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Changes in vole and lemming fluctuations in northern Sweden 1960–2008 revealed by fox dynamics

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Cyclic dynamics with extensive spatial synchrony has long been regarded as characteristic of key herbivores at high latitudes. This contrasts to recent reports of fading cycles in arvicoline rodents in boreal and alpine Fennoscandia. We investigate the spatio-temporal dynamics of boreal red fox and alpine arctic fox in Sweden as a proxy for the dynamics of their main prey, voles and Norwegian lemming, respectively. We analyse data from five decades, 1960–2008, with wavelets and autocorrelation approaches. Cyclic dynamics were identified with at least one method in all populations (arctic fox $n = 3$, red fox $n = 6$). The dynamics were synchronous between populations, or coupled with a 1-yr lag, in 8 of 13 pairwise comparisons. Importantly though, the dynamics were heterogeneous in space and time. All analytical approaches identified fading cycles in the three arctic fox populations and two northern red fox populations. At least one method identified similar patterns in three southern red fox populations. Red fox dynamics were cyclic in the 1970s primarily, while arctic fox dynamics was cyclic until the late 1980s or early 1990s. When cyclic, 4-yr cycles dominated in arctic fox and northern red fox, whilst 3–4-yr cycles was found in southern red foxes. Significant cyclic regimes reappeared in the 1990s or 2000s in two red fox populations and one arctic fox population. Cycles and regionally coupled dynamics appeared associated in northern arctic and red foxes. This study supports accumulating evidence which suggests that cyclic and synchronous patterns in the dynamics of lemmings and voles are nonstationary in space and time. Furthermore, the similar patterns of change in both fox species indicate that persistence of cycles is governed by similar mechanisms in lemmings and voles.

Introduction

Regular population fluctuations are a widespread pattern in animal populations (Kendall *et al.* 1998), and lemmings and voles are classical examples exhibiting cyclic dynamics (Elton 1942). Although pioneers in small mammal research compiled strong evidence for the existence of cycles (Johnsen 1929, Elton 1942, Hagen 1952, Wildhagen 1952), the mechanisms causing cycles remain an intensively debated topic (Graham & Lambin 2002, Korpimäki *et al.* 2005a, Lambin *et al.* 2006). Another debate concerns the link between temporal and spatial dynamics, particularly how large-scale spatial synchrony is connected to cyclicity (Ranta *et al.* 1998, Bjørnstad 2000). Recently, cycles have faded in boreal and alpine Fennoscandia with a breakdown of synchrony, and rodent cycles and the associated large-scale synchrony may be less robust than previously thought (Angerbjörn *et al.* 2001, Henden *et al.* 2009). When and where cyclicity is replaced by nonstationary dynamics could be the key to identify the drivers of cyclic dynamics (Ims *et al.* 2008). Loss of cycles and synchrony could lead to restructuring and regime shifts in northern ecosystems, where arvicoline rodents are key determinants of community dynamics (Ims & Fuglei 2005, Ims *et al.* 2008). This highlights a need for continuous documentation of spatio-temporal patterns in the dynamics of arvicoline rodents, where the possibility of nonstationary dynamics is taken into account.

Fennoscandian research on the dynamics of arvicoline rodents has a strong tradition of pattern analysis (Hanski *et al.* 2001). It has been concluded that the dynamics of voles and lemmings are cyclic with a latitudinal gradient in cycle length, increasing from 3 years in the south to 5 years in the north (Hansson & Henttonen 1985, Bjørnstad *et al.* 1995, Angerbjörn *et al.* 2001, Sundell *et al.* 2004). Another characteristic feature is large-scale synchrony in the dynamics, although northern populations sometimes lag behind southern ones (Myrberget 1973, Ranta & Kaitala 1997, Angerbjörn *et al.* 2001). However, analyses of historic data have shown that periods with strong cycles repeatedly have been interrupted by loss of cyclicity and synchrony (Steen *et al.* 1990, Angerbjörn *et al.* 2001, Henden *et al.* 2009). Hence, in contrast to early interpretations where cyclic patterns found primarily in 1970–1990 were regarded as the rule and later change as disruptions, nonstationary dynamics may be the norm in Fennoscandia (Henden *et al.* 2009). This indicates that previous descriptions of rodent dynamics need to be updated. In boreal Sweden for example, the last large-scale analysis of spatio-temporal patterns in vole dynamics comprised 1964–1980 and concluded that the dynamics were cyclic with a 3–4 year period (Angelstam *et al.* 1985). Furthermore, patterns of nonstationary dynamics in boreal voles and alpine lemmings have not yet been analysed separately and compared. Such comparisons would be interesting, because despite similarities in dynamics, it has been suggested that population cycles are driven by different interactions in boreal voles and alpine/tundra lemmings (Turchin *et al.* 2000, Oksanen *et al.* 2008).

Long-term research programmes on Fennoscandian rodents are typically based on intense sampling on a small spatial scale. The dynamics of predators which depend on rodents, such as birds of prey and foxes, have therefore been used as a substitute for the underlying rodent dynamics in investigations of large-scale spatial patterns (e.g. Angelstam *et al.* 1985, Sundell *et al.* 2004, Henden *et al.* 2009). In this study, we use the population fluctuations of boreal red fox *Vulpes vulpes* and alpine arctic fox *Vulpes lagopus* as proxy variables for vole and lemming dynamics respectively. Although the red fox is considered a generalist predator, food limitation governs red fox dynamics in boreal ecosystems where arvicoline voles constitute their main prey (Englund 1965, Angelstam *et al.* 1984). Hence there is a close relationship between vole abundance and red fox reproductive success, which causes the dynamics of the red fox to reflect that of voles (Englund 1970, Hörnfeldt *et al.* 1986, Lindström 1989). The arctic fox on the other hand, is a true specialist predator where reproductive success and population size closely tracks lemming abundance (Angerbjörn *et al.* 1995, Kaikusalo & Angerbjörn 1995, Strand *et al.* 1999, Elmhagen *et al.* 2000).

This paper provides a comprehensive update of the spatio-temporal dynamics of rodent-dependent foxes in Sweden in 1960–2008. We test the prediction that nonstationary patterns characterise the dynamics. Specifically, we test:

1. When the dynamics in each region were cyclic and the length of the cycle period.
2. If the dynamics in adjacent regions were coupled (synchronous or lagged) and if the degree of coupling was stationary over time.

We use autocorrelation and crosscorrelation

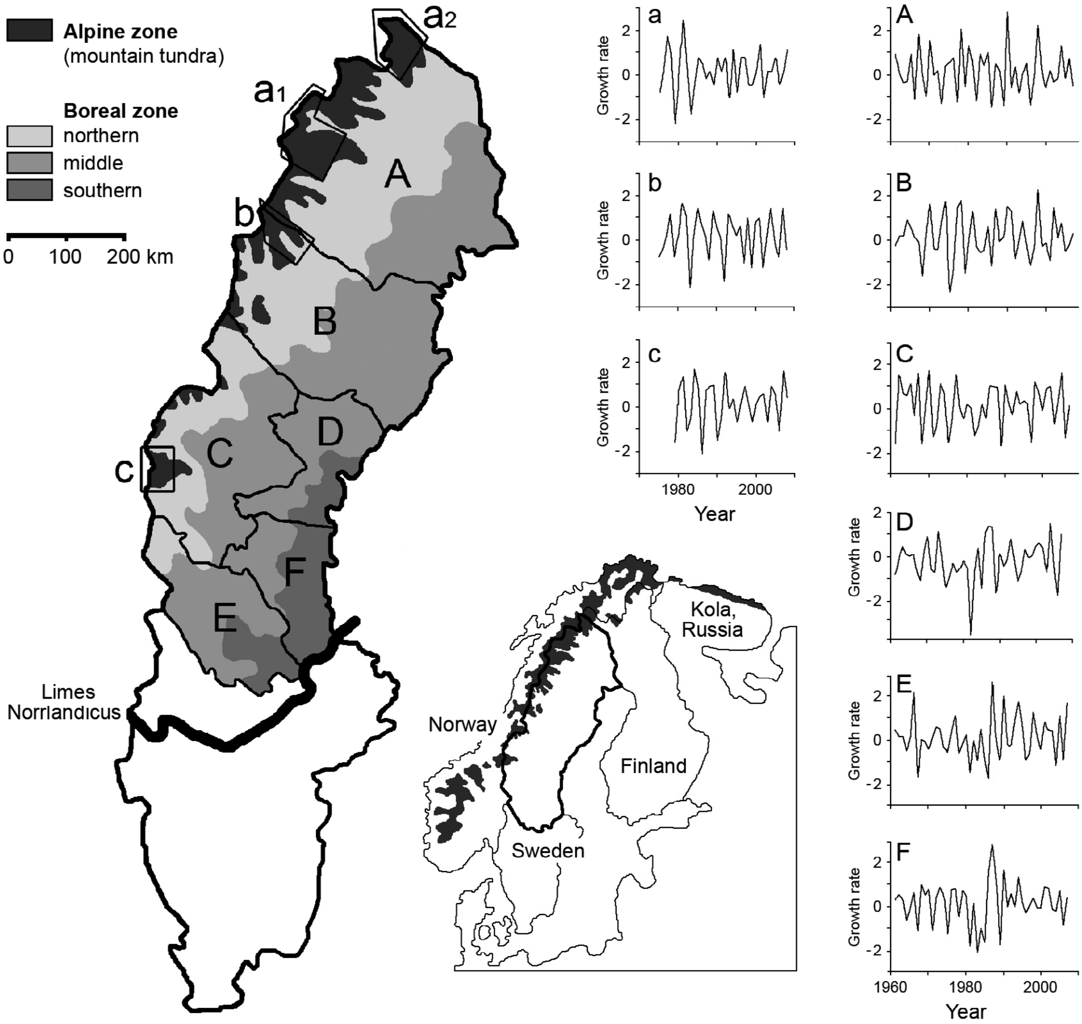

Fig. 1. The study area comprised the Swedish counties A–F, where previous studies found cyclic dynamics. These counties were located north of Limes Norrlandicus, a bioclimatic transition zone which separates the temperate south from the boreal north. The Fennoscandian mountain range runs south from the Arctic tundra in northern Norway and Kola and forms the alpine zone of mountain tundra habitat in north-western Sweden (small map). Red fox bag data were available for each of the counties A–F. Data on arctic fox reproduction were available for four areas; areas a_1 and a_2 in county A, area b in county B and area c in county C. The right panel shows, the dynamics as standardised growth rates over time for each species and region (CAPITAL letters = boreal red fox, small letters = alpine arctic fox).

approaches, as well as the more recently applied wavelet method. This allows us to directly compare our results with earlier studies, which have relied extensively on correlational analyses, but also to compare the outcomes of different methodologies. Furthermore, we analyse the dynamics of arctic and red foxes separately and thus indirectly compare patterns of change in lemming and voles respectively.

Material and methods

Study area

The data were collected from the boreal and alpine vegetation zones in Sweden, 60–70°N (Fig. 1). Temperate vegetation zones were not included because the southern limit of the boreal zone has been shown to coincide with the southern limit of cyclic dynamics in voles and foxes (Angelstam *et al*. 1985, Lindström 1989, Hanski *et al*. 1991).

The boreal zone extends north from Limes Norrlandicus, a distinct geomorphologic and climatic transition zone located approximately 60°N. The length of the snow season ranges from 125 days with snow cover in the south-east, to 200 days with snow cover in the north-west. The growing season is 110–190 days, being shortest in the north-west (averages for 1961–1990; Swedish Meteorological and Hydrological Institute 2011). The vegetation is dominated by coniferous Scots pine *Pinus sylvestris* and Norway spruce *Picea abies* forests.

The Fennoscandian mountain range in north-western Sweden forms the alpine zone, where a belt of birch *Betula* spp. forest separates a mountain tundra ecosystem from the boreal forest. Common vegetation types in the mountain tundra are dry heath, grass heath, meadow and dry fen. The mammal community includes characteristic tundra species such as Norwegian lemming *Lemmus lemmus*, reindeer *Rangifer tarandus* and the arctic fox. The ground is covered by snow 200–225 days, whilst the growing season is < 140 days (averages for 1961–1990; Swedish Meteorological and Hydrological Institute 2011).

Fox data

The data available for the two study species had been collected at different spatial scales with different methods. Arctic fox data were extracted from local surveys of breeding arctic foxes, whilst red fox data were compiled from large-scale records of hunting statistics.

The arctic fox is critically endangered in Scandinavia. Local surveys have therefore been carried out in arctic fox hot spots since the 1970s. Surveys were continued with the same methods but with increased effort and spatial coverage in 1998–2008 within SEFALO, an EU Life-Nature conservation project for the arctic fox (Angerbjörn *et al*. 2008). Arctic foxes use large conspicuous dens for breeding. Most den locations are known and den surveys in summer provide reliable data on the number of litters produced (Angerbjörn *et al*. 1995, Dalerum *et al*. 2002, Herfindal *et al*. 2010). There is a strong positive relationship, without time lag, between arctic fox reproductive success and lemming abundance (Angerbjörn *et al*. 1995, Strand *et al*. 1999). We therefore assumed that between summer changes in the number of arctic fox litters born would reflect changes in lemming abundance. Long term data were available from four areas, those where both local surveys and surveys within SEFALO had been carried out, but data from areas a_1 and a_2 were pooled since they showed the same pattern of between-year variation. The final data set comprised the number of arctic fox litters born in area a_{1+2} in 1974–2008, in area b in 1974–2008 and in area c, where surveys started somewhat later, in 1978–2008 (Fig. 1).

The Swedish Association for Hunting and Wildlife Management has compiled county-wise bag records for red foxes since 1960. The records are based on yearly reports from local hunters and hunting organisations, which state the number of foxes killed within specified areas each winter during the hunting season. The total bag for each county is extrapolated from the number of foxes killed in reported areas to the entire county, using the percent area cover by reports (e.g. Angelstam *et al*. 1985, Carlsson *et al*. 2010). We analysed the time series of red fox bags in boreal Sweden in winters 1960/1961–2007/2008 (county A–F; Fig. 1). There is no time lag between red fox reproductive success and vole abundance, which implies that there is a substantial increase in red fox abundance following summers of high vole abundance (Angelstam *et al*. 1985, Lindström 1989). Previous studies have also found a strong relationship between red fox bags and red fox abundance (Kurki *et al*. 1998, Forchhammer & Asferg 2000, Jarnemo & Liberg 2005). Hence we assumed that the number of red foxes shot in winter would reflect vole abundance in the preceding breeding season, i.e. in the summers 1960–2007. There are alpine areas with lemmings in county A, B and C, but we assumed this would not confound the result since red fox abundance is relatively low in alpine areas. In contrast to arctic foxes, alpine red foxes also establish at low altitudes where voles dominate over lemmings in their diet (Dalerum *et al*. 2002, Elmhagen *et al*. 2002, Killengreen *et al*. 2007).

Furthermore, a large part of the alpine habitat in county A–C is found within protected areas where hunting is often forbidden.

Statistical analyses

Using the classical approach to test if and when the dynamics in each region were cyclic, we calculated the autocorrelation function for (1) each full-length time series and (2) a sliding window, where the autocorrelation function was calculated for segments of each time series as a time window was moved forward with a time step of one year (Steen *et al*. 1990, Ranta *et al*. 1997). To test if and when the dynamics were coupled between regions, we calculated pairwise crosscorrelation functions for adjacent regions for (1) the full-length time series and (2) the sliding window. Both autocorrelation and crosscorrelation analyses require stationary time series. However, the arctic fox declined in the 1980s and 1990s due to low food availability and so did the number of recorded litters, despite increased search effort during SEFALO (Angerbjörn *et al*. 1995, Angerbjörn *et al*. 2008). Similarly, most red fox populations declined in the 1980s due to an epidemic of sarcoptic mange and increased during recovery in the 1990s (Carlsson *et al*. 2010). We, therefore, converted the time series to standardised growth rates before analyses, i.e. the time series were detrended by calculating first-differenced log-abundances, which was then standardised to zero mean and unit variance (Legendre & Legendre 1998, Bjørnstad *et al*. 1999) as follows:

$$r_t = \ln(\text{Count}_t + 1) - \ln(\text{Count}_{t-1} + 1) \quad (1)$$

The length of the time series should be at least four times that of the cycle period (Legendre & Legendre 1998). Hence we used segments of 21 years as the sliding window, which corresponds to 20 data points in a time-differenced time series. In the autocorrelation analyses, we extracted the coefficients for lags 3, 4 and 5 for each segment. However, lag 5 was never significant and we focus on lags 3 and 4 in the results. In the crosscorrelation analyses, coefficients for lags 0, –1, and +1 year were extracted. There was no indication that longer lags were important. Significant lags were identified with a 95% confidence interval (Legendre & Legendre 1998).

A wavelet analysis is particularly useful to locate sudden shifts in temporal dynamics (Cazelles *et al*. 2008). It has thus been applied to investigations of changing cyclicity in voles and lemmings (Saitoh *et al*. 2006, Kausrud *et al*. 2008, Brommer *et al*. 2010). We used a wavelet analysis to determine if and when the dynamics in each region were characterised by cyclic fluctuations. Cycle period was retrieved from the wavelet power spectrum. The analyses were performed on time series detrended in two alternative ways. First, by smoothing the original time series with a cubic regression spline (Wood 2006) where the residuals were used in the analyses. Second, for comparison, on the time series of standardised growth rates which also were used in the autocorrelation analyses. We used the Morlet wavelet as the mother wavelet to carry out the wavelet transform of the time series. From the wavelet transform, which can be regarded as a generalisation of the Fourier transform, we calculated the wavelet power spectrum which estimates the variance distribution for a given time point and scale. Significance of the wavelet spectrum was evaluated with a pointwise test (Torrence & Compo 1998, Maraun *et al*. 2007), assuming a red noise background spectrum as the null hypothesis. The critical values for the pointwise test were determined by 1000 Monte Carlo-simulations. In the wavelet analysis, the time series is extended with zero padding towards both ends in order to avoid ‘wrap around’ effects, creating edge effects in the wavelet transform. The region where edge effects are present is known as the cone of influence. Outside this cone, interpretation should be made with caution.

All analyses were carried out in R ver. 2.11.1 (R Development Core Team 2010). The wavelet analysis was performed with the R-package sowas (Maraun & Kurths 2004, Maraun *et al*. 2007).

Results

As predicted, the dynamics were nonstationary in all study populations. The different analytical approaches produced very consistent results for five of the six north-western populations, arctic fox in areas a–c and red fox in counties B–C, which all where characterised by fading cycles. The autocorrelation function for the full-length time series identified significant (a, c, B) or close to significant (b, C) cycles, with a dominant periodicity of four years in arctic fox a–c and red fox B, but three years in red fox C (Fig. 2; a–c, B–C). The time-variant analyses showed that cyclic dynamics did not persist through time. Both sliding window and wavelets identified fading 4-yr cycles in arctic fox a–c and red fox B. In red fox C, wavelets identified fading 3–4-yr cycles, while the sliding window found a similar tendency. Hence, cyclic dynamics were identified in the 1970s and/or early 1980s in all five populations. The cycles faded in red fox B–C around 1980, while cycles persisted in arctic fox a–c until 1985–1990 (Fig. 2; a–c, B–C).

The dynamics of red fox A and D–F were also nonstationary but the analyses produced slightly different results. The autocorrelation function for the full-length time series found strong, but not significant, 3-yr periodicity in D and E (Fig. 2; D–E). The wavelet analyses suggested that there were periods with significant cycles in all populations, but the pattern was complicated by double periodic components, primarily at 3–4 and 7–8 years (Fig. 2; A, D–F). Wavelets on residuals identified 3–4-yr cycles in the 1960s or 1970s in D–F which then faded. In D, the sliding window supported this result as there was a weak tendency for 3–4-yr cycles in the 1970s. However, wavelets on standardised growth rates found regions with 3–4-yr cycles both in the 1970s and 1980s (Fig. 2; D). In E, the sliding window and wavelets on standardised growth rates identified significant 3-yr cycles only in the middle of the study period (Fig. 2; E). In F, wavelets on standardised growth rates found 3–4-yr cycles in the 1980s, while the sliding window failed to identify cyclic dynamics (Fig. 2; F). In A, wavelets on standardised growth rates identified a short period of 4-yr cycles in the early 1970s and the 1990s, but this result was not supported by the other analyses.

In addition to fading cycles, we found some evidence for local returns to cyclic dynamics in the late 1990s. Both the sliding window and wavelets on standardised growth rates identified a reappearance of significant 4-year cycles in red fox B, and wavelets on standardised growth rates identified significant 3-yr cycles in D. This can be compared to the arctic fox in b where wavelets on standardised growth rates also found significant 3-yr cycles (Fig. 2; b, B, D). Similar patterns in the 2000s were a tendency towards 3-yr cycles in c and C (Fig. 2; c, C).

Pair-wise crosscorrelation between adjacent regions showed that the fox dynamics were significantly coupled for 8 of 13 pairs when the full-length time series were considered. The dynamics tended to be coupled for an additional 3 pairs. However, the sliding window showed that the strength of coupling generally changed over time (Fig. 3). Four patterns could be discerned.

I. In the north, significant coupling (synchrony or 1-yr lags) was found primarily in the early part of the study period when the dynamics were cyclic. This was the case for pairs of arctic fox populations (a–b, b–c), the three pairs of northern red fox populations (A–B, B–C and B–D) and for arctic and red foxes in county B (b–B).
II. In the south, red fox populations showed coupled dynamics throughout the study period, although shifts between synchrony and 1-yr lags occured (continuous synchrony: C–D, E–F; shifts between lagged dynamics and synchrony: C–E, C–F, D–F).
III. Synchrony was the more common form of coupling in both the full-length time series and the sliding window. However, when 1-yr lags occurred, it was always the dynamics of the northern county that lagged behind.
IV. In the later part of study, red fox dynamics were characterised by two large areas with synchronous dynamics, A–B and C–F (Fig. 3).

Discussion

We used the population dynamics of arctic and red foxes as a proxy for fluctuations in alpine lemmings and boreal voles over the last 35–48 years. The results support studies that have demonstrated that cycles and large-scale synchrony are not persistent patterns (e.g. Ranta *et al*. 1997,

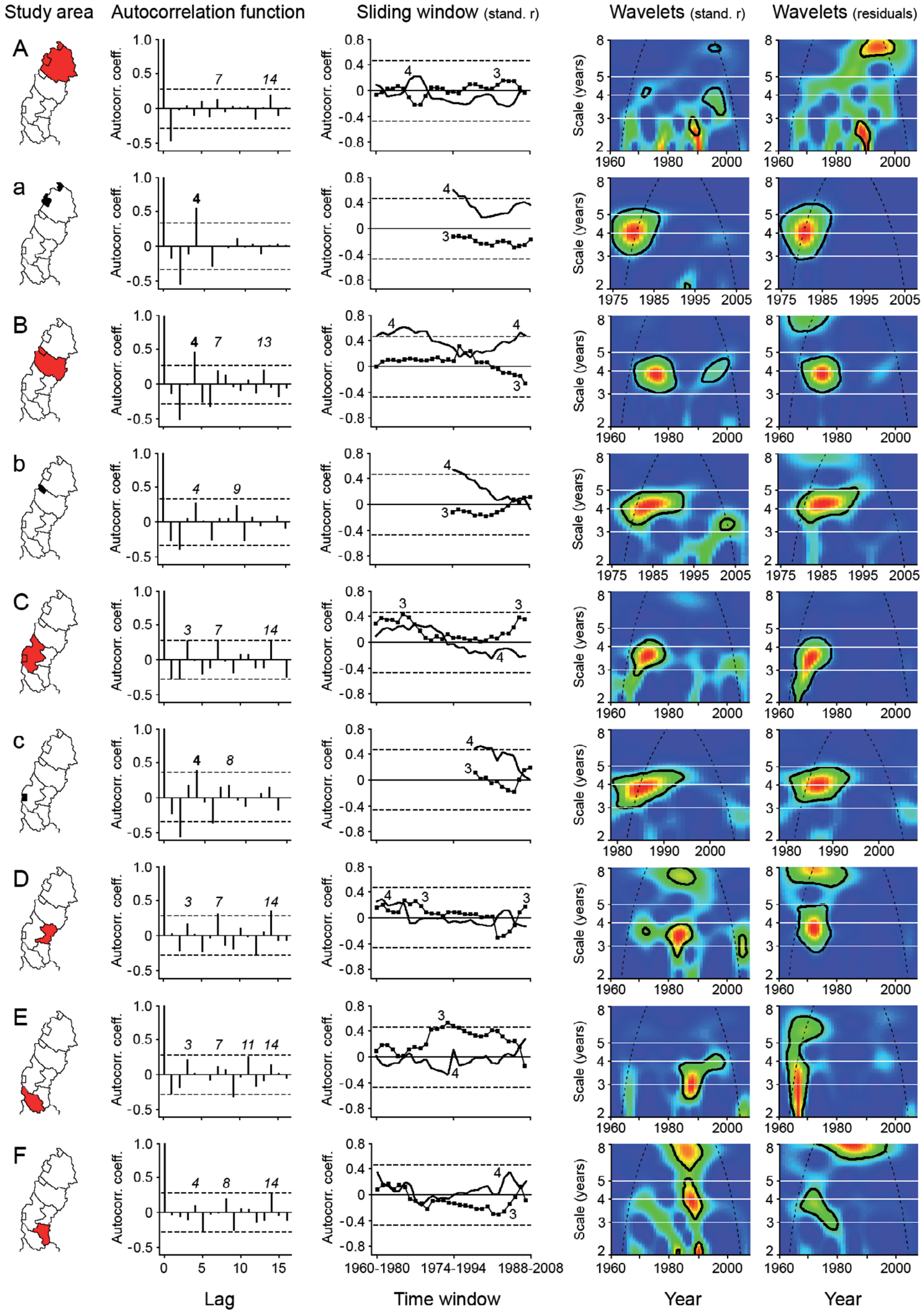

Fig. 2. Patterns in the dynamics of arctic fox in areas a–c (black) and red fox in counties A–F (red). The autocorrelation function shows the dominant periodicity for each full-length time series. Numbers in italics denote strong positive lags, while significant lags are set in boldface (95% CI). The sliding window shows the autocorrelation for lags 3 and 4 for a sliding 20-yr period, using time series of standardised growth rates. The wavelet results shown are for time series detrended by two different methods: standardised growth rates and residuals. The wavelet power spectrum identifies points in time with significant periodicity. The spectral power increases from blue to red and significant regions are bordered by black lines. The scale shows cycle period. Towards both ends of the spectrum is the cone of influence, outside which interpretation should be made with caution. Note the different scales on the *x*-axis (time) in the wavelet periodograms.

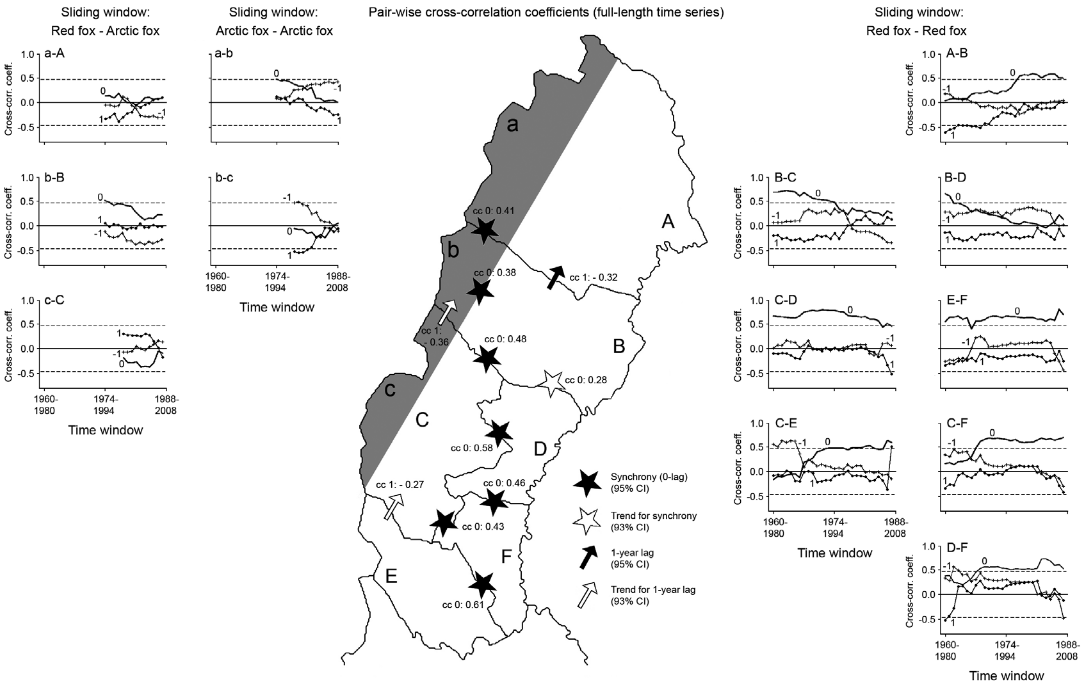

Fig. 3. Pairwise crosscorrelations between adjacent populations. Significant crosscorrelation coefficients for the full-length time series are shown in the map, where stars denote synchrony and arrows denote 1-yr lags. The arrows point the county that lags behind. The small figures show sliding window results for lags 0, –1 and 1 for each pair. Dashed lines mark the 95% confidence intervals. In all cases where there were significant lags of 1 year, the northern population lagged behind. This direction is indicated by a significant positive crosscorrelation for –1 years and/or a significant negative crosscorrelation for 1 year.

1998, Bjørnstad 2000). Our analyses further showed that northern fox populations generally displayed similar dynamics. Arctic fox dynamics were characterised by fading 4-yr cycles in the early part of the study period. Towards the end of the study period cycles or cyclic tendencies reappeared in two of the three arctic fox populations. Likewise, red fox dynamics were generally characterised by 3–4-yr cycles in the 1970s. The cycles then disappeared, to reappear locally in the late 1990s and 2000s. Both alpine and boreal dynamics were also characterised by changing patterns of coupled dynamics, which involved both synchrony and one-year lags of northern populations. Thus, just as Henden *et al.* (2009) found that patterns in fox, and hence rodent, dynamics in Norway changed continuously in the period 1880–1976, change was a characteristic feature of the spatio-temporal dynamics of arctic and red foxes in Sweden in 1960–2008. The observed spatio-temporal heterogeneity in Sweden also agrees with observations of locally retained or reappearing cycles in Norway and Finland in the 1980s–2000s, when the general perception was that the rodent cycle had faded (Strann *et al.* 2002, Huitu *et al.* 2009).

We chose to use a combination of methods in the analyses to be able to directly compare patterns with earlier studies. Autocorrelation and crosscorrelation have been used extensively in previous studies of lemming, vole and fox dynamics in northern Sweden (Angelstam *et al.* 1985, Small *et al.* 1993, Hörnfeldt 1994, Angerbjörn *et al.* 1995, Angerbjörn *et al.* 2001). However, our sliding window analysis suggested that this cyclic dynamics was characteristic of only a relatively short period in the 1970s and 1980s. Consequently, a time-varying approach to time series analysis should be preferred when possible. The sliding window approach reveals non-stationary dynamics as a gradual change in the correlation coefficient for a particular lag, which creates a wave-like pattern as the time window slides along the time series (Ranta *et al.* 1997;

this study, Fig. 3). The approach is robust against changes in the length of the time window as well as changes in the length of the time step by which the window is moved (Cooke *et al*. 1998). The sliding window results also conformed well to wavelet analyses, independent of data treatment. It was only in the southernmost red fox populations that the different analytical approaches produced somewhat different results (discussed below). Thus our main result, the general pattern of fading cycles in alpine and boreal regions in north-western Sweden, appears robust.

We analysed red fox data at the county-level, the lowest level available to us, assuming that the dynamics were synchronous within counties. Previous studies support that population fluctuations in foxes and rodents are synchronised at spatial distances up to 500–1000 km (Lambin *et al*. 2006, Henden *et al*. 2009). Nevertheless, we failed to identify consistent patterns of periodic fluctuations in the largest county A, although cyclic rodent fluctuations were identified by monitoring in the 1970s (Andersson & Jonasson 1986, Bjärvall & Lindström 1991). At the time however, rodents in the western part of the county lagged one year behind the eastern part (compare data in e.g. Nilsson 1981, Andersson & Jonasson 1986, Hipkiss *et al*. 2008). Hence, local variation in dynamics within county A may have kept us from finding evidence for the periodic signals that could be expected at least in the 1970s. Thus, aggregation of population processes over too large areas can erode periodic signals in the data due to mixing of asynchronous local populations (Lindström *et al*. 1997).

Cycles of seven years for rodents and their predators have been interpreted as a methodological artefact caused by a mix of 3–4-yr cycles of varying peak amplitude (Framstad *et al*. 1993, Hellstedt *et al*. 2006). We found similar patterns with autocorrelation, i.e. significant or strong 7 and 14-yr lags in boreal C, D and F. In C and D, the autocorrelation was strong for both lag 3 and 4 in the early part of the study period when wavelet analyses on residuals found cycles with a 3–4-yr period, which indeed suggests a mix of 3–4-yr periods. In our study, the mange epidemic may have contributed to the appearance of 7-yr cycles, since the epidemic in the 1980s caused marked short-term changes in the amplitude of the time series which were not completely removed by detrending, as revealed by double periodicities in some wavelet peridograms. The dynamics of predators such as both fox species are thus not determined solely by rodent abundance in a simple bottom-up fashion, but are also modified by interactions with e.g. parasites, alternative prey and humans (primarily through changes in land use and hunting). Although several studies have showed that there generally is a close relationship between variation in red fox hunting bags and red fox dynamics (Kurki *et al*. 1998, Forchhammer & Asferg 2000, Jarnemo & Liberg 2005), both hunting effort (numerical response) and efficiency (functional response) of hunters may decline when red fox abundance decreases. During a cyclic regime, varying hunting effort is expected to amplify the amplitude in furbearer bag statistics (e.g. Royama 1992), but if mean fox abundance decreases (e.g. following an epidemic) hunting effort could decrease to an extent where fluctations in the fox population is no longer reflected in the number of red foxes killed. A challenge for future monitoring and theoretical work is therefore to separete process variance (fox dynamics) from observation variance (functional and numerical responses of hunters) by developing e.g. state-space models.

Despite potential shortcomings of using bags statistics as a proxy for the dynamics of voles, the available long-term studies of small rodent dynamics in northern Sweden support our general conclusion of fading cycles in boreal vole populations in county B and C in the 1980s and/or 1990s (Hansson 2002, Hörnfeldt 2004). Further, for alpine habitat, a qualitative assessment confirm an absence of high amplitude lemming peaks in the late 1980s and 1990s (Angerbjörn *et al*. 2001) and a trapping study which started in 1995 did not find cyclic peaks in the 1990s (Ecke *et al*. 2010). The 'disturbed dynamics' observed in voles and lemmings in Fennoscandia in the 1980s and 1990s has involved increased seasonality at the expense of cyclicity, a greater irregularity in period length, a higher occurrence of short increase phases and a decrease in cycle amplitude (Hanski *et al*. 1993, Hanski & Henttonen 1996, Oksanen & Henttonen 1996, Angerbjörn *et al*. 2001, Hörnfeldt 2004, Kausrud *et al*. 2008). In this study, we focused on the presence and disappearance of periodic components in the time series. The dynamics of the two fox species shared the same characteristics and nonstationary properties, which strongly suggests that the dynamics of lemmings and boreal voles changed similarly over time. Several lines of evidence suggest that a strong predator–prey interaction with small mustelids causes cycles in Fennoscandian voles (Hanski *et al*. 2001). However, the 'specialist predator hypothesis' has not received general support as an explanation for vole cycles outside Fennoscandia (Graham & Lambin 2002). Neither has it become generally supported as an explanation for lemming cycles in Fennoscandia, where available long-term data support a dominant lemming-plant interaction (Turchin *et al*. 2000, Oksanen *et al*. 2008). However, a recent study from northern Norway suggests that lemming outbreaks are caused by the ability of lemmings to breed in winter and also by apparent mutualism with voles (Ims *et al*. 2011). Although different mechanisms may be involved in the generation of vole and lemming cycles, persistence of cycles over vast areas is therefore likely a community process governed by a similar set of factors independent of species. Our findings of similar dynamics in boreal and alpine regions during the 1970s, and then a concentrated disappearance of cycles over large parts of northern Sweden, support this view. We thus agree with Lambin *et al*. (2006) that "common explanations should be sought for common patterns unless clear ecological differences are demonstrated".

Both direct and delayed density dependence are necessary to generate cycles (Stenseth 1999), but density-dependent factors can interact with or become subordinate to stochastic perturbations and environmental trends. Along this line, several hypotheses have been put forward to explain the disrupted dynamics in the 1980s and 1990s (reviewed by Hörnfeldt 2004). One hypothesis that pertains to cyclic dynamics in general is that periodic disruptions are inherent to stochastic predator–multiprey communities (Hanski & Henttonen 1996). An alternative hypothesis with growing support is 'climate forcing' (Ims & Fuglei 2005, Ims *et al*. 2008). Changes in winter conditions, e.g. the quality of the snow cover, could interfere with the interactions between rodents and their predators (Kausrud *et al*. 2008, Gilg *et al*. 2009) or limit access to food due to ice crust formation (Korslund & Steen 2006), thereby effectively reducing overwinter survival (Aars & Ims 2002).

Regardless of the mechanisms causing fading cycles, available data sets reveal that rodent dynamics in Fennoscandia changed differently over the past 15 years. For instance, high-amplitude vole cycles persisted in northern Norway (Strann *et al*. 2002, Oksanen *et al*. 2008), whereas vole cycles faded and returned in southern Finland (Brommer *et al*. 2010) and along the Swedish mountain range (Ecke *et al*. 2010). We reviewed 13 data sets longer than 14 years and published during the last 13 years. Ten of these data sets showed signs of weaker periodic components, where loss of periodicity in dynamics is typically associated with amplitude dampening (Table 1). Loss of cyclicity also often resulted in loss of geographic as well as inter-specific synchrony in fluctuations, and consequently marked changes in species composition have been observed at several locations. Although recent trends are difficult to analyse as they are located towards the end of the time series (leading to weaker inference), we also found support for a recent shift towards periodic fluctuations with a 4-yr cycle in boreal B and a 3-yr cycle in alpine b. Likewise, we found recent tendencies for a 3-yr cycle in boreal C, D and alpine c. This could be an early indication of another marked change in dynamics, similar to that described by e.g. Brommer *et al*. (2010) in southern Finland, and we suggest that rodent dynamics over much of northern Sweden is in a transient phase. Contrasting experimental studies combined with well-designed monitoring of local changes in ecosystem structure and climate should therefore provide a key to understand the spatio-temporal heterogeneity and nonstationary patterns in Fennoscandian rodent dynamics.

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Table 1. Summary of available recent long-term data sets (duration ≥ 14 years) for voles and lemmings in Fennoscandia. Only published data sources (to 2010) have been included here although several of these time series are continuously updated. Studied species: BV = bank vole (*Myodes glareolus*), GV = grey sided vole (*Myodes rufocanus*), RV = red vole (*Myodes rutilus*), FV = field vole (*Microtus agrestis*), TV = tundra vole (*Microtus oeconomus*), WV = water vole (*Arvicola terrestris*), and NL = Norwegian lemming (*Lemmus lemmus*). Habitat: F = forested areas, M = mountain tundra, A = agricultural land. Changes in rodent dynamics were evaluated for four characteristics associated with cycles; periodicity, amplitude, synchrony (in this case both intra- and interspecific), and changes in species composition. A minus sign (–) indicates decreases in periodicity, amplitude or synchrony, whereas a plus sign (+) indicates return of periodicity, increasing amplitude of fluctuations, higher synchrony and changes in species dominance or composition of the rodent community. –/+ indicates first loss, then return of periodicity and/or synchrony. If no clear trend was detected in the four time series characteristics, this is indicated by “0”. “?” means that this aspect was not considered/studied by the authors of respective reference.

Reference	Study species	Study area	Habitat	Time span	*N* years	Periodicity	Amplitude	Synchrony	Composition
Brommer *et al.* 2010	BV, FV	Heinola & Kirkonummi, Finland	F/A	1986/1981–2008	23/28	–/+	0	–/+	+
Ecke *et al.* 2010	GV	Ammarnäs, Sweden	M/F	1995–2008	14	+	+	?	?
Hansson 2002	BV, FV	South-central & northern Sweden	F/A	1971–2000	30	–/+	–	?	?
Henttonen & Wallgren 2000	GV, RV, FV, NL	Kilpisjärvi, Finland	M/F	1949–1999	51	–	–	–	+
Henttonen & Wallgren 2000	BV, GV, FV	Pallasjärvi, Finland	F	1971–1995	25	–	–	–	+
Hörnfeldt 2004	BV, GV, FV	Vindeln, Umeå	F	1971–2002	32	–	–	?	+
Kausrud *et al.* 2008	NL	Finse, Norway	M	1970–2007	38	–	–	–	?
Kausrud *et al.* 2008	Voles	Finse, Norway	M	1970–2007	38	–/+	–	–	?
Korpimäki *et al.* 2005b	MV, BV, WV	Kauhava/Lapua, Finland	A	1977–2003	27	0	0	0	0
Olofsson *et al.* 2009	Voles	Iesjávri/Joatka, Norway	M/F	1977–2006	30	0	–	?	?
Oksanen *et al.* 2008	NL	Porsanger, Norway	M	1977–2006	30	–	–	?	?
Solonen & Ahola 2010	BV, FV	Lohja & Kirkonummi, Finland	F/A	1981–2006	26	–	–	–	+
Strann *et al.* 2002	GV, RV, FV, TV, NL	Kirkesdalen, Norway	M/F	1985–1998	14	0	0	?	0

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