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Title: Temporal Dynamics of Bird Community Composition: an Analysis of Baseline Conditions from Long-term Data

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Abstract

Numerous anthropogenic activities threaten the biodiversity on earth. Because all ecological communities constantly experience temporal turnover due to natural processes, it is important to distinguish between change due to anthropogenic impact and the underlying natural rate of change. In this study, we used data sets on breeding bird communities that covered at least 20 consecutive years, from a variety of terrestrial ecosystems, to address two main questions: (1) How fast does the composition of bird communities change over time and can we identify a baseline of natural change that distinguishes primeval systems from systems experiencing varying degree of human impact? (2) How do patterns of temporal variation in composition vary among bird communities in ecosystems with different anthropogenic impact? Time lag analysis (TLA) showed a pattern of increasing rate of temporal compositional change from large-scale primeval systems to disturbed and protected systems to distinctly successional systems. TLA slopes of <0.04 were typical for breeding bird communities with natural turnover, while communities subjected to anthropogenic impact were characterised by TLA slopes of >0.04. Most of the temporal variability of breeding bird communities was explained by slow changes occurring over decades, regardless of the intensity of human impact. In most of the time series, medium and short-wave periodicity was not detected, with the exception of breeding bird communities subjected to periodic pulses (e.g. caterpillar outbreaks causing food resource peaks).

Keywords. Community dynamics; Long-term datasets; Periodicity; Primeval forests; Time lag analysis; Time series
Introduction

We live in a rapidly changing world. Numerous anthropogenic activities such as habitat destruction, habitat fragmentation, landscape change, overharvesting, spread of invasive species, pollution, soil erosion and global climate change threaten the biodiversity on earth (Pereira et al. 2010; Sodhi and Ehrlich 2010; Dawson et al. 2011). The detection of the influence of external factors on ecological communities is hampered, however, by the limited information on their natural background rates of change (Magurran et al. 2010). Because all ecological communities constantly experience temporal turnover, we need to know their natural rate of change to be able to identify and evaluate the change that is due to anthropogenic impact. Long-term datasets (LTDS) are indispensable resources for the determination of baselines against which on-going and future community change can be evaluated. Although there exist some well known LTDS with time series of up two almost 150 years (Magurran et al. 2010), the collection of LTDS has received only limited attention. This may possibly be attributed to a general monitoring “phobia” in ecology, noted as early as the 1980s by Franklin (1989). Also, Wiens (1989) commented that long-term studies are often not encouraged by contemporary views of scientific productivity or research funding policies. In the light of environmental problems such as climate change, this attitude is changing, and there is now wider acknowledgement for the need of high-quality, question-driven, statistically-designed monitoring (Collins 2001; Legg and Nagy 2010; Lindenmayer and Likens 2010). There are now many LTDS available on traditionally well-studied communities of short-lived organisms, e.g. phytoplankton and aquatic invertebrates (Korhonen et al. 2010). However, there are few LTDS on the community level of long-lived terrestrial animals, even for well-studied groups such as birds. This is because monitoring efforts have been focussed
on single species or small groups of species, under the assumption that they were adequate indicators of some given environmental change (Lindenmayer and Likens 2010).

Thanks to the foresight of a few pioneering ornithologists, though, there are some LTDS of breeding bird communities that extend several decades, for example, the work of Kendeigh (1982) that commenced as early as in 1934 (Illinois, USA, 43 years), and of Enemar (1966), who in 1953 started the monitoring of a passerine breeding bird community in the South of Sweden (continued until today, Enemar et al. 1994; Svensson et al. 2010). Other LTDS include the bird monitoring in the Hubbard Brook Experimental Forest in New Hampshire, USA (initiated in 1969, Holmes and Sherry 2001; Holmes 2011), and the long-term study of bird community dynamics in the primeval temperate forest of the Białowieża National Park in Poland (since 1975, Wesołowski et al. 2010). Some LTDS have been published in less widely available journals (e.g., Jansen and de Nie 1986, Dutch cultivated mixed forest, 1951 to 1981) or even “hidden” in only locally available journals of ornithological societies (e.g., Sanders et al. 2001, 20-year study in a Dutch recreational forest). Together, these LTDS cover a wide variety from habitats from primeval to successional and heavily managed ecosystems, mainly forests.

The apparent compositional stability of breeding bird communities has been repeatedly reported. These observations stem from extensive primeval ecosystems of hundreds of square kilometres (temperate primeval forest, Wesołowski et al. 2010; Scandinavian alpine vegetation, Svensson 2006), but also from much smaller stands of protected forests (Beven 1976; Enemar et al. 1994). The idea that the study of primeval ecosystems may provide benchmark data for the comparison with man-made systems is not new and the decision to
start the monitoring programme in the Białowieża National Park, for example, was specifically based on that objective (Tomiałojć et al. 1984).

In this study, we used LTDS on bird communities from a variety of terrestrial ecosystems to address two main questions: First, we asked: how fast do the compositions of bird communities change over time and can we identify a baseline of natural change that distinguishes primeval systems from systems experiencing more human impact? For these analyses, we determined the rate of compositional change by means of time lag analysis (TLA), a distance-based method for measuring community dissimilarity between years and regressing it on increasing time-lags (Collins et al. 2000; Kampichler and van der Jeugd 2013). The advantage of this method is its computational simplicity and its output of a single statistic—the regression slope, a measure indicating the rate of compositional change through time—which can be easily compared among communities.

The second question was: how do patterns of temporal variation in composition vary among bird communities in ecosystems with different anthropogenic impact? The many ecological processes that take place over longer time periods, including slow processes, rare events, episodic phenomena, processes with high annual variability, subtle processes and complex phenomena (Franklin 1989), leave signals at different temporal frequencies. We accounted for such non-linear dynamics using a method referred to as redundancy analysis with principal coordinates of neighbour matrices (RDA-PCNM) (Borcard and Legendre 2002; Borcard et al. 2004). This method was originally designed for all-scale analysis of spatial patterns, but can also successfully be applied in time series modelling to identify ecological patterns and processes at different temporal scales and the taxa that contribute to these patterns (Angeler et
We hypothesised that breeding bird communities in large-scale primeval systems would exhibit slow compositional change with a slope of close to (but significantly different from) zero, while those in other systems (disturbed, managed, or small-scale; here, for the ease of communication simply called disturbed) would show steeper slopes, indicating faster change relative to the primeval systems. The rationale for this hypothesis is that the causes of compositional change in primeval systems are due to a combination of neutral processes such as demographic stochasticity (Hubbell 2001) and responses to slow changing environmental variables that are extrinsic to the ecosystem (e.g., climatic conditions). Assuming that disturbed sites are equally influenced by extrinsic factors as primeval systems, any observed higher rates of community turnover there can be attributed to factors that influence communities locally. These local factors may comprise management interventions or local disturbance regimes or—in the case of small patches—landscape effects of the surrounding matrix. Small and isolated ecosystems can be expected to show higher turnover rates due to frequent stochastic extinction and recolonisation events. Regarding non-linear dynamics, we expected temporal variation to be low-frequent (slow changes lasting over many years) in primeval systems, tracking essentially broad-scale environmental variability. In disturbed systems, these dynamics are expected to be high-frequent (rapid changes occurring within a few years); that is, short term changes are due to management measures or forest succession and a generally higher level of anthropogenic disturbance. By distinguishing the community composition dynamics in primeval systems from other systems, we attempted to identify a natural change baseline, based on linear and non-linear patterns, against which observed community change can be integrally judged. Given (i) our interest in detecting general
patterns rather than in identifying the identity of the species responsible for the pattern on a
given site, and (ii) the heterogeneity of available LTDS stemming from various ecosystem
types and even from different continents and thus housing taxonomically different bird
assemblages, no emphasis was laid on species-specific analysis; such analyses are reserved
for in-depth studies of single LTDS.

Methods

Data origin

We searched national and international journals intending to identify all in-depth studies that
met our criteria, i.e., that reported breeding bird abundances from relatively small and well-
defined study plots that had been surveyed for a period of at least 20 consecutive years and
where sampling effort had been standardised and kept constant over time. We did not aim to
detect all grey data sources (such as files of local ornithological societies or articles published
in local newsletters), but added a few additional papers from Dutch regional and local journals
as well as an unpublished Dutch LTDS that were easily accessible to us. Large-scale surveys
such as the Breeding Bird Survey of North America (Sauer et al. 2008) were not included
since they are much wider scale and yield only indices to relative abundances for each species
rather than abundance estimates. In total, we found 15 studies reporting long-term breeding
bird data from 24 study plots. All but two studies in the far north of Sweden were performed
in the temperate zone of the northern hemisphere. The majority of studies (11) report LTDS
from forests (four in the USA, two each in Sweden and the Netherlands, one each in the UK,
Poland and Estonia), two from treeless islands (both in the UK), and one each from alpine
vegetation (Sweden) and coastal dunes (Netherlands). Their characteristics are summarized in Table 1 (see Online Resource 1 for more detailed descriptions of the studied systems). For the majority of LTDS bird abundance was determined by territory mapping. Exceptions are the forests of the Gaisatj and Valle Mountains in Sweden (combination of territory mapping and line transects, Enemar et al. 2004), the Mastbos forest (combination of territory mapping and maximum score method, Jansen and de Nie 1986), and the forest at Gaudineer Knob (repeated transect counts, Hall 1984). Bird abundance measures (number of territories in almost all cases) were obtained directly from the published material (Robert Allerton Park and William Trelease Wood, Kendeigh 1982; Bookham Common, Beven 1976; Farne Islands, Diamond and May 1977; Gaudineer Knob, Hall 1984; Skokholm Island, Lack 1969), through contact with the data holders (Hoekelum Manor, Sanders et al. 2001; Mastbos, Jansen and de Nie 1986; Meijendel) or were contributed by the authors of this paper. In the few cases where data were missing in the time series, these were imputed by species-specific median values or were interpolated by linear or quadratic models when such distinct abundance trends were apparent.

**Time lag analysis (TLA)**

In TLA, community dissimilarity is regressed on increasing time lags (one-year lags, two-year lags, three-year lags, etc.) (Collins 2001). To prevent the smaller number of data points of larger time lags from biasing the result, the time lags were square root transformed. The regression slope is not significant when the relative abundances of the constituent species vary around a constant value over time or when the species abundances vary randomly and without temporal autocorrelation (Kampichler and van der Jeugd 2013). Significant positive slopes indicate communities that veer away from their original state, either directionally driven by
internal or external factors or due to autocorrelated stochastic variability. Significant negative slopes indicate convergent behaviour, e.g. the return of the community to an earlier state in the time series. The absolute slope values characterise the rate of community change or convergence.

For each LTDS, we transformed abundance data according to the Hellinger transformation proposed by Legendre and Gallagher (2001),

\[ N'_{ij} = \sqrt{\frac{N_{ij}}{\Sigma N_i}} \]

where \( N_{ij} \) is the population size of species \( i \) in year \( j \), and \( \Sigma N_i \) is the sum of individuals across all species in year \( j \). Next, the Hellinger distances, i.e., the Euclidean distances of Hellinger transformed data, for all possible pairs of years of a time series are calculated. The application of Hellinger distance as dissimilarity measure distance in TLA has the following advantages: first, it makes assemblages directly comparable independent of their species richness and abundance of their constituent species, thus controlling for sampling variability between studies; second, it can disentangle compositional change (in which we are interested here) from numerical changes (Kampichler and van der Jeugd 2013). Since a time series of length \( n \) yields \((n^2 - n)/2\) pairwise distance measures, the number of degrees of freedom is heavily inflated and the data points are not independent, which impedes the use of the variance for significance determination. We thus followed the suggestion of Thibault et al. (2004) and determined the significance of the slope by a Monte Carlo permutation procedure. We randomly shuffled the positions of the year columns in the species x year matrix 10,000 times and calculated the error probability as the number of slopes larger than the observed slope divided by 10,000. As a measure of year-to-year variability we used the mean of the \( n - 1 \)
Hellinger distances measured at lag 1.

Redundancy analysis with principal coordinates of neighbourhood matrices (RDA-PCNM)

The RDA-PCNM (Borcard and Legendre 2002; Borcard et al. 2004) is a multivariate time series modelling approach that decomposes the overall temporal structure of communities into independent patterns shown by different groups of species that comprise a community (Angeler et al. 2009, 2011). The method is based on Redundancy Analysis (RDA), where time is modelled with a Principal Coordinate of Neighborhood Matrices (PCNM) approach. In a first step, the analysis converts a time vector comprised of n years in a series of PCNM variables akin to a Fourier transform; that is, a number of different sine waves with different temporal frequencies is obtained through conversion of a single variable (i.e., the time vector). The number of PCNM variables depends on the length of the time vector and equals 2n/3. Their wavelengths range from n+1 to 3 years. Through a forward selection procedure, these PCNMs are related to the community data sets by means of RDA. The RDA retains significant PCNM variables, and these are linearly combined in ways to extract temporal patterns from the species x time matrices of each community; that is, the RDA identifies species with similar temporal patterns in the species x time matrix and uses their temporal pattern to calculate a modelled species group trend for these species based on linearly combined PCNMs. The significance of the temporal patterns of all modelled species groups revealed by the RDA is tested by means of permutation tests. The temporal patterns and frequency structure that can be discerned have upper bounds set by the limit of the temporal extent of the data series, and lower bounds set by the frequency of sample collection.
The RDA relates each modelled species group trend with a significant canonical axis. It generates linear combination (lc) score plots, which visually present the modelled temporal patterns of species groups that are associated with each canonical axis. Based on the number of significant canonical axes, the number of modelled species groups with different temporal patterns can be deduced. The ecological relevance of these temporal patterns can be quantified, using adjusted $R^2$ values of the canonical axes. The overall temporal structure of the whole community can then be deduced from the number of significant canonical axes in the RDA models. Since RDA-PCNM is designed to identify periodical or non-linear dynamics, potential linear trends are eliminated from the data prior to analysis. Online Resource 2 presents a flow chart summarizing the steps of time series modelling with RDA-PCNM and a calculated example with sample plots.

We used the R function quick PCNM by D. Borcard (URL http://biol09.biol.umontreal.ca/ULaval08/quickPCNM-77.R) which invokes the R packages ape (Paradis et al. 2004), ade4 (Dray and Dufour 2007) and vegan (Oksanen et al. 2010) as well as functions of the R package packfor (Dray 2009). All analyses (TLA, RDA-PCNM) were made with R (R Development Core Team 2011).

**Results**

**Rate of compositional change**

As expected, all breeding bird assemblages showed a highly significant directional change of
community composition ($p < 0.0001$) over time (Table 2). The slope of TLA, and thus the rate of community change, varied widely between the studies. The breeding birds in the primeval subalpine birch forests on the Gaisatj and Valle Mountains displayed the slowest change; the fastest change was observed in the successional forest of Robert Allerton Park (Table 2, Fig. 1a and b; see Online Resource 3 for diagrams for all sites).

Year-to-year variability of bird communities, measured as the mean Hellinger distance at lag 1, also varied considerably and ranged from 0.159 on Skokholm Island to 0.445 at Gaudineer Knob (Table 2, Fig 1c and d).

The rate of compositional change and year-to-year variability were not significantly correlated ($r_P = 0.288$, $p = 0.28$) and breeding bird communities with slow change did not necessarily display low year-to-year variability. For example, slowly-changing Kraipe (plot K1) ranked second in terms of ascending rate of compositional change but showed considerable year-to-year variability and ranked 17th in terms of ascending year-to-year variability, while the rather fast-changing Skokholm Island community (ranked 19th in terms of ascending TLA slope) had the lowest year-to-year variability (Fig. 2). Fast compositional change and large year-to-year variability coincided only for the two successional forests at Gaudineer Knob and in Robert Allerton Park, which had the highest values for TLA slope and Hellinger distance at lag 1 among all study sites.

Temporal patterns

The adjusted $R^2$ of the RDA varied between 0.0791 on Hanikatsi Island and 0.6500 on
Skokholm Island (Table 2), indicating a range of model fit from low to quite good. In some of the LTDS no temporal patterns were detectable at all and no RDA models could be fitted (Kraipe plot K1, Białowieża National Park plot CM, Mastbos and Gaudineer Knob). The proportion of variance explained by the first two canonical axes ranged from 0.4565 for Birdsong Valley to 1.0 for Hoekelum Manor (Table 2), averaging at 0.6245.

The linear combination score plots of temporal dynamics of bird communities that were associated with the first canonical axis in the RDA models across study sites are shown in Figure 3. The first canonical axis captures the most important trend in the data, in terms of variance explained. The lc scores represent a synthetic measure of temporal dynamics, based on the patterns of groups of individual species that show similar temporal dynamics, identified by the RDA. In our analysis, most bird communities fluctuated at frequencies of roughly 10 - 30 year intervals (see Fig. 3a-e for a community from a large-scale primeval system and four examples of communities from other systems; see Online Resource 4 for the lc score plots of all study sites). This result indicates that processes at long time scales are the main cause of variability in breeding bird communities, regardless of the intensity of human impact (Table 2). An exception is the breeding bird community from the Gaisatj and Valle mountains (Fig. 3f), which shows a periodicity of roughly 5 years. Considering temporal patterns associated with the remaining canonical axes in the RDA models across communities and sites, we found that the shortest periodicity in compositional change varied between three and 12 years (Table 2; see Online Resource 5 for the significant principal coordinates of all study sites). These results show that the RDA-PCNM approach makes fluctuation frequencies of bird communities at independent temporal scales tractable.
Comparison among bird communities

In order to identify general patterns in the data we aimed to classify the bird communities into different categories based on the degree of human impact in each study site and to compare the outcome of TLA and RDA-PCNM in a statistical analysis. Apart from primeval ecosystems, none of the different ecosystem types represented in the available LTDS (large protected forest, small and isolated forest, successional forest and regrowth, managed and recreational forest, protected dunes, treeless islands), however, was sufficiently replicated to allow the definition of a human impact category of its own and to allow a proper statistical analysis. We thus decided to form only one more or less homogeneous category, namely the bird communities from large-scale primeval ecosystems, and contrast them to the remaining bird communities from all other systems by a type 3 sum of squares ANOVA. As an alternative we applied a regression analysis, using all site characteristics (see Table 1) as explanatory variables for the results of TLA and RDA-PCNM. None of these analyses, however, yielded any significant difference between primeval and other ecosystems or any significant regression model (results not shown; see Online Resource 6 for a closer description of the used methods).

Discussion

Rate of compositional change

As expected, all bird communities in our sample displayed compositional change over time. When ordered according to ascending TLA slope, the top ranks were mostly occupied by bird
communities from pristine systems (Gaisatj and Valle, Białowieża, Kraipe) (Fig. 2) indicating the tendency that they experienced the slowest compositional change among the different systems represented in this study. Also within-study comparisons support the assumption that undisturbed systems show slower compositional change. For example, in the Białowieża National Park, the TLA slope varies between 0.025 and 0.034 for most of the sites with exception of plots NE and NW, which show considerably faster rate of compositional change (slopes: 0.040 and 0.053, respectively) (Table 2, Fig. 2). These two plots have experienced distinct natural disturbance in the past decades, including large gaps created by tornadoes in 1987 and 2002, and a bark beetle outbreak in 2002–2003. The latter killed numerous spruces, reducing the number of living canopy spruces by almost 50% (Wesołowski et al. 2010).

The bird communities from successional systems (Gaudineer Knob, Robert Allerton Park) showed the fastest change (Fig. 2). Protected forests which cannot be regarded as pristine but which have been left undisturbed for a long time (Birdsong Valley, Bookham Common, Hubbard Brook, William Trelease Woods) were located between the extremes (primeval vs. successional). Of course, natural succession occurs also in undisturbed systems. Those protected systems where distinct successional changes (maturation of trees, disappearance of certain species due to diseases or pests etc.) have been reported (William Trelease Woods, Hubbard Brook) (Kendeigh 1982; Holmes and Sherry 2001) showed the fastest rate of change following the purely successional systems.

Plotting TLA slopes against Hellinger distances allows for an evaluation of the position of each LTDS in a plane spanned by speed of change and interannual variability. Four quadrants can be defined: “slow change – low variability”, “slow change – high variability”, “fast
change – high variability” and “fast change – low variability” (clockwise beginning at bottom left) (Fig. 2). Along the TLA slope axis, the results more or less correspond to the expected increasing rate of compositional change: primeval systems > protected systems > successional systems. Interestingly, disturbed forests (Hoekelum, Mastbos) show comparably slow compositional change of bird communities over time with rates close to those of primeval systems and an interannual variability even lower than the primeval Białowieża plots not suffering from natural disturbance (plots L, K. MS, W) (Table 2, Fig. 2). Continuous forest management (Mastbos) obviously imposes stability on the bird community, since it inhibits natural forest succession by harvesting mature trees and planting young ones. While at the plot scale there may be temporal variation as a result of forest management measures (clear-cutting, understory removal etc.), the forest as a whole may display more constancy being composed of a stable mosaic of stands with trees of different age. Also the use of forests as recreation areas seems to affect breeding bird composition less than might be expected. While the researchers abandoned Hoekelum Manor after 20 years of bird monitoring because of the increasing density of strollers, joggers and dog-owners letting their pets running free (Sanders et al. 2001), its breeding bird community showed a high degree of stability with a surprisingly low rate of compositional change. Remarkably, the Hellinger distances at lag 1 of the managed and disturbed forests of Mastbos and Hoekelum Manor indicate lowest year-to-year variability among all studies (only equaled by the treeless islands) and underscore the high stability of their breeding bird communities as already indicated by their low TLA slopes. Consequently, they were located in the “slow change – low variability” corner together with the primeval forests of the Białowieża National Park and the Gaisatj and Valle mountains (Fig. 2). In contrast the successional forests Robert Allerton Park and Gaudineer Knob were located in the “fast change – much variability” quadrant. This finding is contrary to those of
several studies that report the effects of anthropogenic management and disturbance on forest
bird communities (Hobson and Schieck 1999; Canterbury et al. 2000; Drapeau et al. 2000).
None of these latter studies, however, were based on long uninterrupted community time
series. Hansen et al. (1995) reported a non-linear response of species' abundances to tree
density across a wide range of natural and managed stand structures and ages. Probably
Mastbos and Hoekelum Manor maintain a tree density above the threshold at which bird
abundance changes dramatically. Both stands have been forested for two centuries and longer
(see details of land-use history in Online Resource 1) and no fundamental land-use change
occurred in this period (with the exception of a change of the dominant tree species) which
might have created quite stable conditions for the breeding bird community apart from
forestry measures at the stand scale.

Another interesting case is Hanikatsi Island, a protected forest that showed slow
compositional change but high year-to-year variability—almost as high as the successional
forests in Robert Allerton Park and on Gaudineer Knob. This can be explained by a distinct
in-and-out-effect (Diamond and May 1977) of species that repeatedly become extinct and
then immigrate, while at the same time the regional species pool from which the Hanikatsi
community may draw is restricted due to the effect of its isolated location on an island.

The position of the bird communities on treeless islands in the speed of change – year-to-year
variability plot (Fig. 2) is hard to explain. Both Skokholm Island and the Farne Islands
showed very low inter-annual variability, but Skokholm Island underwent a faster
compositional change, probably related to the marked increase in population size of a few
abundant species (Lack 1969).
In conclusion, the TLA slopes ($b$) show a gradient from primeval ($b < 0.04$) over managed or disturbed ($0.04 < b < 0.06$) (Mastbos and Hoekelum) and protected ($0.06 < b < 0.1$) (Birdsong Valley, Bookham Common, Western Trelease Woods, Hubbard Brook and Meijendel) to successional ($b > 0.1$) (Robert Allerton Park and Gaudineer Knob) systems; year-to-year variability was highest in successional forests and lowest in managed and disturbed forests. While these conclusions seem to be ecologically plausible, they are of a hypothetical nature since none of these differences were statistically significant. We must not prematurely conclude, however, that there is no difference between large-scale primeval systems and other systems as long as there are no data available that allow for higher statistical power (Steel et al. 2013). It is evident that more LTDS—particularly from forests subjected to forestry—would be desirable to confirm our conclusions.

**Temporal patterns**

In almost all of the time series analysed, one of the long-wave principal coordinates (PCMN 2 in most cases) was the one with the highest importance (Table 2), indicating that most of the temporal variability was explained by slow changes lasting over many years. In many time-series, medium and short-wave principal coordinates did not appear in the model at all or had only little importance, showing that there was little short-term variation. Thus, the results are particularly interesting as they deviated from our expectations. It is increasingly recognised that anthropogenic stress increases the short-term temporal variability of ecological communities (e.g., Angeler and Moreno 2007; Hillebrand et al. 2010), and that this increased temporal variance in ecological systems can even be used as an early warning signal of
impending catastrophic regime shifts in ecosystems (Carpenter and Brock 2006). Based on these previous findings—although from communities rather different from avian ones in temporal as well as spatial scales—, we expected that anthropogenic impact should increase the temporal variability in stressed communities relative to assemblages in pristine sites, and that this should be manifested in the increased importance of principal coordinates with medium to high-frequent wavelengths in the RDA models. The lack of such patterns, and the finding that long-wave principal coordinates similarly influence bird community dynamics across our habitat categories, suggests that environmental factors that are extrinsic to the system have a proportionally stronger influence than factors associated with local-scale anthropogenic stress. Although speculative, we attribute this finding to the dispersal capacity of birds, especially migratory species. Their capacity to carry out long-distance migration may enhance source-sink dynamics allowing for the colonization of sites that would otherwise be unsuitable to sustain populations in the long-term (Wesołowski and Tomiałojć 1997; Wesołowski et al. 2009). Long-term metacommunity dynamics could help mitigate local-scale human impact on bird communities, provided that regional species pools and/or habitat characteristics are not deteriorated. Another more simple explanation could be that through learning and phenotypic adjustment birds may tolerate a rather high degree of human impact so that their communities are robust assemblages provided that the human stressors do not become too strong. This kind of mechanism could be tested if systems with varying degrees of human pressure could be compared in this respect, but this is not possible with the available LTDS data. Moreover, we can state for some of the study areas, for example, the Białowieża forest, that the majority of birds are not site tenacious (e.g. Piotrowska and Wesołowski 1989, Wesołowski et al 2009, Wesołowski and Rowiński 2012), so every spring the community consists of a new set of “naïve” breeding birds, which have no former
knowledge of the local conditions.

Regarding the importance of local vs. regional scale dynamics it is interesting to note that the bird community inhabiting the primeval subalpine birch forest in the Gaisatj and Valle mountains tracked the cyclic appearance of masses of caterpillars of the Autumnal Moth *Epirrita autumnata*, which provides a superabundant food resource at approximately ten-year intervals (Enemar et al. 2004). These mass appearances clearly transcend ecological dynamics at the plot scale to influence community dynamics over broader spatial extents, enabling us to detect these changes by means of the RDA-PCNM. The dominant periodicity as identified by RDA-PCNM occurred at a wavelength of 0.30 of the study period representing a periodicity of 11 years. Also the principal coordinates with the third largest weight had a wavelength of 10 years, which is in agreement with the periodicity of the moth caterpillar outbreaks and emphasises their impact on the periodical compositional variability of the breeding bird community. Interestingly, in the original publication of these data, Enemar et al. (2004) stated that “*Fringilla montifringilla* increased in density during the first two years of each caterpillar outbreak, whereas the other species responded only weakly”. This substantiates the potential of RDA-PCNM for detecting periodic community dynamics that might remain unidentified with other methods. Also in the Białowieża forest, caterpillars outbreaks are regularly observed. There, however, they do not lead to detectable effects on breeding bird numbers (e.g. Wesołowski and Tomiałojc 1997; Wesołowski et al. 2009, 2010), and no indications of periodic community dynamics tracking these outbreaks were found by RDA-PCNM.

Although we did not aim to analyse which species or species-groups contribute to the temporal patterns of the different breeding bird communities—an exercise beyond the scope
of this paper—it is worth noting that some species occur remarkably often among those correlated with the significant PCNM, as can be seen in the biplots delivered by RDA-PCNM (see Online Resource 7 for biplots for all LTDS). For example, winter wren *Troglydytes troglodytes* (Białowieża forest, Birdsong Valley, Bookham Common, Hanikatsi Island, Hoekelum Manor, Meijendel dunes), chiffchaff *Phylloscopus collybita* (Białowieża forest, Birdsong Valley, Hanikatsi Island, Meijendel dunes) and willow warbler *Phylloscopus trochilus* (Białowieża forest plot L, Gaisatj and Valle Mountains, Hanikatsi Island, Meijendel dunes) appear in various of the European LTDS among the most influential bird species. Interestingly, in open systems—such as the Meijendel dunes—these species mostly appear in up-coming shrubs, while in closed forests they prefer disturbed places with sufficient understory (Haffer 1985a, b; Tiainen 1985), thus characterising local successional dynamics. Not surprising, the winter wren is among the species most closely related to low-frequent PCNM in those plots of Białowieża forest with natural disturbance in the form of storm damage (plots NE and NW) while in the stable plots it seems to have less influence on temporal community patterns. In-depth studies of the single sites where the LTDS were collected certainly will elucidate the relationships between single species population dynamics and more global community patterns.

*A natural baseline?*

We acknowledge that the correlative nature of our approach can be very useful for examining patterns, while it falls short of elucidating mechanisms. However, the generation of patterns alone can be insightful and inform ecological theory and management. For example, contrasting rates of compositional change across habitats with different anthropogenic
influence serves to identify an “ecologically meaningful”, empirical baseline close to the natural composition change in terrestrial breeding bird communities. The “real” baseline that corresponds to natural turnover not being impacted by any form of anthropogenic impact is illusive, because past or already occurring continental or global scale consequences of human activities (acid rain, airborne nutrients, climate change), cannot be fully accounted for. It has to be underlined, however, that various of the time series analysed here have been either collected, or initiated, well before any climate change effects had became discernible. Moreover, though some warming was observed, until now its effects were modest. For example, changes observed in the Białowieża Forest remained within the range of natural variation recorded before the onset of warming, and up to now no climate forced directional changes in composition of tree or birds communities have been recorded (Wesołowski and Cholewa 2009, Wesołowski et al. 2010). Thus the predicted large scale turnover of fauna due to climate change (Pereira et al. 2010; Sodhi and Ehrlich 2010; Dawson et al. 2011) has not occurred yet.

Patterns of periodic dynamics do not vary much among systems with different levels of human influence. Regardless of the duration of the LTDS, the low frequency dynamics always seem to be the most important ones and are overridden by high frequency dynamics only under peculiar circumstances, for example, periodic food outbreaks, which may be due to metacommunity dynamics that are specific to birds (i.e., their high dispersal capacity). It will be interesting to determine the generality of this finding in time series analyses in other groups of organisms.

Conclusions
Despite the determination of baselines of temporal compositional change being important for assessing and managing ecological systems in face of environmental change, the paucity of available data sets, particularly for longer-lived organisms such as terrestrial vertebrates, currently limits strong inference. Our use of LTDS in this paper demonstrates the potential value of so-called passive monitoring (as opposed to question-driven monitoring), which can provide valuable data even when not all of the possible analyses can be anticipated at the outset. Due to the moderate number of available independent LTDS for temperate bird communities our study was hampered by the heterogeneity in the systems other that large-scale primeval ones, which prevented the definition of more specific categories of human impact and their statistical comparison. As a result, our attempts of comparison between bird communities from large-scale primeval systems and other systems did not yield any statistically significant differences, neither did our approach to regress community change, interannual variability and temporal community patterns on the characteristics of the sites where the LTDS were collected. Nevertheless, specific patterns in the data call for more information and closer analysis (e.g. the comparison between primeval and successional forest systems). Although our results must be viewed with caution, we believe that our approach serves as an instructive example on how baselines of compositional change can be compared and evaluated.

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publication xxxx.

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Fig. 1 Time lag analysis (TLA) results of the breeding bird communities from different ecosystem types—a) Gaisatj and Valle Mountains (primeval subalpine birch forest), b) Robert Allerton Park (successional forest on abandoned fields), c) Gaudineer Knob (second-growth spruce forest) and d) Skokholm Island (small treeless island)—showing the Hellinger distances between all pairs of years at different time lags and the fitted regression line.

Fig. 2 Position of the study sites (large filled circles: large-scale primeval systems; large open circles: other systems) in the variable space of rate of community change (characterised by the TLA slope) and interannual variability (characterised by the Hellinger distance at lag 1). At the seven sites in Białowieża National Park (Wesołowski 2011) and the three sites in the dunes of Meijendel, the numbers of birds tended to be highly synchronous across years. These plots are thus not regarded as independent. In the figure their means of community change and interannual variability are shown with values of their single plots represented as small filled (Białowieża) and as small open circles (Meijendel).

Fig. 3 Linearly combined scores of principal coordinates of neighbourhood matrices on the first redundancy axis for four sites from different ecosystem types characterised by long periodicity: a) Białowieża National Park (plot K) (primeval forest), b) Meijendel (middle zone) (protected dune ecosystem), c) Hoekelum Manor (managed forest), d) Skokholm Island (small treeless island); and for two sites characterised by shorter periodicity: e) Robert Allerton Park (successional forest on abandoned fields), and f) Gaisatj and Valle mountains (primeval subalpine birch forest).
Figure 1

(a) Gaisatj and Valle Mountains
(b) Robert Allerton Park
(c) Skokholm Island
(d) Gaudineer Knob

Hellinger distance vs. Time lag (square root of years)
Figure 2
Online Resource 1 Detailed description of studied systems

Online Resource 2 Short guide through Redundancy Analysis (RDA) with Principal Coordinates of Neighbourhood Matrices (PCNM)

Online Resource 3 Time lag analysis results of all breeding bird communities included to the analysis, showing the Hellinger distances between all pairs of years at different time lags and the fitted regression line. See Table 2 in the main document for statistical parameters of the regression.

Online Resource 4 Results of redundancy analyses with principal coordinates of neighborhood matrices (lc score plots) of all breeding bird communities included to the analysis. See Table 2 in the main document for statistical parameters of the analysis.

Online Resource 5 Significant principal coordinates of neighborhood matrices (PCNM) for all breeding bird communities included to the analysis. The PCNM are characterised by their wave-lengths expressed in years.

Online Resource 6 Methods applied for the comparison of TLA and RDA-PCNM results among bird communities

Online Resource 7 RDA-PCNM biplots of all breeding bird communities included to the analysis. No RDA models could be fitted to Kraipe plot K1, Białowieża National Park plot CM, Mastbos and Gaudineer Knob. See Online Resource 2 for an explanation of how to read an RDA-PCNM biplot.
Table 1. Studies of breeding bird communities with time series of at least 20 years used in the analyses. Studies are alphabetically ordered by site names. System size = contiguous habitat in km² in which study plots were embedded.

<table>
<thead>
<tr>
<th>Name and location</th>
<th>Habitat</th>
<th>Bird community</th>
<th>Species number</th>
<th>Time series</th>
<th>Plot size [ha]</th>
<th>System size</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Białowieża National Park, Poland (plots CM, K, L, MS, NE, NW and W)</td>
<td>primeval mixed forest</td>
<td>all</td>
<td>51 (CM)</td>
<td>1975–2009 (all except L)</td>
<td>24 (CM)</td>
<td>&gt;1400</td>
<td>Tomiałojć et al. 1984; Tomiałojć and Wesołowski 1994, 1996; Wesołowski et al. 2002, 2006, 2010</td>
</tr>
<tr>
<td>Birdsong Valley, Sweden</td>
<td>protected isolated deciduous forest</td>
<td>passerines</td>
<td>41</td>
<td>1953–2009</td>
<td>13</td>
<td>0.13</td>
<td>Enemar 1966; Enemar et al. 1994; Svensson et al. 2010</td>
</tr>
<tr>
<td>Bookham Common, UK</td>
<td>protected mature oak-wood group of rocky islands</td>
<td>all</td>
<td>44</td>
<td>1949–1975</td>
<td>16</td>
<td>1.12</td>
<td>Beven 1976</td>
</tr>
<tr>
<td>Farne Islands, UK</td>
<td></td>
<td>land birds</td>
<td>16</td>
<td>1946–1974</td>
<td>32</td>
<td>0.32</td>
<td>Diamond and May 1977</td>
</tr>
<tr>
<td>Gaisatj and Valle, Vindel mountain nature reserve, Sweden</td>
<td>primeval subalpine birch forest</td>
<td>passerines</td>
<td>46</td>
<td>1963–1999</td>
<td>900</td>
<td>&gt;1000</td>
<td>Enemar et al. 2004</td>
</tr>
<tr>
<td>Hanikatsi Island, Estonia</td>
<td>protected isolated forest patch on an island</td>
<td>all</td>
<td>33</td>
<td>1974–2004</td>
<td>10</td>
<td>0.1</td>
<td>Leito et al. 2006</td>
</tr>
<tr>
<td>Hoekelum Manor, Netherlands</td>
<td>recreational forest</td>
<td>all</td>
<td>50</td>
<td>1981–2000</td>
<td>69</td>
<td>1000</td>
<td>Sanders et al. 2001</td>
</tr>
<tr>
<td>Location</td>
<td>Habitat Description</td>
<td>Bird Groups</td>
<td>Population Size</td>
<td>Study Period</td>
<td>Abundance</td>
<td>Reference</td>
<td></td>
</tr>
<tr>
<td>------------------------------</td>
<td>--------------------------------------------</td>
<td>-------------</td>
<td>-----------------</td>
<td>--------------</td>
<td>-----------</td>
<td>-----------------------------------------------</td>
<td></td>
</tr>
<tr>
<td>Kraipe, Vindel mountain</td>
<td>primeval alpine vegetation</td>
<td>all</td>
<td>26 (K1)</td>
<td>1964–2001</td>
<td>100 (K1)</td>
<td>300 Svensson et al. 1984; Svensson 2006</td>
<td></td>
</tr>
<tr>
<td>nature reserve, Sweden</td>
<td></td>
<td></td>
<td>19 (K2)</td>
<td>1964-1999</td>
<td>114 (K2)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>300</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mastbos, Netherlands</td>
<td>cultivated mixed forest</td>
<td>passerines</td>
<td>18</td>
<td>1955–1981</td>
<td>50</td>
<td>5.7 Jansen and de Nie 1986</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meijendel, Netherlands</td>
<td>protected coastal dunes</td>
<td>all (except</td>
<td>60 (seaward)</td>
<td>1986–2008</td>
<td>12.2 (seaward)</td>
<td>30 van Ommering and van der Salm 1990³</td>
<td></td>
</tr>
<tr>
<td>(seaward, middle and</td>
<td></td>
<td>colonial</td>
<td>98 (middle)</td>
<td></td>
<td>166.7 (middle)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>landward zone)</td>
<td></td>
<td>breeders)</td>
<td>89 (landward)</td>
<td></td>
<td>68.4 (landward)</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Robert Allerton Park, Illinois, USA</td>
<td>successional forest on abandoned fields</td>
<td>all</td>
<td>51</td>
<td>1946–1971</td>
<td>24.3</td>
<td>1.8 Kendeigh 1982</td>
<td></td>
</tr>
<tr>
<td>Skokholm Island, UK</td>
<td>treeless island</td>
<td>land birds</td>
<td>18</td>
<td>1946–1967</td>
<td>96</td>
<td>0.96 Lack 1969</td>
<td></td>
</tr>
<tr>
<td>William Trelease Woods,</td>
<td>protected isolated deciduous forest</td>
<td>all</td>
<td>59</td>
<td>1934–1976</td>
<td>24</td>
<td>0.24 Kendeigh 1982</td>
<td></td>
</tr>
<tr>
<td>Illinois, USA</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>30</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

- Including plot names when more than one plot was monitored

- Colonial breeders such as cormorants and gulls move their breeding sites from one place to the other within a few years, for example, from within a study plot to outside or vice versa. Since colony movement might misleadingly appear to indicate huge abundance changes and, thus, bias the results, we skipped colonial breeders from the analysis.

- This paper describes the study area and reports earlier investigations on its breeding bird community. The time series from 1986 through 2008 used in our analysis has not been published before.
Table 2. Model outputs of time lag analysis (TLA) and redundancy analysis (RDA) with principal coordinates of neighbourhood matrices (PCNM) for breeding bird community time series of at least 20 years. The PCNM with the largest weight in the RDA model is expressed as proportion of the time series length, the shortest PCNM in the RDA model is expressed in years. ND, not determined since no RDA model could be fitted.

<table>
<thead>
<tr>
<th>Name</th>
<th>TLA slope</th>
<th>Mean Hellinger distance at lag 1</th>
<th>Adjusted R² of RDA model</th>
<th>Explained variance of RDA axes 1 and 2</th>
<th>PCNM with largest weight in RDA model</th>
<th>Shortest PCNM in RDA model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Białowieża National Park (plot CM)</td>
<td>0.029</td>
<td>0.28</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
</tr>
<tr>
<td>Białowieża National Park (plot K)</td>
<td>0.034</td>
<td>0.23</td>
<td>0.30</td>
<td>0.52</td>
<td>0.74</td>
<td>7</td>
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<tr>
<td>Białowieża National Park (plot L)</td>
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<td>0.24</td>
<td>0.22</td>
<td>0.52</td>
<td>0.70</td>
<td>3.5</td>
</tr>
<tr>
<td>Białowieża National Park (plot MS)</td>
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<td>0.23</td>
<td>0.34</td>
<td>0.47</td>
<td>0.74</td>
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<td>Białowieża National Park (plot NE)</td>
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<td>0.34</td>
<td>0.20</td>
<td>0.50</td>
<td>0.74</td>
<td>6</td>
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<tr>
<td>Białowieża National Park (plot NW)</td>
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<td>0.30</td>
<td>0.24</td>
<td>0.57</td>
<td>0.74</td>
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<tr>
<td>Białowieża National Park (plot W)</td>
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<td>0.24</td>
<td>0.27</td>
<td>0.59</td>
<td>0.74</td>
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<td>0.46</td>
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<td>Bookham Common</td>
<td>0.071</td>
<td>0.27</td>
<td>0.24</td>
<td>0.63</td>
<td>0.74</td>
<td>8</td>
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<td>Farne Islands</td>
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<td>0.44</td>
<td>0.58</td>
<td>0.69</td>
<td>6</td>
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<tr>
<td>Gaisatj and Valle mountains</td>
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<td>0.22</td>
<td>0.14</td>
<td>0.67</td>
<td>0.30</td>
<td>10</td>
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<tr>
<td>Gaudineer Knob</td>
<td>0.106</td>
<td>0.45</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
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<tr>
<td>Hanikatsi Island</td>
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<td>0.42</td>
<td>0.08</td>
<td>0.79</td>
<td>0.71</td>
<td>9</td>
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<td>Hoekelum Manor</td>
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<td>0.11</td>
<td>1.00</td>
<td>0.75</td>
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<tr>
<td>Hubbard Brook</td>
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<td>0.42</td>
<td>0.59</td>
<td>0.74</td>
<td>3.5</td>
</tr>
<tr>
<td>Kraipe (plot K1)</td>
<td>0.020</td>
<td>0.30</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
<td>ND</td>
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<tr>
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<td>ND</td>
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<td>0.091</td>
<td>0.26</td>
<td>0.34</td>
<td>0.52</td>
<td>0.70</td>
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</tr>
<tr>
<td>Location</td>
<td>Value 1</td>
<td>Value 2</td>
<td>Value 3</td>
<td>Value 4</td>
<td>Value 5</td>
<td>Value 6</td>
</tr>
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<td>Meijendel (middle zone)</td>
<td>0.085</td>
<td>0.17</td>
<td>0.42</td>
<td>0.58</td>
<td>0.70</td>
<td>5</td>
</tr>
<tr>
<td>Meijendel (seaward zone)</td>
<td>0.103</td>
<td>0.27</td>
<td>0.41</td>
<td>0.68</td>
<td>0.70</td>
<td>3.5</td>
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<td>0.17</td>
<td>0.71</td>
<td>0.54</td>
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<td>0.75</td>
<td>0.77</td>
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<td>0.52</td>
<td>0.56</td>
<td>0.70</td>
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