies in *S. araneus* showed levels of nondisjunction or germ cell death high enough to affect the fertility of heterozygotes (e.g., Jadwiszczak and Banaszek 2006), the data suggest that Rb heterozygotes do not suffer from infertility as substantially as other taxa (Searle 1993; Narain and Fredga 1997; Banaszek et al. 2000) and that hybrid individuals forming long chain of chromosomes are not sterile (Jadwiszczak and Banaszek 2006). Thus, the impact of chromosomal rearrangements in *S. araneus* might be less important than in other taxa.

Second, demographic, geographic, or historical factors might have a stronger effect than chromosomes in structuring the hybrid zones. In agreement with previous studies (Andersson et al. 2004; Jadwiszczak et al. 2006; Lundqvist et al. 2011; Moska et al. 2011), we observed a low genetic differentiation among chromosomal races of *S. araneus*. This low genetic differentiation might be explained by the recentness of chromosome differentiation, as karyotypic evolution was proposed to occur between 15,000 and 7000 years ago in the *S. araneus* group (Searle 1984; Wójcik 1993). Moreover, chromosome differentiation was hypothesized to be a fast process (Andersson et al. 2005; Lundqvist et al. 2011), which could be largely independent of the genetic differentiations acquired in allopatry during the last glaciations (e.g., Taberlet et al. 1994). In addition, recent common ancestry from a shared glacial refugium may also explain a low genetic differentiation (Jadwiszczak et al. 2006; Lundqvist et al. 2011).

Third, we considered in our study that the impact of rearrangements would affect globally all the rearranged chromosomes. This is a rough proxy and rearranged chromosomes are certainly not affected identically by rearrangements. However, a similar approximation had already been used at interspecific level (Basset et al. 2006a, 2008; Yannic et al. 2009) and the results of these studies confirmed the impact of chromosomal rearrangements on the *S. araneus* group differentiation. Additionally, Rb heterozygotes (i.e., the presence of a chromosomal arm in either the acrocentric or metacentric state within the same race) may occur in each karyotypic race (Wójcik et al. 2002). These heterokaryotypes may have a nonnegligible impact on gene exchange by diluting or increasing the divergence between races. This effect might be strong in zones with high frequency of Rb polymorphism (i.e., Ox–He hybrid zone, Hatfield et al. 1992) but it could be neglected in other hybrid zones with very low frequency of polymorphism (i.e., Dn–Bi, Wójcik et al. 2002).

Fourth, the *Sorex* genetic markers are only mapped at the chromosome level and no information is available about localization within a chromosome. The position within chromosomes might be an important parameter because the recombination rate varies along chromosomes and according to the chromosomal configuration (acrocentric vs. metacentric; Borodin et al. 2008). The impact of the position within rearranged chromosomes has for example been confirmed in several house mouse chromosomal hybrid zones (Panithanarak et al. 2004; Franchini et al. 2010). Finally, at the low genetic differentiation observed in these hybrid zones, it might be necessary to have a larger microsatellite resolution to detect a subtle impact of chromosomal rearrangements.

In conclusion, and in contrast to what was observed at the interspecific level (i.e., Basset et al. 2006a; Yannic et al. 2009), our data did not confirm the impact of chromosomal rearrangements on the genetic differentiation between the karyotypic races of *S. araneus*. Although equating a low F_{ST} or F_{CT} with extensive gene flow should be done with caution (e.g., see Holsinger and Weir 2009), the effect of chromosomal rearrangements might be negligible—or at least undetectable—within the genetically homogeneous *S. araneus* species. Further studies are necessary to understand the real impact of chromosomal rearrangements on the genetic differentiation of the group.

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Supporting Information

The following supporting information is available for this article:

Table S1. Number of alleles (Na), observed heterozygosity (H_O), expected heterozygosity within (H_S) and between (H_T) samples, and values of F_{IS}, estimated per locus, per chromosome class (common or rearranged) and across all loci, in each of the five studied hybrid zones of the *Sorex araneus* group.

Table S2. Hierarchical *F*-statistics per locus, across common, rearranged, and all loci in each hybrid zone of *Sorex araneus*.

Table S3: Model selection based on Akaike information criterion (AICc).

Supporting Information may be found in the online version of this article.

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