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Short-term variations in gene flow related to cyclic density fluctuations in the common vole

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Abstract

In highly fluctuating populations with complex social systems, genetic patterns are likely to vary in space and time due to demographic and behavioural processes. Cyclic rodents are extreme examples of demographically instable populations that often exhibit strong social organization. In such populations, kin structure and spacing behaviour may vary with density fluctuations and impact both the composition and spatial structure of genetic diversity. In this study, we analysed the multiannual genetic structure of a cyclic rodent, *Microtus arvalis*, using a sample of 875 individuals trapped over three complete cycles (from 1999 to 2007) and genotyped at 10 microsatellite loci. We tested the predictions that genetic diversity and gene flow intensity vary with density fluctuations. We found evidences for both spatial scale-dependant variations in genetic diversity and higher gene flow during high density. Moreover, investigation of sex-specific relatedness patterns revealed that, although dispersal is biased toward males in this species, distances moved by both sexes were lengthened during high density. Altogether, these results suggest that an increase in migration with density allows to restore the local loss of genetic diversity occurring during low density. We then postulate that this change in migration results from local competition, which enhances female colonization of empty spaces and male dispersal among colonies.

Keywords: cyclic rodent populations, gene flow, genetic diversity, *Microtus arvalis*, migration, spatial genetic structure

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Introduction

Under demographically stable conditions, neutral genetic patterns are expected to be stable over time as a result of an equilibrium between genetic drift and migration (Wright 1931, 1943). However, numerous natural populations, in particular fluctuating populations, exhibit important spatio-temporal variations in size. In such populations, both the composition and spatial structure of neutral genetic diversity are likely to vary in space and time. Quantifying temporal changes in neutral genetic patterns in relation to density fluctuations has emerged as an important topic to better understand demographic and microevolutionary processes in natural populations (Schwartz *et al.* 2007). In this field, genetic comparative studies, between populations being in different demographic states or temporal demo-genetic monitoring, have proved to be very useful approaches to better understand the role of dispersal in the maintenance of genetic diversity in populations regularly affected by low numbers (Østergaard *et al.* 2003; Berthier *et al.* 2006; Ehrich *et al.* 2009; Rikalainen *et al.* 2012) and in spatial synchrony and spread of outbreaks (Berthier *et al.* 2005, 2013; Chapuis *et al.* 2008, 2009). Comparing patterns for both neutral and adaptive genetic variation may also provide insight on density-dependent changes in selection pressures such as

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parasitism (Bryja *et al.* 2007). Moreover, analysing temporal genetic data can provide information on how spacing behaviours (i.e. individual movements driven by behavioural interactions) may vary with density fluctuations (Sutherland *et al.* 2005; Piertney *et al.* 2008; Pilot *et al.* 2010).

Cyclic microtine rodents are a well-known example of species exhibiting huge fluctuations in densities. Their populations often undergo 3–5 year cycles with 10- to 100-fold changes in density (Stenseth 1999). Surprisingly, despite recurrent demographic bottlenecks, cyclic rodent populations generally maintain high level of genetic diversity (Ehrich & Stenseth 2001; Ehrich *et al.* 2001, 2009; Berthier *et al.* 2005, 2006; Ehrich & Jorde 2005; Vuorinen & Eskelinen 2005; Rikalainen *et al.* 2012). Cyclic rodents also often exhibit complex social organization with individuals forming kin groups and colonies. Within colonies, related individuals (usually females) may interact altruistically while interactions among non-related would be mainly aggressive (Pilot *et al.* 2010). Assuming that kin structure changes with density, some theoretical models have predicted that the subsequent impact on spacing behaviour could in return induce important density fluctuations (Charnov & Finerty 1980; Lambin & Krebs 1991). Nowadays, this hypothesis is no longer considered as a strong candidate to explain cyclic dynamics in rodents. However, the two proposed models, which differ in their predictions on the correlation between population density, dispersal and relatedness, still provide a very interesting framework to address the central question of density-dependant dispersal. According to Charnov & Finerty (1980), local relatedness (i.e. within colonies) is higher at low density due to low immigration and inbreeding. When density increases, immigration into colonies will increase as well and, as a result, relatedness declines rapidly. In contrast, according to Lambin & Krebs (1991), relatedness is higher during high density due to female philopatry and low immigration. Home range sharing between related females would reduce competition for space and then facilitate local increase in density. Demographic decline would further result from aggressive interactions, leading to local kin groups breaking due to mortality.

Expectations from both models, in terms of genetic diversity, temporal genetic differentiation and relatedness patterns, are well summarized in Pilot *et al.*'s study (2010 – see table 1). Basically, according to Lambin & Krebs (1991), no significant temporal changes are expected locally as dispersal is negatively correlated with density. Moreover, relatedness and spatial distance among related females should be positively and negatively correlated to density, respectively. These predictions have been partly verified from different studies (Sutherland *et al.* 2005; Ehrich *et al.* 2009; Pilot *et al.* 2010). In contrast, from the model of Charnov & Finerty (1980), we can expect significant temporal variations in genetic diversity and differentiation patterns, a negative correlation between relatedness among females and density and, finally, a positive correlation between spatial distance among related females and density. Two empirical studies have corroborated the local loss of genetic diversity at low density and its subsequent restoration through immigration during increasing and peak phases (Berthier *et al.* 2006; Rikalainen *et al.* 2012). Considering a larger spatial scale, Berthier *et al.* (2006) extended Charnov & Finerty (1980) predictions to a metapopulation framework and proposed a demo-genetic scenario involving temporal variations in gene flow along the cycle. Under this scenario, at low density, voles would be distributed in small isolated demes (i.e. groups of neighbour colonies) subject to genetic drift (i.e. loss of genetic diversity) while genetic diversity would not be affected at the metapopulation scale as different alleles are retained within different demes. When population density increases, previously isolated demes merge into a continuous population and local genetic diversity is restored through gene flow. Therefore, discrepancies between findings from previous studies could partly result from differences in the spatial scale considered, that is, regional (metapopulation), local demes or isolated colonies. Temporal and multi-scale demo-genetic studies are needed to better understand relationships between density fluctuations, dispersal, kin structure and genetic patterns from local to metapopulation scales.

In this study, we conducted a genetic monitoring (*sensu* Schwartz *et al.* 2007) on a rodent species, the common vole, *Microtus arvalis*, over an area of 430 km^2 located in central-western France. In this region, vole populations undergo well-marked demographic cycles of 3 years (Lambin *et al.* 2006). The common vole, which has a lifespan that does not exceed a few months, is a social species living in colonies and producing three to five generations per year (Martinet & Spitz 1971; Le Louarn & Quéré 2003). Related females build burrow networks harbouring colonies and cooperate for breeding and maternal care while, males are more likely to be solitary and promiscuous, moving constantly among colonies to mate (Boyce & Boyce 1988; Dobly & Rozenfeld 2000; Gauffre *et al.* 2009). A previous population genetics study, based on a snap shot sampling conducted in 2006 across the same study area, showed that *M. arvalis* forms a genetically homogeneous unit slightly shaped by an IBD (isolation-by-distance) pattern (Gauffre *et al.* 2008).

In this study, rodents were trapped over a period covering three demographic cycles, between 1999 and 2007.

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Individuals were considered as independent genetic sampling units (i.e. individual-based sampling) and were genotyped at 10 highly variable microsatellite loci. Multilocus genotypes were used to test the predictions drawn from the models of Charnov & Finerty (1980) and Lambin & Krebs (1991) at spatial scales ranging from the region (i.e. the whole study area: 430 km^2) to the colonies (i.e. a 100-m trap line). First, we tested for density-related variations in genetic diversity and investigated whether those variations could be scale dependant as suggested by Berthier *et al.* (2006). Second, we tested for changes in allelic frequency distribution (i.e. temporal differentiation) and spatial structure (i.e. IBD strength) along the cycles at the regional scale. Finally, we assessed potential density-related changes in kin structure and spacing behaviour by estimating (i) relatedness among females at the scale of the colonies and (ii) the spatial extend of relatedness patterns for males and females separately as dispersal in the common vole is sex-biased toward males (Gauffre *et al.* 2009).

Material and methods

Study area and sample collection

The study area, the LTER 'Zone Atelier Plaine & Val de Sèvre', covers about 430 km^2 of an intensive farmland in central-western France (Région Poitou-Charentes, 46.11° N, 0.28° W). Landscape in the study site is a complex mosaic of crops containing winter cereals (42% of the whole agricultural area), spring cereals (maize and sunflower, 27%), oilseed rape (13%), grassland (10%), alfalfa (4%) and a few other miscellaneous rare crop types.

Genetic sampling and estimation of abundance were carried out twice a year, in April and June, between 1999 and 2007 using a trap line protocol (no genetic samples were collected in 2000). A trap line was a 100-m transect with 51 single-capture live traps spaced every two metres and set for 24 h in an agricultural field. Sampled fields were selected to represent each major crop type while covering homogeneously the whole study area. This area was thus subdivided into nine sectors of similar sizes (see Fig. 1). Hence, for a given sector and for each trapping session, 10 fields were selected with respect to a homogeneous stratification among crop types (2–3 winter cereals, 1–2 oilseed rape, 1–2 alfalfa, 1–3 meadows, 1–2 spring crop and 0–1 rare crop type, including pea or flax) along a transect crossing the sector. Trap lines were located in different fields each year and session (June transect was set orthogonally to April transect). In the course of the study, a total of 1480 trap lines were set up (10 trap lines × 2 sessions × 7 years × 8 sectors between 1999 and 2005 – the western sector has not been sampled during this period – or 9 sectors between 2006 and 2007). Spatial coordinates were recorded from the centre of each trap line using a Global Positioning System (GPS) with a precision of ~10 m. Distance between two trap lines varied from 30 m (two adjacent fields) to 26.5 km. All animals were sexed, weighted and checked for reproductive status. A small piece of ear was collected for genetic analyses.

Common vole abundance

In western France, the common vole exhibits a clear cyclic dynamics, synchronous over hundreds of km^2,

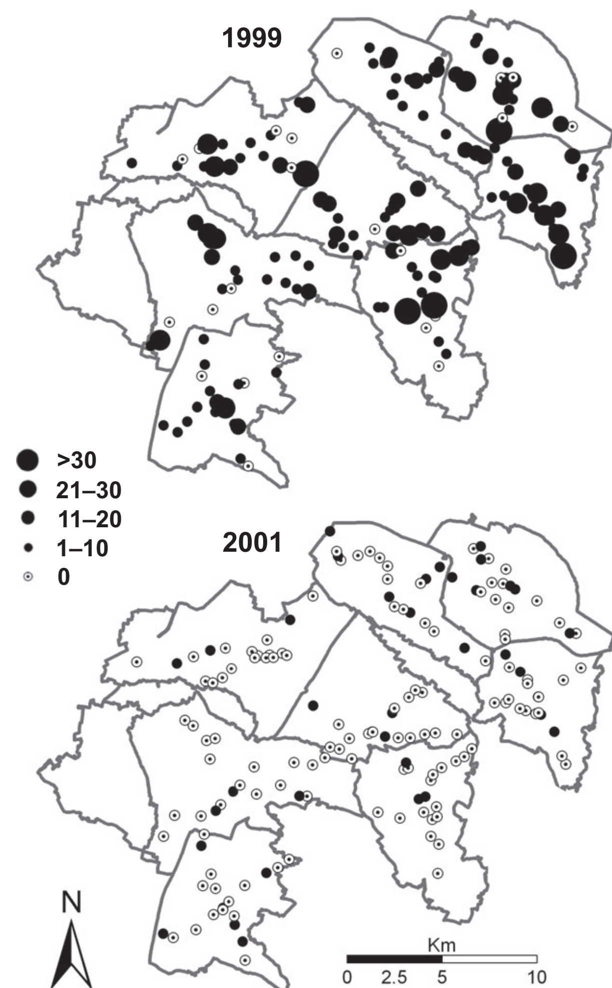

Fig. 1 Spatial location and common vole abundance from the 160 trap lines set up in 1999 and 2001, the two most extreme years in terms of abundance. Common vole presence was detected from 136 to 37 of the 160 trap lines sampled in 1999 and 2001, respectively. Grey lines indicate sectors boundaries, and dots indicate trap lines location. Dot size and colour represent common vole abundance (number of common vole caught per 100 trap and 24 h).

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and characterized by a 3-year period and cycle amplitude up to 200-fold (Lambin *et al.* 2006; Fig. 1a). As for other cyclic systems, common vole populations exhibit successive density phases of increase, peak, crash and stagnation at low numbers (Krebs & Myers 1974). As the peak is very sharp in this species (see Fig. 2), we considered years of increase and maximum densities as peak phases (i.e. 1999, 2002, 2005 and 2007). Years marking the end of the rapid decrease in densities were considered as crash phases (i.e. 2003 and 2006), and years corresponding to the transition between low numbers and the beginning of the next density increase were considered as low phases (i.e. 2001 and 2004). For each trapping session, an abundance index was first calculated at the scale of the trap lines as the number of common voles caught per 100 traps in 24 h (Lambin *et al.* 2006; see Fig. 1). Then, abundance indices were averaged according to crop type, and a global abundance index was calculated at the scale of the study site by averaging densities across crop types (details on the method, applied on the same data set, are presented in Inchausti *et al.* 2009). A value of seven individuals per 100 traps in 24 h approximately corresponds to 50 common voles/ha over the whole study site (Lambin *et al.* 2006). Annual population growth rate (PGR) was estimated as the ratio of the estimated population abundance into two consecutive years (N_t/N_{t-1}) using June trapping session estimates as it exhibits the highest amplitude of fluctuation (Inchausti *et al.* 2009).

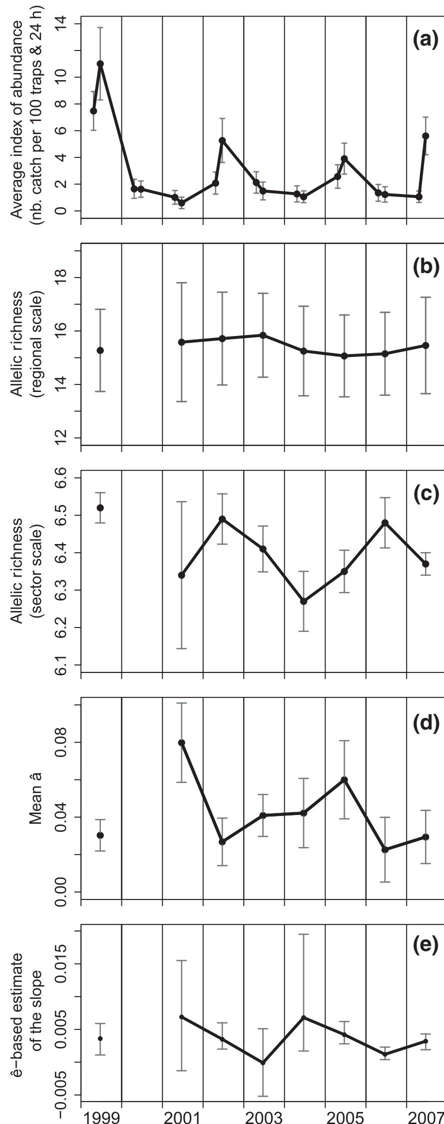

Fig. 2 Demographic and genetic changes in the common vole population: time series of abundance at the regional scale (a); variations in allelic richness (mean ± SE) computed for a sample size of 34 individuals at the regional scale (b) and five individuals at the sector scale (c); mean (±SE computed by bootstrapping over loci) level of between-individuals differentiation based on the â statistic (d) and slope of the regression of the genetic distances (based on the ê statistic) against the logarithm of the geographical distances with 95% CI estimated by bootstrapping over loci (e).

Microsatellite genotyping

Tissue samples were stored in 95% ethanol prior to DNA extraction, which was carried out using a standard Chelex protocol. DNA was amplified using the polymerase chain reaction and genotyped with a multiplex panel of 10 microsatellites (see details in Gauffre *et al.* 2007, 2008) using an automated sequencer ABI PRISM 310 GENETIC ANALYSER (Applied biosystems). Genotypes were determined using GENESCAN and GENOTYPER software (Applied Biosystems). Ten individual genotypes were randomly repeated for each year separately to assess the repeatability of the method. This procedure indicated a repeatability of 100%. Detailed analyses of genotypic linkage disequilibrium using the G-test implemented in GENEPOP 4.0 (Rousset 2008) previously demonstrated that our loci were not physically linked (Gauffre *et al.* 2008).

Statistical analyses

Variation in genetic diversity. Deviation from Hardy–Weinberg equilibrium (HWE) for each locus, and for all loci considered together, was tested for each year (pooling April and June sampling sessions) using the Markov chain method implemented in GENEPOP 4.1 (Rousset 2008). We used the false discovery rate (FDR) approach to account for multiple testing (Benjamini & Hochberg 1995). Deviation from HWE was quantified by computing F_{IS} according to Weir & Cockerham (1984). Genetic variation was estimated over all loci and for each year by calculating the unbiased expected (*He*;

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Nei 1987) and observed (H_O) heterozygosities using GENETIX 4.05.2 (Belkhir 2004). We used the rarefaction procedure implemented in F_{STAT} 2.9.3.2 (Goudet 1995, 2001; El Mousadik & Petit 1996) to compute allelic richness corrected for sample size (*Ar*). As *Ar* is more sensitive than *He* to detect a reduction in population size (Schwartz *et al.* 2007), it was used to test for density-related variations in genetic diversity at two different spatial scales: (i) the regional scale (i.e. 430 km^2, the whole study site) using a subsample of 34 individuals (the smallest number of individuals typed for a locus in a year) and (ii) the sector scale (on average 43 ± 10 km^2) using a subsample of five individuals. Sectors for which less than five individuals were caught in a given year were excluded from the analysis. A total of 45 individuals from 16 sectors were thus excluded (the number of sectors considered was three in 1999, three in 2001, eight in 2002, six in 2003, four in 2004, eight in 2005, eight in 2006 and nine in 2007). Overall, sectors mean *Ar* was then computed for each year.

Following the approach of Ehrich *et al.* (2009), we used linear models to test for variation in *Ar* along the demographic cycle at the regional and sector scales. To account for differences in allelic diversity among loci, each locus was included in all models as a fixed effect. First, we tested for change in *Ar* using the phase of the cycle as a factorial variable with three levels as described above (i.e. peak, crash and low phases). Second, we challenged a set of models using three demographic parameters as covariates: (i) the abundance index during the current year (June estimates: N_t); (ii) the abundance index during the previous year (June estimates: N_{t-1}) and (iii) the annual PGR. As the annual PGR is a combination of the two former covariates, we did not test models including the three covariates simultaneously. As the proportion of the study area covered by the genetic sampling can vary among years (Table 1), we included the number of sectors as a fixed effect in the models performed at the regional scale. Linear models with different combinations of explanatory variables were compared using Akaïke Information Criterion (AIC, Burnham & Anderson 2002). The model with the lowest AIC was retained as the best model. We assessed homoscedasticity, linear relationships and the presence of outliers by visually inspecting the distribution of the residuals. Tests were performed using the statistical software R 2.10.1 (R Development Core Team 2012).

Temporal differentiation. We investigated whether the (meta)population significantly differentiated between years by computing pairwise F_{ST} values (Weir & Cockerham 1984) and testing for genotypic differentiation, between pair of years, using GENEPOP 4.1 (Rousset 2008). We used the false discovery rate approach (FDR) to account for multiple testing (Benjamini & Hochberg 1995).

Spatial genetic structure. To test for possible changes in the spatial genetic structure along the demographic cycle, we used GENEPOP 4.1 (Rousset 2008) to compute, for each year, the mean pairwise genetic distances between individuals using the statistics â (Rousset 2000) and ê (Watts *et al.* 2007). Due to their intrinsic characteristics, these estimators have slightly different behaviour. The ê estimator tends to decrease when individuals harbour alleles that are common in the whole population, hence giving more weight to rare alleles in the measurement of genetic distances. As a result, ê has a lower variance and is asymptotically biased (high divergences between individuals are underestimated). By contrast, â is considered as an unbiased estimator of genetic distances (Watts *et al.* 2007). We used the software R 2.10.1 (R Development Core Team 2012) to test, at the regional scale, whether the mean level of differentiation between individuals (i.e. â statistics) was different between all pairs of years. To do so, we applied the procedure described in Coulon *et al.* (2006), which allows to account for the nonindependence of pairwise data. This procedure consists in generating 1000 random resampling sets without replacement, such that each individual occurs only once in a given set. The difference in the mean differentiation (Δâ) between 2 years is then calculated for each resampled set. Under the null hypothesis that the mean level of differentiation is not different, Δâ is expected to follow a normal distribution centred on zero. Under the alternative hypothesis, Δâ is expected to be significantly different from zero.

To assess whether the IBD pattern revealed in Gauffre *et al.* (2009) was a constant regional structure irrespective of cycle phases, we used Mantel tests (5000 permutations) to assess for each year (pooling April and June sampling sessions) the correlation between genetic and log-transformed geographical distances computed among individuals. Confidence intervals around the slopes of the regressions were estimated by bootstrapping over loci using GENEPOP 4.1 (Rousset 2008). The slope of the IBD regression is inversely proportional to the product of effective density (D_E) and second moment of the dispersal distance (σ^2) (Rousset 2000). Therefore, assuming constant or positive (Charnov & Finerty 1980) density-related dispersal, the slopes are expected to be high after low numbers due to genetic drift effects and to flatten after high densities due to increasing gene flow. Alternatively, negative density-related dispersal (Lambin & Krebs 1991) should prevent genetic drift effect during low density, and

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Table 1 Characteristics of the eight genetic temporal samples: sample size (*N* ind), number of fields (*N* Fields) and sectors in brackets (*N* Sectors). Mean (±SD) allelic richness (*Ar*), calculated at the regional and sector scales (corrected for a sample size of 34 and five individuals, respectively), and mean (±SD) observed (H_O) and expected (H_E) heterozygosities. Intrapopulation fixation indices (F_{IS}) and probability associated with the rejection of the Hardy–Weinberg equilibrium [HWE (*P*)],

Year	*N* ind	*N* fields (*N* sectors)	*Ar* (regional scale)	*Ar* (sector scale)	H_O	H_E	F_{IS}	HWE (*P*)
1999 (peak)	89	24 (4)	15.27 ± 4.86	6.52 ± 0.07	0.853 ± 0.072	0.878 ± 0.081	0.03	0.044
2001 (low)	36	23 (7)	15.58 ± 7.03	6.34 ± 0.34	0.812 ± 0.109	0.876 ± 0.091	0.074	**0.002**
2002 (peak)	163	76 (8)	15.72 ± 5.49	6.49 ± 0.19	0.855 ± 0.097	0.877 ± 0.097	0.026	**<0.001**
2003 (crash)	63	45 (8)	15.84 ± 4.96	6.41 ± 0.15	0.84 ± 0.081	0.877 ± 0.081	0.042	**0.013**
2004 (low)	59	31 (8)	15.25 ± 5.3	6.27 ± 0.16	0.826 ± 0.128	0.872 ± 0.095	0.048	0.046
2005 (peak)	128	55 (8)	15.07 ± 4.84	6.35 ± 0.16	0.821 ± 0.095	0.868 ± 0.098	0.056	**<0.001**
2006 (crash)	112	62 (9)	15.15 ± 4.9	6.48 ± 0.19	0.858 ± 0.086	0.877 ± 0.089	0.022	0.373
2007 (peak)	225	95 (9)	15.41 ± 5.7	6.37 ± 0.09	0.844 ± 0.084	0.869 ± 0.099	0.029	0.106

Significant probabilities after FDR corrections are indicated in bold.

then, IBD's slopes should not vary significantly along the cycle. The linear relationship between genetic and geographic distances is expected to hold best at distances greater than the mean parent–offspring dispersal distance (σ) and to progressively deviate from linearity at distances larger than 50σ. For these reasons, we excluded pairwise comparisons between individuals separated by <250 m (Rousset 2000; Vekemans & Hardy 2004; Gauffre *et al.* 2008). IBD tests were performed using the ê statistic, which provides higher statistical power and slope estimates with lower mean square error than the â statistics (Watts *et al.* 2007). Moreover, as ê gives more weight to rare alleles, it is also less dependent on past demographic events (Leblois *et al.* 2004; Watts *et al.* 2007). Then, when investigating changes in IBD slopes in cyclic species, such as the common vole, ê-based analyses are expected to be more accurate.

Following the same approach as for *Ar*, we used linear models to test for changes in the slope of the IBD regression according to, first, the demographic phases of the cycle taken as a factor with three levels (peak, crash and low phases) and, second, three demographic parameters as covariates: (i) N_t, (ii) N_{t-1} and (iii) annual PGR. As previously, we did not test models including the three covariates simultaneously and selected the best model using AIC. The slopes were estimated by locus, and each locus was included in all models as a fixed effect.

Sex-specific relatedness patterns. To test the predictions detailed in Pilot *et al.* (2010) regarding density-dependent changes in relatedness patterns among females, we computed sex-specific relatedness coefficient between pairs of individuals. We used the program SPAGEDI 1.2 (Hardy & Vekemans 2002) to compute an estimator derived from Li *et al.* (1993), which often shows a low variance compared with other estimators, with a sample size correction (Wang 2002, see also SPAGEDI User's manual). Allelic frequencies calculated over the whole data set were used as references to compute relatedness among individuals trapped the same year. For each sex, we divided the data in two categories of density. The first one corresponded to high-density years (i.e. pooling peak phases: 1999, 2002, 2005 and 2007) and the second to low-density years (i.e. pooling together crash and low phases: 2001, 2003, 2004 and 2006). Crash and low phases were merged in a single category as relatedness provides a more direct and instantaneous measure of gene flow than classical genetic distances estimates, which integrate population demographic history. The changes in the spatial extent of males and females relatedness patterns were tested using correlograms as implemented in the software SPAGEDI and considering nine distance classes. The first class corresponded to individuals trapped on the same trap line, and subsequent distance classes were lagged every 2500 m. Significance of relatedness coefficients was tested by permuting individuals trapped during the same year of sampling.

To specifically test whether relatedness among females within colonies (i.e. at the scale of the trap line) varied with density, we compared coefficient's values between low (2001, 2003, 2004 and 2006) and high (1999, 2002, 2005 and 2007) density years. We applied the procedure described in Coulon *et al.* (2006) and generated 1000 random resampling sets without replacement, such that each individual occurs only once in a given resampled set.

Results

Common vole population dynamics

Time series of population abundance from both April and June trapping sessions clearly revealed the 3-year

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cycle (Fig. 2a) already described for this population (Lambin *et al.* 2006). Peaks occurred in 1999 and every third year thereafter at the exception of the 2007 peak, which occurred after only 1 year of low density. In total, 875 tissue samples were collected between 1999 and 2007 and used for genetic analyses (Table 1). Among those 875 individuals, 186 could be considered as juveniles as they weighted <14 g (Bonnet *et al.* 2013). In 1999 and 2001, the two most extreme years in terms of abundance, the common vole was present in 85% and 23% of the 160 trap lines, respectively. This suggests that colonies are continuously distributed over the landscape during peak years while spatial structure is probably a lot more patchy during low-density years (Fig. 1).

Variation in genetic diversity

After FDR correction, 4 years (2001, 2002, 2003 and 2005) displayed a significant heterozygote deficiency, with F_{IS} values ranging from 0.026 to 0.074 (Table 1). At the regional scale, allelic richness (*Ar*), estimated over loci, varied from 15.07 in 2005 to 15.84 in 2003 (mean = 15.42 ± 0.28, reference sample size = 34 – Table 1 and Fig. 2b). At the sector scale, mean *Ar* varied from 6.27 ± 0.16 in 2004 to 6.52 ± 0.07 in 1999 (mean = 6.41 ± 0.17, reference sample size = 5 – Table 1 and Fig. 2c, details for each sector and year are available in Table S1, Supporting information).

At the regional scale, linear models did not reveal any effect of the cycle's phase ($F_{2,79}$ = 0.06, P = 0.94) or demographic parameters (i.e. N_t, N_{t-1} and PGR) on *Ar* (results not shown). At the sector scale, the best linear model (i.e. with the lowest AIC) showed a significant positive effect of annual PGR and a marginally significant positive effect of vole density in the previous year (N_{t-1}) (Table 2). Hence, at the sector scale, *Ar* was estimated to increase of 0.26 (~4%) for a 10-fold increase in density. Three competing models had a ΔAIC <2 with the best model. However, they did not reveal any significant effect of the cycle's phase ($F_{2,489}$ = 1.34, P = 0.26) or demographic parameters retained: N_t and PGR, respectively (see Tables S3 and S4, Supporting information).

Temporal differentiation

Estimated pairwise F_{ST} values between years varied between −0.0014 and 0.0035 (Table 3), indicating thus very small variations in allelic frequencies along the demographic cycles at the regional scale. Some of these slight variations were, however, significant (Table 3). In particular, a significant differentiation was found between the peak in 2002 and the crash in 2003 as well as between two successive years of peak, that is, 2005 and 2007. There was no significant correlation (Mantel test, P = 0.34) between genetic (F_{ST}) and temporal (years) distances.

Table 2 Parameter estimates for the best models, selected from AIC, for the effects of the annual population growth rate (PGR) and density in the previous year (N_{t-1}) on (i) the allelic richness estimated at the sector scale and (ii) the slope of the regression of genetic distances (ê-based estimator) against the logarithm of geographic distances. Each locus was included as a fixed effect in the models (coefficients not shown)

Response variable	Effect	Estimate	Std. error	*t*-value	*P*-value
Ar sector scale	Intercept	5.978	0.1264	47.29	<0.001
	PGR	0.0265	0.0129	2.06	**0.04**
	N_{t-1}	0.0465	0.0253	1.83	0.067
ê-slope	Intercept	0.0085	0.004	2.069	0.042
	PGR	−0.0007	0.0004	−1.75	0.084
	N_{t-1}	−0.0019	0.0008	−2.77	**0.026**

Significant effects are indicated in bold.

Spatial genetic structure

The Figure 2d shows the variations, along the demographic cycles, in the mean level of differentiation (â) at the regional scale. Between-individuals differentiation was significantly higher in 2001, which was the year characterized by the smaller index of abundance (details of the tests between all pairs of years are presented in Table S2, Supporting information). Overall, individuals were, in average, less differentiated during peak than low-density years, with the exception of 2005, which was the peak of lowest amplitude in the time series.

For all years but 2003, we found a significant IBD pattern using the ê statistic with IBD's slopes ranging from −0.0001 to 0.0068 (Table 4). The best linear model revealed a significant effect of the cycle's phase ($F_{2,79}$ = 3.5, P = 0.035). The slopes were significantly stronger during low phases than during crash phases (0.007 ± 0.002, P = 0.01) and, though marginally, peak phases (0.005 ± 0.002, P = 0.06). There was no difference between crash and peak phases (0.003 ± 0.002, P = 0.28). One model had a ΔAIC <2 with the best model and, consistently, it showed a significant negative effect of vole density in the previous year (N_{t-1}) and a marginal negative effect of the annual PGR (Table 2 and Table S3, Supporting information). The distributions of the residuals showed some outliers, which all concerned the locus Ma81. When this locus was excluded from the analysis, the best model still showed a significant negative effect of vole density in the previous year (N_{t-1}).

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Table 3 Pairwise F_{ST} values computed between annual samples

	1999 (peak)	2001 (crash)	2002 (peak)	2003 (crash)	2004 (low)	2005 (peak)	2006 (crash)
2001 (low)	0.0015						
2002 (peak)	0.0009	−0.0007					
2003 (crash)	**0.0019***	0.0003	**0.0026***				
2004 (low)	0.0015	0.0010	0.0005	**0.0035***			
2005 (peak)	**0.0028***	0.0020	0.0002	**0.0020***	0.0010		
2006 (crash)	0.0010	−0.0014	0.0001	**0.0009***	0.0001	0.0000	
2007 (peak)	**0.0015***	0.0014	0.0005	**0.0022***	−0.0003	**0.0013***	0.0002

Bold and * indicate significant P-values (<0.05).

Table 4 Summary statistics for the regression analyses of genetic distances (ê statistic) against log-transformed geographic distances computed between pairs of individuals: Mean (±SD) values of the ê statistic, Mantel test P-values (IBD P), intercept and slope with 95% CI estimated by bootstrapping over loci

Year	ê-slope [95% CI]	IBD P
1999 (peak)	**0.0036** [0.0011–0.0059]	**0.002**
2001 (low)	0.0069 [−0.0014 to 0.0155]	**0.034**
2002 (peak)	**0.0035** [0.002–0.0059]	**<0.001**
2003 (crash)	−0.0001 [−0.0052 to 0.0051]	0.593
2004 (low)	**0.0068** [0.0017–0.0195]	**0.002**
2005 (peak)	**0.0042** [0.0029–0.0063]	**<0.001**
2006 (crash)	**0.0012** [0.0004–0.0023]	**0.041**
2007 (peak)	**0.0032** [0.0019–0.0043]	**<0.001**

Significant Mantel tests are indicated in bold.

Sex-specific relatedness patterns

Relatedness between individuals decreased with increasing geographic distance whatever the sex or density category considered (Fig. 3). However, behind this general pattern, the mean level of relatedness between females at very short distances (i.e. trap line scale) was two times greater during high than low density (0.086 vs. 0.04); this difference was, however, found as nonsignificant when using the resampling procedure ($P = 0.21$). Moreover, the spatial scale of positive and significant relatedness between females extended from the trap line (100 m) at low density to 2500 m at high density. The spatial extent of relatedness between males also increased from 5000 to 7500 m between low and high density (see Fig. 3), while the mean level of relatedness at very short distance did not vary (0.031 for both high and low-density years).

Discussion

This study presents the result of a 9-year demo-genetic survey of a vole population with large multiannual fluctuation in density (up to ~100-fold). Our large scale study site and the individual-based approach allowed us to sample enough individuals for population genetics analyses even during low densities. Our design also enabled us to explore direct and time-lagged effects of population density on genetic diversity, spatial genetic structure and relatedness patterns at spatial scales varying from the regional (whole study site) to the colonies (trap lines).

Genetic diversity and geneflow variation along cycles

At the regional scale, genetic diversity did not vary significantly through the demographic cycles and it remained high, which is in line with previous studies on cyclic rodent populations (Ehrich & Stenseth 2001; Ehrich *et al.* 2001, 2009; Østergaard *et al.* 2003; Berthier *et al.* 2005, 2006; Ehrich & Jorde 2005; Vuorinen & Eskelinen 2005; Rikalainen *et al.* 2012). However, if the number of alleles did not vary, we found evidences for slight variations in their frequencies. For example, the whole population differentiated between the 2002 peak and 2003 low-density year. This finding can be explained by the different picture that emerged at the sector scale. When the spatial scale was reduced, allelic richness exhibited slight, but clear, variations along the demographic cycles (Fig. 2c). At this scale, the best linear model indicated a significant positive effect of the annual PGR and a marginal positive effect of past density on allelic richness. The lack of power in our statistical approach may be due to the low number of individuals sampled during crash and low phases. It is also likely to be due to the individual-based approach adopted for this study. Indeed, the sector scale (~40 km^2) is the smaller spatial scale at which allelic richness could be computed for each sampling year. Moreover, our estimates were based on a low-reference sample size of five individuals. Adopting a population-based sampling to estimate genetic diversity at a smaller scale (ideally one or few adjacent fields) would have probably enhanced our ability to detect significant variations in allelic richness with density. Our results, however, strongly suggest that variations in genetic

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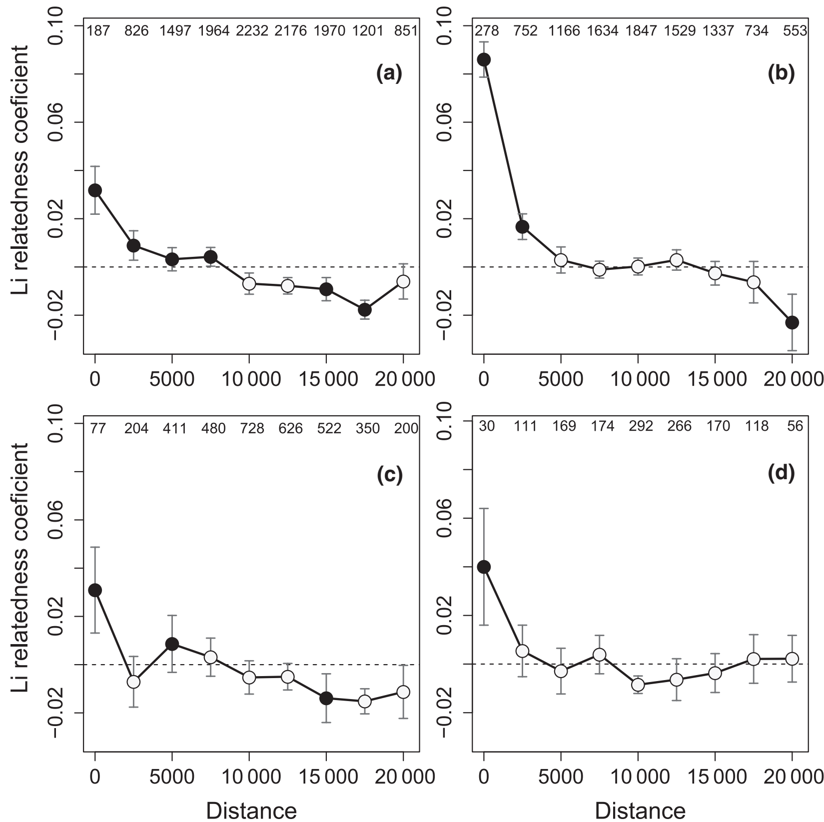

Fig. 3 Spatial autocorrelation analyses based on Li's relatedness coefficient. Correlograms are presented for males (a) and females (b) in high-density years (1999, 2002, 2005 and 2007) and for males (c) and females (d) in low-density years (2001, 2003, 2004 and 2006). SE computed by bootstrapping over loci is plotted for each coefficient. Coefficients were computed for nine distance classes (in metres), and the first distance class (0 m) represents pairwise comparisons between individuals from the same trap line. Black dots indicate distance classes for which the observed value significantly departed from the mean permuted value ($P < 0.05$).

diversity are scale dependant (Berthier *et al.* 2006; Devillard *et al.* 2011). Finally, as the variations are slight, using more microsatellite loci (e.g. 20) would have probably improved the statistical power in our analyses.

The level of genetic structure and the pattern of IBD within the population varied through the demographic cycles, which suggests that geneflow intensity covaried with density fluctuations. First, excepted in 2005, which was the peak with the lowest amplitude, genetic differentiation was lower during high-density years. In contrast, the highest level of differentiation was observed in 2001, the year with the lowest number recorded. Second, the best linear model (i.e. cycle phase model) showed that the ê-based slopes of the IBD regressions were stronger during low density than during crash and peak phases. The weakest slopes were recorded during the crash phases (see Fig. 2), suggesting then a delayed effect of density (i.e. under direct demographic effects, weakest slopes should be observed when densities are the highest). This delayed effect was supported by the second best linear model (ΔAIC <2) which revealed a significant negative effect of vole density in the previous year (N_{t-1}).

The delay in the changes of IBD slopes, and to a lesser extent in allelic richness, according to cyclic fluctuations is an originality of our study. This could be due either to our early sampling in spring, when maximum density during peak years usually occurs in autumn, or to genetic inertia. Common voles breed and potentially migrate all year round, although at reduced rates during winter. Then, the pattern observed 1 year is most likely shaped over the autumn and winter of the previous year. Genetic inertia stands for the accumulation of demographic effects on genetic parameters over generations (Whitlock & McCauley 1999; Leblois *et al.* 2006). This effect is not equivalent for all genetic parameters, and consistently, we found that the effect of previous year density is less marked on *Ar*, which is expected to respond more rapidly to demographic crashes than the slopes of the IBD regression (Leblois *et al.* 2006; Schwartz *et al.* 2007). Thus, the weak IBD slopes during a crash year would be the delayed result of the previous peak year while stronger slopes build up through two consecutive years of low density (when the population undergoes crash and low phases). Altogether, these results suggest that the balance between genetic drift and gene flow is biased toward the former during low density and the later during high density as expected under constant or positive density-related dispersal.

Density- and sex-dependent dispersal

Many studies have suggested that negative density-dependant dispersal could be the rule in microtine

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rodents (e.g. Smith & Batzli 2006; Ehrich *et al.* 2009; Le Galliard *et al.* 2011). In our study, the observed variations in genetic diversity and genetic structure support the hypothesis that dispersal can only counterbalance genetic drift effects when population experiences high density (Berthier *et al.* 2006). However, as we used indirect measures of gene flow, the observed pattern depends on both effective population size (De) and second moment of the dispersal distance (σ^2). Then, we cannot infer the relationship between density and dispersal (i.e. distinguishing between constant or positive density-dependant dispersal) as an increase in any of these two parameters would result in a larger number of migrants and then gene flow. In this context, approaches comparing relatedness measures can provide further insights into the processes shaping observed genetic patterns (Iacchei *et al.* 2013). When using such an approach for the common vole, we found evidences that the spatial extent of relatedness actually increases with density for both sexes (Fig. 3). This suggests that common voles move at longer distances when density increases.

Altogether, the variations in genetic diversity, allelic frequencies and both IBD and spatial relatedness patterns are more consistent with model's predictions from Charnov & Finerty (1980), which assumes positive density-related dispersal. However, regarding kin structure at the local scale, we did not find the negative correlation between density and females' relatedness that should have resulted from increasing immigration into pre-existing colonies. We actually observed the opposite signal as local relatedness among females was two times greater in high (0.086) than low density (0.04). Although not significant, this result appears more consistent with the alternative model from Lambin & Krebs (1991), which assumes negative density-related immigration. This apparent contradiction could be explained by between sex differences in dispersal behaviour. In the common vole, dispersal is biased toward males, which are mainly involved in the spread of genes among colonies through repeated dispersal events while female dispersal mostly translates in the colonization of empty patches through new colonies foundation (Boyce & Boyce 1988; Dobly & Rozenfeld 2000; Gauffre *et al.* 2009). When local density increases, female emigration is enhanced by competition and females colonize more intensively the fields surrounding their natal patch (Aars *et al.* 1999). Moreover, it has also been suggested that new colonies are established from small groups of related females (Boyce & Boyce 1988). Such a mechanism can explain why the spatial extent of significant relatedness between females increases during high-density years without inducing a strong reduction in female relatedness within colonies. Establishment of numerous new colonies by females in different fields could in turn allow males to reproduce in different patches or fields over long distances by moving from one colony to another. Indeed, when local density increases, males are less successful at settling in the nearest patches due to high competition (Andreassen & Ims 2001; Gundersen *et al.* 2002). As a result, distance moved by males before mating will increase, as suggested by the larger distance separating related males (Fig. 3). Conversely, during low density, male dispersal would be efficient more locally because of the scarcity and patchy distribution of colonies in the landscape and lower competition for mating. Hence, when discussing density-dependent dispersal in the common vole, it is important to distinguish between interpatches dispersal, which is mainly a male process, and colonization of empty patches that would be primarily performed by females. Colonization is even more likely to be a key process in highly dynamic agroecosystems such as the one studied here. Indeed, ploughing of annuals crops, which cover more than 80% of the studied area, leads to local eradication by direct killing and destruction of colonies (Jacob 2003; Bonnet *et al.* 2013). Hence, aside from density fluctuations, most of the landscape patches (i.e. fields of annual crops) are emptied annually by ploughing. Therefore, common vole metapopulation dynamics strongly depends on colonization events.

Conclusions

In this study, we revealed density-related variations in genetic patterns in a cyclic population of the common vole. We found evidences that variations in genetic diversity with density are scale-dependent, that is, genetic diversity fluctuates at the local scale but remains constant at the regional scale. At the metapopulation scale, changes in spatial structure (mean differentiation and IBD) and relatedness patterns suggest that gene flow is temporarily slowed down at low density as expected from the model of Charnov & Finerty (1980), which assumes positive density-related dispersal. Gene flow is thereafter enhanced during high density probably as a result of local competition that increases both empty patches colonization by females and male dispersal among newly established colonies. These results highlight the potential key role of extinction and recolonization processes in driving temporal variations in the composition and spatial structure of neutral genetic diversity in populations exhibiting large density fluctuations.

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B.G. performed field work, laboratory work and statistical analyses. B.G. and K.B. wrote the manuscript with contributions from P.I., V.B. and J.-F.C. Y.C. collected the DNA samples. V.B. and J.-F.C. obtained funding and designed the study with B.G. All authors read, edited and approved the manuscript.

Data accessibility

Microsatellite and abundance data sets have been posted on Dryad (doi:10.5061/dryad.jf7sn).

Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Mean (±SD) allelic richness (*Ar*), calculated for each sector and year.

Table S2 Resampling tests applied to test for temporal differences in the mean genetic differentiation among individuals (â statistic).

Table S3 Model selection for allelic richness (*Ar*) and IBD $\hat{e}$-slope variations, considering (i) the cycle's phase as a factorial variable (three levels: peak, crash and low phase) and (ii) three demographic parameters as covariates [population abundance (N_t), previous year population abundance (N_{t-1}) and annual population growth rate computed as N_t/N_{t-1} (PGR)].

Table S4 Parameter estimates for the three models having a ΔAIC <2 with the best model explaining variations in allelic richness (*Ar*) at the sector scale.

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