Dispersal, landscape and travelling waves in cyclic vole populations

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Abstract

Travelling waves (TW) are among the most striking ecological phenomena emerging in oscillating populations. Despite much theory, understanding how real-world TW arise remains a challenge for ecology. Herein, we analyse 16-year time series of cyclic vole populations collected at 314 localities covering 2500 km² in France. We found evidence for a linear front TW spreading at a speed of 7.4 km year⁻¹ along a north-west/south-east direction and radiating away from a major landscape discontinuity as predicted by recent theory. The spatial signature of vole dispersal was assessed using genetic data collected at 14 localities. Both data sets were handled using similar autocorrelation approaches. Our results revealed a remarkable congruence of the spatial extent and direction of anisotropy of both demographic and genetic structures. Our results constitute the first empirical evidence that effective dispersal is limited in the direction of TW while most of the individual exchanges occur along the wave front.

Keywords

Anisotropy, autocorrelation, cyclic populations, dispersal, dynamics, genetics, landscape obstacles, travelling wave, voles.

INTRODUCTION

Understanding the spatial dimension of population dynamics is an endeavour in which the dialogue between theoretical and empirical studies has been particularly fruitful (Bjørnstad et al. 2002; Johnson et al. 2006; Sherratt & Smith 2008; Fox et al. 2011). It is established that several processes may concurrently shape patterns of population synchrony (Bjørnstad et al. 1999; Koenig 1999, Liebhold et al. 2004). They include common environmental influences such as weather affecting separate populations sharing the same density-dependent structure (Moran 1953); frequent local or rarer long-distance dispersal binding populations over distances exceeding mean dispersal distances (Sherratt et al. 2000), as well as trophic interactions (Ims & Andreassen 2000). Disproportional depletion by predators of populations more abundant than their neighbours can equalise densities and bring population into synchrony.

Some of the most dramatic examples of spatial synchrony in nature come from species that experience population cycles, a type of dynamics classically viewed as arising from trophic interactions. Indeed, cyclicity is said to beget synchrony. In space with the spatial and temporal oscillations combining to give the appearance of a wave in population density. As in ‘Mexican waves’, however, there is no net propagation of individuals. Mathematical theory on periodic TW, crisply summarised by Sherratt & Smith (2008), uses reaction-diffusion equations of interacting species at different trophic levels involved in cyclic oscillations (predator–prey, pathogen–host, plant–herbivore, plant–herbivore–parasitoid), which generate the density fluctuations, and a diffusion process. The diffusion process may be through dispersal of individuals belonging to either one or all trophic levels involved in cyclic oscillations (Sherratt & Smith 2008). Reaction-diffusion models assume isotropic dispersal. However, to keep the spatial shift in population growth, which characterise linear and unidirectional TW, dispersal leading to successful immigration (effective dispersal) should be directional, at least at large spatial scales: weaker in the direction of propagation than along the front of the wave. For a given set of ecological parameters, and when diffusion coefficients

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of the interacting species are sufficiently similar, there is a range of possible values for the speed, wavelength, time period and amplitude of periodic TW solutions (Sherratt & Smith 2008).

Much theory indicates that heterogeneities in landscape are instrumental in generating TW by impacting dispersal (Sherratt et al. 2002, 2003; Johnson et al. 2004). Outbreak waves may originate at the edges of obstacles to movement (Sherratt et al. 2002), but the nature of the obstacle seems to matter. When large-scale landscape features are modelled under absorbing boundary conditions (individuals encountering obstacles ‘die’), they will tend to organise the spatiotemporal dynamics into periodic waves moving away perpendicular to obstacles, especially for long and thin obstacles (Sherratt et al. 2003). Where TW have been detected in natural systems, evidence that obstacles to dispersal were involved in wave generation is at best equivocal (Moss et al. 2000; Mackinnon et al. 2001; Bjørnstad et al. 2002; Johnson et al. 2004). Heterogeneities in landscapes are ubiquitous, but, at least in the Kielder Forest field vole empirical system that motivated the theory developments by Sherratt et al. (2002, 2003), the observed pattern of a TW seemingly passing through a large lake that cuts vertically through the study area (Lambin et al. 1998) does not match the predictions of waves travelling perpendicularly away from obstacles. TW theory is in its infancy and landscape heterogeneities may act in various ways. For instance, Johnson et al. (2004, 2006, 2010) showed that historical larch budmoth outbreaks in the Alps originate in epicentres of high-quality habitat and then subsequently spread to low-quality habitat and such pattern can be reproduced in simulations models. Sherratt & Smith (2008) concluded that at present, there is no conclusive evidence for any specific wave generation mechanism applying in a particular ecological system that exhibits periodic TW.

An excellent model to confront outcomes of the theory of periodic TW to a real ecological system is provided by the fossorial water vole, Arvicola terrestris (Linnaeus, 1758), a meadow dwelling subterranean rodent. In the Jura Mountains of France and Switzerland, this species undergoes well-marked abundance cycles over 5–8-year periods (Saucy 1994; Weber et al. 2002). During a cycle, densities vary from less than one animal to several hundred per hectare and regular outbreaks cause important agricultural and economic losses (Giraudoux et al. 1997). Changes in vole population abundance were monitored over 16 years (1989–2004) over a large area (>2500 km²). Using graphical analyses and abundance data from an entire demographic cycle (1989–1994), Giraudoux et al. (1997) suggested that outbreaks emerge from epicentres localised in a south-west/north-east strip, and then spread as a TW from north-west to south-east over more than 2500 km² at a speed exceeding 10 km year⁻¹. Moreover, a genetic study conducted in 2002 and encompassing the area studied by Giraudoux et al. (1997) suggested the presence of major physical obstacles to vole dispersal (Berthier et al. 2005).

In this study, using appropriate statistical analyses and longer term demographic data (1989–2004), we reinvestigated the spatiotemporal dynamics of the fossorial water vole occurring over the same area to: (1) assess the synchrony in vole density fluctuations, and (2) test for the presence of a unidirectional TW, and estimate the direction and speed of this wave. We also reanalysed the genetic data collected over the same area to determine: (1) whether gene flow (effective dispersal) is directional and (2) the maximum spatial scale at which dispersal still has some homogenising genetic effects taking into account for the potential anisotropy in gene flow. We then compared the spatial demographic and genetic patterns to determine if vole dispersal meets theoretical expectations for TW emergence. On the basis of TW theory, we expected: (1) spatially restricted vole dispersal contrasting with large-scale dispersal being, in extremis, expected to synchronise the fluctuations over large areas, (2) directionality in gene flow as effective dispersal should be weaker along the propagation axis of the wave to allow the spatial shift in demographic phases and (3) the presence of landscape obstacles, oriented perpendicularly to the wave propagation, that could act as absorbing boundaries against vole dispersal in the long term.

MATERIALS AND METHODS

Study site

The study was conducted on the Jura Plateaus, an area of altitude ranging from 400 m to 1200 m in the Franche-Comté region (47.11 °N, 6.24 °E), in the Middle East of France (Fig. 1). Within this area, the landscape consists largely of open permanent grasslands interrupted by conifer and beech forests, and areas of mixed pasture, woodland and hedgerows of different sizes and shapes. The study area is bounded by major landscape discontinuities oriented along a south-west/north-east direction. To the north-west, lays the edge of the Jura Plateaus, fringed by the Doubs River, which marks an abrupt transition between the plateaus, above 400 m of altitude and dominated by grasslands, and the plain of the Doubs an area of altitude lower to 400 m characterised by arable farming and urbanised areas. To the south-east, along the border between France and Switzerland, lays the ‘Haute-Chaine’ of the Jura Swiss Mountain culminating at 1720 m and behind which are located two long and narrow major bodies of water (Lake Neuchâtel and Lake Biel, 218 and 39 km² in area respectively). In the middle, a third elevation discontinuity, the Loue river valley bisects the southernmost third in a meandering pattern roughly along a north-west/south-east direction. The later has recently been identified as a physical barrier to vole dispersal (Berthier et al. 2005).

Vole abundance data

The survey data were collected in autumn by the technicians of the FREDON (regional federation of defence again pest organisms) over an area of about 2500 km². The method developed to assess vole abundance is based on the density of earth mounds tumuli that reflects vole activity and is roughly proportional to water voles abundance (Giraudoux et al. 1995, 1997). Vole abundance was recorded at the commune/township scale (mean area = 9 km²; referred to hereafter as localities) according to the following categories: 0 = no
Figure 1 Map of the major landscape features of the study area. Red triangles and side panels show the location and shape of six illustrative examples among the 314 abundance time series recorded within the study area between 1989 and 2004 and analysed in this study. Black squares depict the 14 sampling localities for genetic data (numbers refer to population codes in Berthier et al. 2005). The upper scatter plots show the spatial variations in (a) mean elevation and (c) permanent grassland ratio within our localities ordered north-west to south-east (135° to north). Each dot represents a locality and a smoothing spline was fitted to the data with 95% confidence envelope of the smoothing function indicated with dashed lines.

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colony, 1 = some isolated colonies, 2 = colonies present in many grasslands, 3 = very numerous colonies and serious damages to grassland. This index method provides reliable information to describe qualitatively, or semi-quantitatively, the spatiotemporal variation in vole abundance (Fig. 2). Overall, 314 localities time series of 16 years (1989–2004) were analysed to investigate the spatial patterns of abundance by performing statistical analyses using this abundance index.

Synchrony

A measure of the synchrony of change in abundance between two distinct localities was derived using an approach similar to that advocated by Bjørnstad et al. (1999) with the following adjustments made to cater for the semi-quantitative nature of our data. Growth rates between two successive observations of abundance in the same locality were calculated as \( Z_t = N_t / C_0 \), where \( N_t \) is the abundance at time \( t \). Pairwise Spearman rank correlations between time series of growth rate were used as measures of synchrony. Regional synchrony was the average Spearman rank correlation between the time series of growth rate. As cross-correlation coefficients are not independent, their significance was evaluated using a bootstrap confidence interval generated by sampling with replacement among the time series. The relationship between synchrony and Euclidean distance between localities’ centroids was quantified using the spline correlogram approach, which provides bootstrap confidence envelopes for the shape of the covariance function (Bjørnstad et al. 1999). The \( x \)-intercept of the spline correlogram was used to estimate the extent of local synchrony.

Following Lambin et al. (1998), we tested for the presence of anisotropy in the spatial pattern of synchrony. We calculated the distance between pairs of localities after their projection onto an axis passing through the centroid position of the localities with an angle of \( \theta \) to north. For 63 integer angle value of \( \theta \), varying between 0° and 180°, the Mantel correlation was calculated between cross-correlation coefficient and distance between localities after their projection. The angle value corresponding to the strongest negative Mantel correlation between synchrony and distance was considered as the direction with the greatest spatial dependency. Significance of each Mantel coefficient was assessed using a randomisation test with 1000 permutations. Finally, we estimated the spatial scale of synchrony accounting for directionality by calculating anisotropic spline correlograms for 12 different bearings from 0° to 165° to north.

**Figure 2** Annual maps of vole abundance recorded at the commune scale in the Doubs department (ca. 2500 km²) between 1989 and 2004. \( n \) is the number of localities with data for a given year. Year 2001 is not presented as there was numerous missing data. Vole abundance categories are represented as follows: red for high abundance, orange for medium abundance, yellow for low abundance, light yellow for absence and grey for missing data.
Travelling wave estimates

We tested for the presence of a periodic TW using general additive models (GAM) following Lambin et al. (1998). We fitted a model assuming a linear front, constant speed TW moving towards a direction $\theta$ from the north. The equation of the fitted model was as follows: $A(i,t) = m + s(t + rd(\theta)) + e(i,t)$, with $A(i,t)$ the observed abundance at site $i$ and time $t$, $m$ the overall mean, $s(t)$ the smoothing spline describing the temporal change in abundance, $rd(\theta)$ the distance of site $i$ from the centroid of the localities after projection of the site $i$ onto an axis of angle $\theta$ to north and passing through the centroid of the localities, $r$ the inverse of the wave speed and $e(i,t)$ the residuals. The number of degrees of freedom (d.f.) used for fitting the TW model was determined by repeated fitting of GAM, assuming no wave, and observing both the reduction in the Akaike Information Criteria (AIC) and the shape of the fitted response curve. Maximum likelihood estimates (MLE) of the parameters $r$ and $\theta$ were calculated assessing the AIC of the model for 10,000 combinations of $r \cos \theta$ and $r \sin \theta$.

TW emergence

In the Jura Mountains, the cycle period of vole populations has been reported to vary from 5 to 8 years (Saucy 1994; Weber et al. 2002). The cycle period can be influenced by local direct density-dependent processes (strictly speaking also delayed density dependence, although to a lesser extent) that could be spatially structured over a large scale. Therefore, demographic patterns resembling a TW signal may emerge at large scale. Recent theoretical works also suggest that heterogeneities in landscape are instrumental in generating TW either by acting as dispersal barriers (Sherratt et al. 2002, 2003) or by generating spatial gradients in habitat quality that reflect on intrinsic rates of population increase (Johnson et al. 2006). Elevation in our study area clearly exhibits a monotonic gradient from the edges of the Jura Plateaus (north-west) to the Haute-Chaîne (south-east) (Fig. 1a). This area also includes sharp elevation changes such as the Loue Valley, which has been identified as a barrier to vole dispersal (Berthier et al. 2005). To contrast these hypotheses on TW emergence, we derived three population dynamics estimates from our time series.

First, we estimated the dominant period in abundance fluctuations within each locality using Lomb-Scargle periodograms (Lomb 1976), which perform better than classical Fourier-based periodograms in detecting sinusoidal rhythms from noisy and short-term data (Glynn et al. 2006; Refinetti et al. 2007). For each time series, we tested a limited range of frequencies in the periodogram corresponding to periods between 3 and 9 years. The statistical significance of the dominant period detected compared to noise-induced signal was evaluated using 95% bootstrap confidence intervals generated by sampling the series 100 times with replacement. Second, for each locality, we derived a mean growth rate computed as the median of all positive growth rates occurring in a time series. Finally, we estimated the local delay in outbreaks occurrence between any given locality and each of its neighbours computed as 1 – Spearman coefficient between time series.

For both non-paired estimates (cycle period and mean growth rate), we tested if there was a monotonic gradient occurring in the direction of the wave’s movement by ordering the localities along the wave propagation axis. We also analysed variations in synchrony’s delay as a function of three landscape features: mean elevation, slope (taken as standard deviation of mean elevation) and grassland ratio. These features were computed from raster images by drawing 1-km radius buffers around the straight lines linking the centroids of adjacent localities. For all these analyses, we used Spearman correlation tests.

Spatial genetic pattern

In a previous study, Berthier et al. (2005) analysed the spatial genetic structure of water voles using eight neutral microsatellite loci and samples collected in 2002 from 23 localities covering a larger area. Here, we reanalysed those data considering only the 14 localities sampled within the demographic study area (Fig. 1 and Table S1). The spatial pattern of genetic variation was investigated using Mantel correlograms. Mantel coefficients between genetic distances ($F_{st} –$Weir & Cockerman 1984) and Euclidean distances among all pairs off localities were computed for 10 distance classes. The first Mantel coefficient no longer positive and significantly different from zero provides information on the distance at which the localities are, on average, as similar as two localities randomly chosen from the sample (Vekemans & Hardy 2004). This distance can be interpreted as the maximum extent of the spatial genetic structure. When a correlogram steadily decreases until reaching that distance class with no other trends at longer distances, this means that dispersal is spatially restricted at the studied scale (the so-called isolation-by-distance pattern – IBD), with a mean dispersal distance lower than this distance. This particular distance class provides information on the spatial extent at which dispersal can still have some genetically homogeneous effect through both stepping stone dispersal and rare long-distance dispersal events.

We tested for anisotropic gene flow using bearing analyses (Rosenberg 2000). In such analyses, the geographic distance between two points is weighted according to the degree of alignment with a fixed bearing. As with demographic data, Mantel correlations were first computed between pairwise genetic distances ($F_{st}$) and weighted distances for each of the 63 values of $\theta$, varying between 0° and 180°. We then computed Mantel bearing correlograms using the same 10 distance classes as for the non-directional genetic correlogram and the 12 bearings as for the anisotropic spline correlograms. Significance of Mantel coefficients was assessed with 1000 permutations. The angle values for which Mantel coefficients are not significant inform on the directions of low distance dependency of gene flow. This could mean that localities arranged along these directions are either highly and similarly connected by gene flow whatever the distance between them or, by contrast, poorly connected by gene flow and then largely influenced by genetic drift. As previous genetic studies on A. terrestris revealed strong IBD patterns at various spatial scales.

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(Berthier et al. 2005, 2006; Aars et al. 2006; Bryja et al. 2007; Deter et al. 2007), the high gene flow explanation can be ruled out. Indeed, because of this IBD, we expected the direction of highest spatial dependency, which will be indicated by significant Mantel coefficients over longer distances, to be the direction of highest gene flow.

RESULTS
Spatial pattern of synchrony
The regional mean synchrony in changes in abundance was 0.14 (Cl95% = [0.12–0.17]). The spatial scale of synchrony estimated from the isotropic spline correlogram was 25.4 km (Cl95% = [21.6–31.5], Fig. 3a). There was evidence for anisotropy in the spatial pattern of synchrony. The strongest negative Mantel correlation between synchrony and distance was obtained after projection of the localities onto an axis at 132° to north (r = −0.43, P < 0.001; Fig. 3b). The spatial scale of synchrony estimated from the anisotropic spline correlograms was the smallest, ~14 km (Cl95% = [12.4–15.3]), along that general direction (120°–135° to north; Fig. 3c). The strongest positive Mantel correlations between synchrony and distance were obtained after projection of the localities onto approximately perpendicular axes, i.e. 45° to north, r = −0.12, P < 0.001. The spatial scale of synchrony estimated from the anisotropic spline correlograms was the largest, ~26 km (Cl95% = [13–45]), along that general direction (45°–75° to north; Fig. 3c).

Travelling wave estimates
The GAM supported the existence of a pattern resembling a TW over the entire area. The best smoothing spline, describing the temporal change in abundance without a TW, was obtained with 14 d.f. The fit of the model was substantially improved by incorporating a TW (ΔAIC = 237). MLE for the angle θ was 135° to north (Cl95% = [113.2–176.3]) and for speed (1/r) = 7.37 km year⁻¹ (Cl95% = [3.88–23.01]). The fitted model showed clearly that vole populations fluctuate with a 5- to 6-year period (Fig. 4). The direction of propagation of the wave (north-west/south-east) is almost perfectly perpendicular to the direction (south-west/north-east) of the longer axis of the large landscape discontinuities bounding the study area, i.e. the edge of the Jura Plateau, the Haute-Chaine of the Jura Mountains and the lakes Biel and Neuchatel (Fig. 1).

Cycle period, growth rate and local synchrony’s delay
Statistically significant cycle periods were determined for 294 times series of the 314 analysed. For all but one locality the dominant period detected ranged from 5 to 9 years, mean = 6 years and did not show any gradient in period lengths along the north-west/south-east propagation axis of the wave (correlation = 0.084, P = 0.191; Fig. 5a, b). The mean growth rate within locality varied from 1 to 3 (abundance index/year) and exhibited a slight increasing trend along the propagation axis (correlation = 0.15, P = 0.007; Fig. 5c, d). Spearman correlation tests between synchrony delay among adjacent localities and landscape features revealed a strong and positive correlation with elevation slopes (correlation = 0.30, P < 2.2e⁻¹⁶; Fig. 6).

Spatial genetic pattern
Mantel correlogram of genetic data showed a pattern of decreasing similarity with distance consistent with IBD. The spatial extent of the genetic structure estimated from the upper bond of the larger distance class that still show a positive and significant Mantel coefficient was 18 km (Fig. 3d). Further tests supported the existence of anisotropy in gene flow. Mantel correlations between genetic and geographic distances calculated for 63 bearings were weak and non-significant along the north-west/south-east directions (100°–165° to north; Fig. 3e). This result was supported by Mantel bearing correlograms, which showed that genetic and geographic distances were significantly and positively correlated only over a maximum distance of 12 km along the north-west/south-east axis (135°–165° from north) with no other significant correlation at larger distances (Fig. 3f). In contrast, Mantel correlations were significant along the north-east/south-west direction (45°–105° from north; Fig. 3f), with positive correlations up to 18 km and negative correlations for largest distances (36–48 km).

DISCUSSION
Our results bridge theory and empirical studies on spatial population dynamics. Joint analyses of demographic, genetic and landscape data yielded three main discoveries. First, we presented striking empirical evidence of TW in a cyclic system closely approaching an idealised linear front, constant speed TW spreading at a mean speed of about 7–8 km year⁻¹. Second, the landscape context of the wave provides novel empirical support for the theoretical prediction that TW emanate from obstacles. Finally, we provided striking evidence of congruence between genetic and demographic patterns, with limited gene flow in the direction of the wave, supporting for the first time the contention of limited effective dispersal in the direction of the wave but more individual exchanges among populations located along the wave front.

TW evidence
Water vole populations experience high amplitude cyclical oscillations with a period of 5–9 years sweeping from north-west to south-east across the grass-rich area of the Jura Plateaus (Fig. 1, 2). Our results are partly congruent with Giraudoux et al. (1997)’s graphical analysis of a subset of the data presented here (1989–1994) that led them to correctly detect the existence of a wave-like pattern. However, while they correctly inferred that vole outbreaks emanated from epicentres with a fast spread to the south-east, with the possible exception of the near region-wide outbreak in 1997–1998 (Fig. 2), we find no evidence for their suggestion of bidirectional spread. Instead, the data were strikingly consistent with a hypothetical linear front, constant speed TW. The standard of evidence provided here is much stronger, including formal
Figure 3 Isotropic and anisotropic analyses of the demographic and genetic structures. Isotropic spline and Mantel correlograms computed from (a) abundance time series and (d) genetic distance ($F_{st}$). Spline correlogram (a) is presented with its 95% CI (dashed lines give). Mantel correlations (d, b, e) are presented with black and white circles depending whether coefficients are or are not significantly different from 0 at $\alpha = 0.05$. Mantel correlations between (b) synchrony coefficients and distances between localities after projection on an axis orientated along 63 different fixed bearings and (e) genetic distances ($F_{st}$) and geographic distances weighted according to their degree of alignment with the 63 fixed bearings. Anisotropy in the spatial extent of (c) synchrony (black line) and its 95% CI (grey lines) and (f) genetic structure (dark and light grey areas represent the distance classes with significant positive and negative Mantel coefficients, respectively).
estimates of anisotropy in the scale of synchrony of population growth, and estimation of wave parameters using a statistical model specifically designed for detecting such patterns. Fitting this model yielded estimates wave speed of about 7.4 km year$^{-1}$ with confidence limits widely overlapping with the higher estimate (19 km year$^{-1}$) found in Scotland for the field vole, Microtus agrestis, a much smaller but related vole species with shorter 3–4 year cycles and inhabiting highly fragmented grassed patches that form after clear felling in a man-made forest (Lambin et al. 1998; Mackinnon et al. 2001). The much larger scale of the sampled area for water voles provides more convincing evidence of a linear wave front than any other studies. This study adds to evidence that organised spatial patterns predicted by theory do indeed occur in natural systems.

Congruence of demographic and genetic patterns

This study demonstrates congruent isotropic and anisotropic patterns in demographic and genetic structures of a cyclic species (Fig. 3). For both structures, anisotropic scales of autocorrelation were smaller along the wave propagation axis, 13 and 12 km, than perpendicular to it, 25 and 18 km respectively. Isotropic and anisotropic Mantel correlograms of genetic data clearly reflected that vole dispersal is highly restricted in space at this regional scale. Dispersal nevertheless may still have some homogenising effect up to 18 km along the wave front and 12 km along its propagation axis. This means that, while mean dispersal distance is far less than 18 and 12 km along these two directions, its influence at these scales is likely to result from the cumulative impact of stepping stone dispersal through generations. This anisotropic gene flow suggests that when populations increase in size, individuals are more successfully colonising along a north-east/south-west axis. Interpreting how genetic signatures arise in fluctuating populations is complex as gene flow reflects the effective number of migrants between populations and depends on population sizes and migration rates. The genetic structure observed at a given time results from past and current demographic events impacting the populations. A temporal genetic survey conducted during the increasing phase of synchronous populations of A. terrestris suggested that this phase marks the transition from a patchy demic-structure, during low density, to a continuous population as individuals from growing demes are colonising all the space available, with vole tumuli becoming continuously distributed (Berthier et al. 2006). Then, the observed higher scale of gene flow in the direction parallel to the wave front may result from the recurrent redistribution of the genetic diversity during each outbreak between populations fluctuating in synchrony. By contrast, along the propagation axis of the wave, populations that do not fluctuate in synchrony will not merge demographically and hence less genetically. Thus, synchronous populations will only differentiate during short periods of time (low phases) while populations not synchronised in their fluctuations could diverge under the influence of long-term genetic drift as they never fully merge demographically. While the spatial layout of our genetic sampling sites probably results in varying power for anisotropic analyses of gene flow for some combinations of angle and distance, this reflects a striking biological reality. Indeed, despite intensive fieldwork in the Eastern part of the study area, we only found one vole population located in the extreme south-east, which was likely to be a relic of the previous outbreak in this area. An even wider spatiotemporal genetic survey would be required to fully test our hypothesis about long-term effects of gene flow and genetic drift along the propagation and front directions of the wave.

**TW and landscape heterogeneity**

The TW detected emerges and spreads from the edge of the Jura Plateaus, an area with a high ratio of permanent grasslands favoured by voles. It then climbs a strong gradient in elevation from north-west to south-east (Fig. 1). The slight increasing trend in population growth rates along the north-west/south-east propagation axis of the wave is at odds with theoretical considerations that TW may spread from most to least productive areas (Johnson et al. 2004, 2006). Instead, it implies that population growth rates would be higher in higher altitude parts of the study area where the ratio of permanent grassland decreases drastically (Fig. 1). In contrast, the direction of the wave’s movement along a north-west/south-east direction supports theoretical insights on the role of landscape obstacles in generating TW (Sherratt et al. 2002; Sherratt & Smith 2008). As was the case with two previous empirical instances of cyclic vertebrate populations experiencing multi-annual cycles (Lambin et al. 1998; Moss et al. 2000), the water vole wave moves orthogonally to large-scale obstacles lying to the south-east and north-west, with their long axis perpendicular to the direction of the waves ($80^\circ$–$90^\circ$; Fig. 1). The first discontinuity is the Haute-Chaîne, a subalpine mountain range culminating at 1720 m and dominated by large forests and rugged terrain. South-east of the Haute-Chaîne are the lakes of Neuchâtel and Biel surrounded by
tilled land unsuitable for water voles. To the north-west, lays the edge of the Jura plateaus with a south-west/north-east alignment. This area is fringed by the river Doubs and marks an abrupt transition between permanent grasslands on the plateaus to the lower altitude of the plain of the Doubs to the north-west, an area less suitable for large populations of voles as grassland is largely replaced by arable farming and urbanised areas. All these landscape features bounding the area where the TW is detected are likely to act as obstacles to vole effective dispersal. However, in continuous time models,
no-flux boundary conditions, meaning that individuals cannot enter or leave the domain, do not generate stable TW in oscillating populations (Sherratt et al. 2002). In contrast, assuming that population densities are always zero on the obstacle edge (individuals crossing the obstacle die or are lost to the system) readily gives rise to TW moving out from the obstacle and

Figure 6 Map of the local lag in synchrony computed as 1– the synchrony coefficient between each locality and all its neighbours. Each locality is represented by a star which has as many branches as neighbours; each branch is proportional to the value of 1– the synchrony coefficient computed between the focal locality and the adjacent locality along the direction of the branch. The lower scatter plots show the relationships between the measures of the local lag in synchrony and (a) the mean elevation, (b) the standard deviation in elevation and (c) the ratio of permanent grassland computed within 1 km radius buffers drawn around the straight lines linking the centroids of all pairs of adjacent localities.

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through the domain. While we lack behavioural data on the response of dispersing voles, large-scale changes in land use as occurring in the plain of the Doubs are much more likely to act as absorbing boundaries than hard obstacles such as lakes. Tentalling support for the crucial role of the edge of the Jura plateaus is also provided by the fact that water vole outbreaks are altogether virtually absent beyond this obstacle (Giraudoux et al. 1997). In contrast, water vole cycles still occur in the Haute-Chaine of Jura Mountains and further to the south-east, beyond the lakes Neuchâtel and Biel, reportedly with a time lag of one year relative to our study area (Saucy 1988, 1994), hence consistent with the TW continuing its spread in a south-east direction. The strong correlation between local variations in synchrony’s delay and elevation slopes strongly supports a role for physical obstacles in shaping TW not only where they emerge but also where they spread. Indeed, abrupt changes in elevation that act as physical barriers to vole dispersal such as the Loue river valley (Berthier et al. 2005) tend to locally disorganise the synchrony pattern (Fig. 6). However, irrespective of their orientation they do not disrupt the larger scale demographic wave. The impact of these obstacles that are small relative to the scale of the demographic process is seemingly swamped by the rapid colonisation. These results highlight the importance of the size of the obstacles interfering with dispersal in generating a TW (Sherratt et al. 2003).

CONCLUSION

Our study provides empirical evidences consistent with theoretical expectations on TW emergence in ecological systems. First, the wave detected in the water vole, one of the larger reported to date, adds to the list of empirical examples supporting the theory that periodic TW solutions do occur in natural populations undergoing multi-year cycles (Lambin et al. 1998; Moss et al. 2000; Grenfell et al. 2001; Bjørnstad et al. 2002; Cummings et al. 2004; Johnson et al. 2004; Sherratt & Smith 2008; Tenow et al. 2013). Second, the wave we describe spreads as a linear front away from a major landscape obstacle oriented along a direction almost perfectly perpendicular to the wave propagation as predicted by recent theory (Sherratt & Smith 2008). Finally, we found some support for limited dispersal in the direction of the wave as expected to keep the spatial shift in population growth that characterise the TW (Sherratt et al. 2000; Vasseur & Fox 2009).

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AUTHORSHIP

KB analysed both demographic and genetic data. KB and XL wrote the manuscript. SP collated the environmental data, managed the GIS framework and analysed the data with KB. RD and DT provided the time series of vole abundance. JFC, PG and JCF contributed to the interpretation of the results and to the writing of the manuscript.

REFERENCES


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