

Is the seasonal variation of abundance and species richness in birds explained by energy availability?

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Abstract. Energy availability explains the spatial variation of species richness. However, in arctic to temperate regions species richness in birds shows also a seasonal pattern with high species numbers in summer and low numbers in winter. Is it possible to explain this pattern by high energy availability in summer and low availability in winter? The ‘energy availability hypothesis’ rests on a positive correlation between abundance and species richness. Using weekly counts along a transect in Northern Bavaria (S Germany), we found the expected seasonal annual as well as biannual cycles in species richness (108 species observed in total). In contrast, the number of individuals showed no clear seasonal cycle, but erratic fluctuations particularly in winter. Weather conditions had only small effects on the number of individuals and on species richness. Adding weather variables to analyses increased explained variance only by 1.5% to 10%. The energy availability hypothesis is not able to explain the seasonal variation of species richness in temperate regions. However, bird assemblages during winter consist of species able to feed on various resource types, in particular seeds produced during summer. These left-overs provide the resources for diet generalists to survive the winter.

Key words: seasonal patterns, species richness, niche breadth, energy-availability hypothesis

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INTRODUCTION

Among the most celebrated general patterns in ecology (see Lawton 1999) is the latitudinal decline in biodiversity towards the poles (Rosenzweig 1995). In birds, most of latitudinal analyses concentrate on the breeding season (e.g. Hawkins et al. 2003, but see Dalby et al. 2014). In birds, however, long-distance migration leads to a fascinating seasonal component of diversity, particularly in temperate, boreal and arctic regions. This component is based on a heritable circannual rhythm, which evolved as an adaptation to the availability of resources (Gwinner 1996, Berthold 2001). In addition to long-distance migration, local movements follow weather conditions (Richardson 1978) as well as the availability of food resources (Jenni 1987). All these movements lead to a reorganization of the assemblages

across seasons (Saavedra et al. 2016). Assemblages of birds, therefore, show characteristic changes in abundance, species richness and species composition throughout the year (Bezzel 1980). In our paper we use “abundance” to indicate the general concept. There are several metrics to estimate abundance, such as the number of individuals counted in a sample. We use the term “number of individuals” always when we refer to our particular data set.

The ‘energy-availability hypothesis’ (Wright 1983) is invoked as the dominant process leading to spatial changes in species richness (e.g. Bonn et al. 2004, Evans et al. 2006, Mönkkönen et al. 2006), but may also apply for seasonal patterns. The general idea is that available energy determines how many individuals are able to coexist, which limits abundance. Furthermore, species richness increases with abundance and therefore with the

available energy (Preston 1948, 1962, Gotelli & Colwell 2001, Currie et al. 2004). From these arguments we expect a high abundance and species richness of birds in summer (high energy availability) and a low abundance and species richness during winter (low availability). Furthermore, passage migrants should lead to two peaks in species richness during the migratory seasons in spring and autumn. Of course this hypothesis is simplistic and there are alternative and additional explanations of the seasonal variations of species richness. We want to mention two of such alternatives. Harsh climatic conditions during winter might limit the occurrence of certain species due to physiological constraints (Root 1988). Furthermore, the accessibility of resources shows seasonal changes and may limit the occurrence of species that use certain types of resources (Newton 2008, 2013, Somveille et al. 2015). For example, most insectivores have to leave temperate and arctic regions due to the low availability of insects during winter (Rogers 2005, see also Fristoe 2015). Species that use a broad spectrum of diet should be better able to survive during winter in temperate and or arctic regions than should specialist feeders. This predicts characteristic seasonal patterns in the niche of species in respect to diet. Note that this is a variant of the 'niche breadth hypothesis' invoked to explain the variation of the size of distributional ranges across species (Brown 1984, 1995).

Despite the enormous efforts expended on monitoring birds, only very few studies are available that analyse the seasonal variation in the abundance of terrestrial bird assemblages and its correlation with species richness from an ecological perspective (see also Marra et al. 2015 for a plea for more full annual cycle research). Here we use approximately weekly censuses of birds along a 4 km transect passing through a Central European landscape to evaluate seasonal variation of the abundance and species richness of co-occurring bird species. In particular, we test the following hypotheses: 1) The abundance and species richness of birds show a clear seasonal pattern with low values of both metrics in winter, high values in summer. Local weather conditions only modulate this general pattern; 2) The seasonal variation in the abundance and species richness is closely correlated and therefore seasonal variation in the abundance explains a large proportion of the seasonal variation in species richness; 3) There are clear seasonal changes in the composition of bird assemblages with respect to their dietary niche

breadth with many specialists in summer and generalists in winter.

METHODS

Study area and data sampling

The analysis is based on weekly counts of birds along a transect of exactly 4 km in length between 1st January 2010 and 31st December 2014, passing through a landscape of northern Bavaria (Germany, Bavaria, Bayreuth: 11°38.7' E, 50° 1.0' N; elevation between 390 and 400 m a.s.l.; Fig. 1). 2.3 km of the transect crossed open agricultural landscapes with fields of maize, other cereals and meadows (58% of the total transect), with single trees (oak, lime, birch) and a small wetland with reed-beds, willows and ditches. 1.7 km (43%) passed through small woods and cultivated landscape with hedges and trees.

The climate of this area is characterized by mean temperature of 7.9 °C and mean yearly rainfall of 724 mm (measured at the Ecological Botanical Gardens of the University of Bayreuth, 11 km distant from the sampled transect). For closer analysis of the relationship between actual weather conditions and bird assemblages we used daily temperatures as well as daily records of precipitation recorded at the Ecological Botanical Gardens (period from 2009 to 2014, Micrometeorology, Prof. Dr. Thomas, BayCEER, University of Bayreuth, Appendix 1).

To minimize bias, all counts were undertaken by one observer (RP) during good weather conditions (not during heavy rainfall, fog or stormy weather; Bibby et al. 1992). Each survey lasted two hours and started between 8:00 and 14:00 and the transect was always followed in the same direction to minimize bias by circadian rhythms in the activity of birds (Fig. 1). During each expedition all signs of occurrence of bird individuals by optic, acoustic or other characteristics (in individual cases fresh tracks from rare species, e.g. plucked feathers of a Snow Bunting *Plectrophenax nivalis*) were recorded. The observer made all possible efforts to avoid double counts. Furthermore, counts were not restricted to a fixed distance band. The reason for this was that we wanted to record the complete species set of the area. With a fixed band it is impossible to record large species (Hildén 1987). We summed up all records, including individuals heard only, to create a metric for abundance. Obviously the distance between the observer and detected sign of occurrence differs

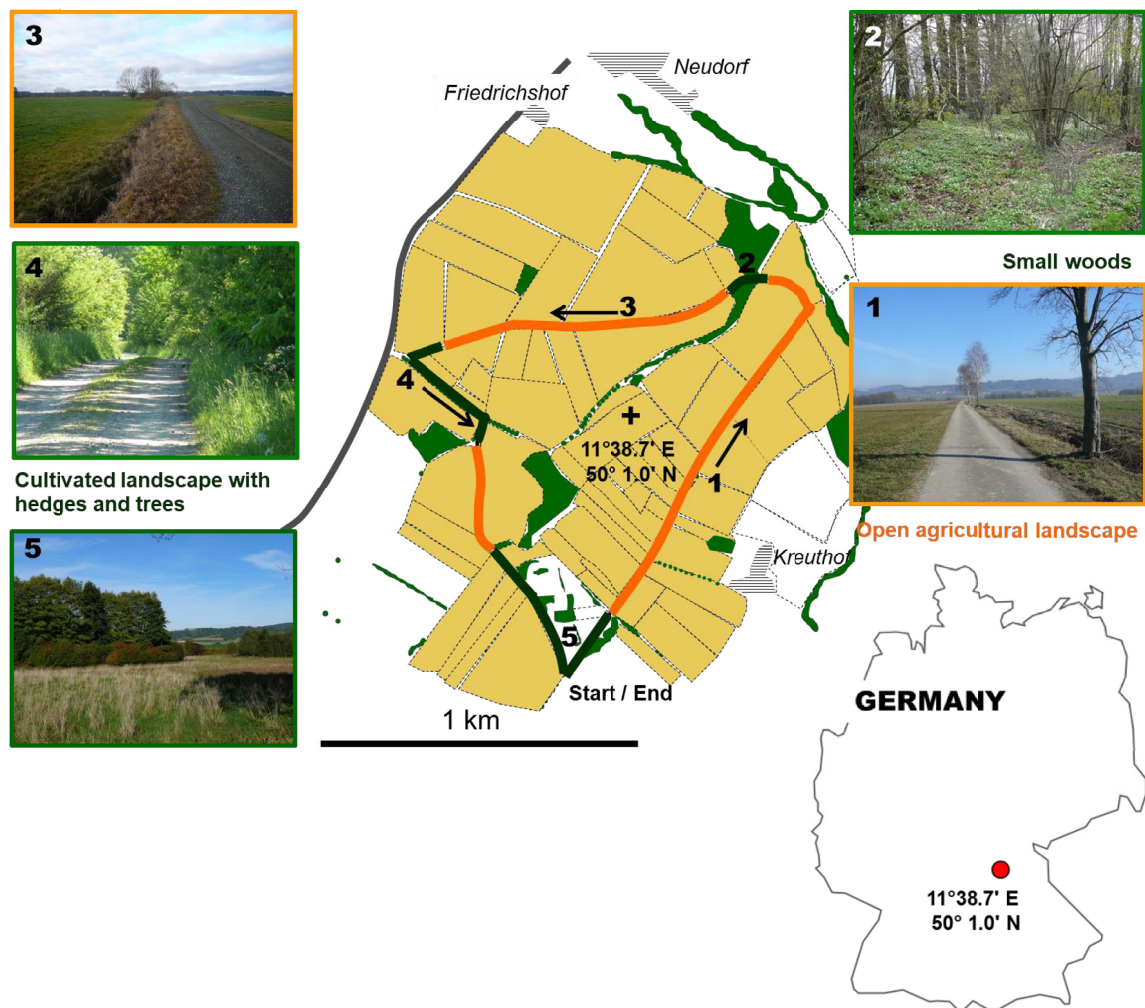


Fig. 1. Location of the transect used for recording birds. The transect is a loop track between the villages Kreuthof, Neudorf and Friedrichshof in northern Bavaria (S Germany) and was followed always in the same direction during all visits (see arrows). The track passes various vegetation types indicated by green and orange colours of the track and numbers. The orange parts of the track pass through open agricultural landscapes (types 1 and 3; see photographs), whereas the green parts of the track pass through small woodland or cultivated landscapes with hedges and trees (types 2, 4, 5).

between species. Large soaring raptors or storks were recorded up to larger distances than cryptic species like Dunnocks *Prunella modularis* or non-singing Grasshopper Warblers *Locustella naevia*. Such differences were not taken into account in our metric of abundance. Of course this introduces a bias. However, assuming that the mean distance up to which a species is recorded remains more or less similar across the year this bias should have only a minor influence on our analyses. Of course, we are also aware that detectability varies between seasons (Bibby et al. 1992). But the differences between species are so large that these seasonal variations in detectability are assumed to be of minor importance for the general analyses. Therefore, we believe that the transect

counts provide a fair metric for abundance across seasons and years. All signs of occurrence were determined to species to estimate species richness. For the present paper, data from 232 counts were available for analyses (Fig. S2 in Appendix 2). Three individuals of Dark-headed Wagtail *Motacilla thunbergi* on September 23rd 2012 were considered conspecific with Yellow Wagtails *Motacilla flava*.

Statistical analysis

To test for seasonal patterns in the number of individuals, species richness and niche breadth we used the *cosinor*-approach with the three mentioned metrics as response variables (Barnett & Dobson 2010; for an alternative approach see also Appendix 2). To model the expected seasonal

variation, we need to implement an “annual cycle” to capture the annual variation and a “biannual cycle” to model the migration seasons in spring and autumn. Note that we use here the term “cycle” in a statistical sense. To implement these two cycles, we created for each cycle a sine and cosine term using the appropriate functions in the R-package *season* (see also Crawley 2007, p. 709 for details). The estimates of the sine and cosine terms were tested for significance following Barnett & Dobson (2010). We accepted significance for each of the two cycles if at least one of the two terms reached the level of significance after accounting for multiple testing using the Bonferroni approach. With four regression coefficients the adjusted significance level is $p = 0.05/4 = 0.0125$. The distribution of the number of individuals recorded during each day was skewed and therefore we \log_{10} -transformed this variable.

The above analyses allow only to test whether the data show the seasonal pattern predicted from the migration movements of birds. In a next step we want to test the importance of weather conditions for the variation in the bird counts. Therefore, we first modelled the annual cycles and proceeded to add weather conditions in a period of 10 days before each excursion (mean temperature and sum of rainfall; see Fig. S3b in Appendix 3). The increase of explained variance between these two models using adjusted R^2 (R_{adj}^2 ; significance tested by an ANOVA comparing the two models) estimates the importance of weather conditions for the response variable.

We expected from the ‘energy availability hypothesis’ that the number of species should follow closely the number of individuals. Therefore, we also calculated a model that first predicted species richness by the number of \log_{10} -transformed individuals. In a next step we added terms to model seasonal variation and weather conditions. If the energy availability predict the seasonal changes of species richness, these sine and cosine terms should provide little additional information to predict species richness. Finally, we added also the diet niche breadth. The idea behind this exercise is that during winter only species with a broad niche (see next paragraph) are able to exist in an area.

To estimate niche breadth in respect to diet, we extracted for all recorded species information on the diet using information given by del Hoyo et al. (1992–2011). We decided to use six categories: plants, seeds, fruits, invertebrates, fish and terrestrial vertebrates. For each species we noted

whether the respective diet category is known to be used by that species. This is the only available and reliable information for all recorded species. With these data it is possible to estimate dietary niche breadth, by counting the number of categories listed for each species. High values (maximum 6) indicate a broad niche in respect to diet, low values (minimum 1) a narrow niche. In a next step we calculated the mean niche breadth of the species recorded during a transect count. We calculated an unweighted mean across recorded species as well as weighted mean. For the latter we averaged niche breadth across individuals using the same number of diet categories for all individuals of a species. This is equivalent to using the relative proportion of species as weights. The analysis of niche breadth showed almost the same pattern irrespective of whether we used the unweighted (across species) or weighted (across individuals) metric and we present only the metric calculated across individuals. Note that we extracted the diet categories used by a species from the literature and our measure of niche breadth integrates across the whole year.

RESULTS

Number of individuals recorded during each count varied between 13 (December 24th 2010) and $\approx 5,500$ (March 22nd 2013) individuals. Overall these individuals represent 108 species. Across all species most individuals were Starlings *Sturnus vulgaris*, whereas the Carrion Crow *Corvus corone* was recorded during more counts than any other species (Fig. 2).

The maximum number of species found during a particular count was 40 (September 28th 2012). At the minimum, only 2 species were recorded (January 30th 2010; Carrion Crow and Redpoll *Carduelis flammea*). In general, we found high numbers of species during late spring when the breeding period of some species overlapped with the occurrence of passage migrants (e.g. Honey Buzzard *Pernis apivorus*), and in late summer, with the latest breeding birds and the first migrants of the beginning post-breeding migration (e.g. Whinchat *Saxicola rubetra* or Wheatear *Oenanthe oenanthe*; Fig. 3). Lowest richness was found in winter (Fig. 3).

Across the five years (2010 to 2014), the number of individuals showed evidence of biannual cycles with peaks in spring and autumn but not of a general annual cycle with low numbers in winter and

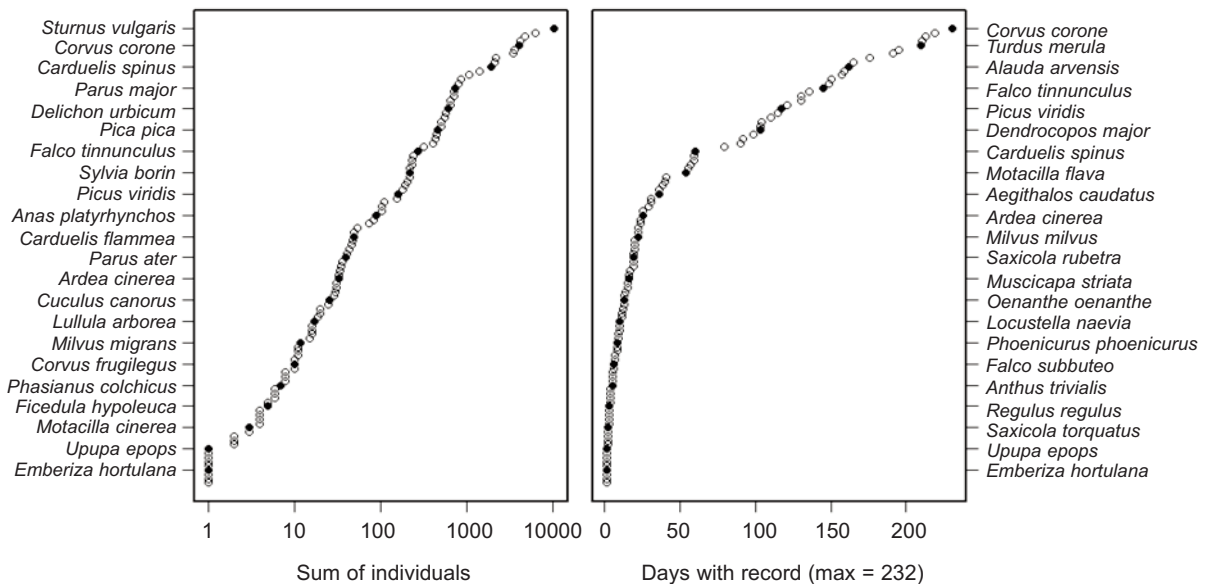


Fig. 2. Plot of the total number of individuals recorded across all 232 counts for each of the 108 species (left panel) as well as the number of counts during which a species was recorded (right panel). For simplicity we give only the name of every fifth species (symbols in black).

high numbers in summer (Table 1, Fig. 3 and Fig. S2 in Appendix 2). Fitting sine and cosine terms for annual and biannual cycles explained only 8.5% of the variability in the number of individuals. Only one term of the biannual cycle was significant (Table 1). Adding weather variables to

the model increased explained variance by 1.5 % to 10 % (Table 1). This increase was significant ($p = 0.046$). In contrast, species richness showed the expected annual as well as biannual cycles (Table 1; Fig. 3). Again weather conditions increased explained variance by only 2.9% ($p < 0.001$).

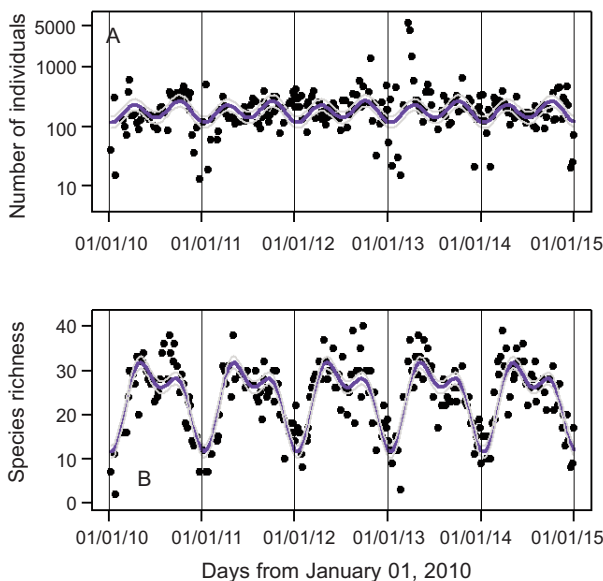


Fig. 3. Variation of the number of individuals (log₁₀-transformed; A) and species richness (B) across the five years of bird sampling. The blue lines are the predicted values (± 2 standard deviations — grey lines) using a *cosinor*-approach fitting an annual as well as a biannual cycle. Note that the number of recorded individuals shows a biannual cycle (Table 1).

The number of recorded species increased with the number of log₁₀-transformed individuals ($R_{adj}^2 = 29\%$; Table 1; Fig. 4a). For a given number of individuals we recorded many more species in summer than in winter (Fig. 4a) and the slopes of the relationship between the number of individuals and species richness differed between seasons. Adding the sine and cosine terms for cycles with a periodicity of one year and half a year increased R_{adj}^2 to 75% ($p < 0.001$). Both cycles were significant (Table 1; see also Fig. 3 and Fig. S2 in Appendix 2). Thus the number of individuals is not sufficient to explain the annual and biannual cycles. Nevertheless, after accounting for seasonal cycles and weather conditions, there was still a positive relationship between number of individuals and species richness (Fig. 4a).

As predicted, bird assemblages during summer had a lower niche breadth in respect to diet than during winter (Fig. 4c). Weather had no influence on the niche breadth (Table 1). The relative number of individuals that feed on a particular diet category changed also across the year. For example, during winter almost all individuals belong to species that are able to feed on seeds. Plotting raw

Table 1. Summary of models used for evaluating the influence of biological rhythm as well as weather variables (mean temperature [°C] and rainfall [mm] in a period of ten days before each excursion) and other factors on three response variables: \log_{10} (number of recorded individuals), species richness and weighted mean niche breadth in respect to diet. We present the t-values of the individual regression estimates (estimate divided by standard error; significant t-values in bold). For the test of the importance of biological rhythms we used a multiple *cosinor*-approach, fitting simultaneously an annual and biannual cycle (see Barnett & Dobson 2010). To evaluate significance, we tested the four individual terms using $p = 0.05/4 = 0.0125$ to correct for multiple tests. Furthermore, we present the adjusted R^2 and AIC-values for the fitted models. For species richness we also present a series of models where the first model included only \log_{10} (number of individuals) and proceeded by fitting additional variables for testing the influence of rhythms, weather and niche breadth on species richness. All models are based on 232 excursions. A conservative guide for significance is $|t| = 2$ and $|t| = 2.6$ for the sine and cosine terms.

Dependent Variable	Cycle -year		Cycle - half a year		Weather		$\log_{10}(\text{Ind.})$	Niche	R_{adj}^2	AIC
	sine	cosine	sine	cosine	°C	mm				
$\log_{10}(\text{Individuals})$	-1.26	-1.16	-1.14	-4.61					0.085	149.2
	0.342	0.766	-1.20	-5.16	1.13	2.28			0.10	146.9
Richness	0.358	-17.50	-5.08	-9.92					0.66	1379.2
	2.56	-4.40	-5.33	-10.9	2.40	3.23			0.68	1367.7
							8.56		0.24	1560.2
	1.29	-8.46	-5.35	-8.46			10.3		0.76	1292.1
	2.84	-5.75	-5.56	-9.06	2.12	2.34	9.33		0.77	1286.5
	2.45	-5.52	-4.61	-8.22	1.83	2.21	9.33	-2.83	0.78	1280.4
Niche breadth	-0.988	8.31	4.52	4.53					0.32	361.6
	-2.12	1.39	4.63	4.86	-1.84	-1.23			0.33	360.8

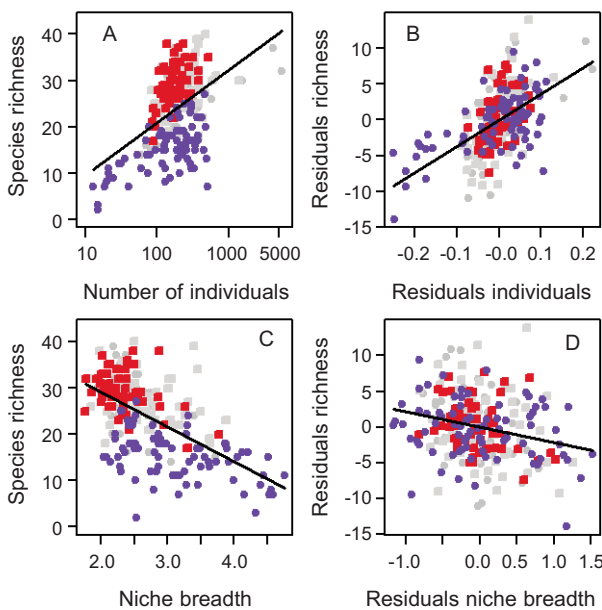


Fig. 4. Relationship between the number of individuals (\log_{10} -transformed) and species richness as well as niche breadth in respect to diet and species richness. The left row (A & C) plots the original values, whereas the right column plots (B & D) the residuals of models incorporating for each dependent variable the annual and biannual cycles as well as weather conditions. To visualize the differences between summer and winter we used colours. The line presents a univariate regression line across all data points. Symbols: grey circles — spring (March, April); red squares — summer (May to July); grey squares — autumn (August to October); blue circles — winter (November to February).

values, we found a clear inverse relationship between niche breadth and species richness, mainly driven by the seasonal pattern (compare in Fig. 4c the location of points across the four seasons). After accounting for the number of individuals as well as biannual and annual cycles, the negative correlation remained with no differences between the four seasons (Fig. 4d). Weather conditions explained only little additional variation although the increase in R_{adj}^2 was significant ($p = 0.009$; Table 1).

DISCUSSION

In our study we found a clear seasonal pattern of species richness with two peaks: one in spring and one in autumn. However, the expected seasonal pattern for the number of (recorded) individuals, with low numbers in winter and high numbers during summer, was not found. Weather conditions had only small effects on the number of individuals and on species richness. Finally, we document that the average food niche breadth is high during summer and low during winter.

The most astonishing finding was that the number of individuals is similar during summer and winter. Therefore, the 'energy availability hypothesis' in its simplest version is not sufficient to explain the seasonal variation in the number of individuals forming the bird assemblages (see also

Currie et al. 2004). Furthermore, from the finding of roughly constant numbers of individuals across the year and a clear seasonal pattern of species richness, it follows that the mean abundance per species must be lower in summer compared to winter (Fig. 4a; see also Hurlbert 2004 for a similar finding in a spatial context). This increase in the abundance per species from summer to winter must be the outcome of the inflow of individuals. This inflow has two reasons. First, some individuals are winter visitors from more northern populations (e.g. Jackdaw *Corvus monedula*, Redwing *Turdus iliacus* or Siskin *Carduelis spinus*). Second, outside the breeding season many species do not defend territories and are therefore able to engage in regional movements (e.g. Senar et al. 1992). Species can thus react to spatial variations in resource supply (e.g. see Jenni 1987) as well as food accessibility because foraging is not constrained by breeding activities. All these regional movements lead to non-cyclic local fluctuations in abundance. Although the general influence of weather conditions is low, exceptional weather conditions influence the local abundance of birds for short time periods. The conditions during March 2013 illustrate this. During that month, large parts of Germany north of the low mountain ranges was covered by snow, while in southern Germany the weather was as expected for early spring (Gelpke et al. 2013). The study site was exactly on the meteorological divide leading to a situation called “Zugstau”, a temporary barrier to migration. At least 5,500 birds were counted along the transect on March 22nd 2013, among them 200 Lapwings *Vanellus vanellus*, 290 Song Thrushes *Turdus philomelos*, 2,600 Starlings *Sturnus vulgaris*, 490 Fieldfares *Turdus pilaris*, 330 Skylarks *Alauda arvensis* and 1,300 Wood Pigeons *Columba palumbus*. Such situations are too rare for a rigorous statistical analysis with our comparatively short time series (4 years).

In contrast to our estimate of abundance, we found symmetric biannual as well as annual cycles that explain the seasonal variation of species richness even after accounting for the number of individuals. This underlines the importance of endogenous processes that trigger seasonality of migration and breeding. Again weather conditions had only slight effects on the general pattern. But this was expected, as birds rely for structuring their seasonal behaviour not on weather conditions, but on endogenous rhythms (Gwinner 1996). Weather is far too unpredictable for important decisions with long-term effects on

survival or reproduction. Nevertheless, local weather conditions modify the local details of migration activities (Richardson 1978).

High levels of species richness were associated with a low average niche breadth in resource use, even after accounting for other confounding factors (Fig. 4d). The straightforward explanation of this pattern is that the species, which are able to live the whole year in the area, and also winter migrants, are species, which use a broad range of food categories (broad niche). Few species feed exclusively on arthropods during winter (e.g. Goldcrest *Regulus regulus*, Thaler 1990). Insects are only available in sufficient numbers during summer and therefore specialists feeding only on insects have to leave more northern regions in autumn (Alerstam et al. 2003). However, it is well-known that e.g. tits feed in summer on insects and during winter additionally on seeds (see also Fig. 5b). This result may therefore be interpreted as a variant of the ‘niche breadth hypothesis’, which states that the range size of species increases with the extent of a species’ niche (Brown 1984, 1995). In addition to dietary breadth, other adaptations of species that optimize foraging efficiency contribute also the ability of a species to survive harsh weather conditions. First, corvids and tits evolved efficient explorative searching behaviour to locate

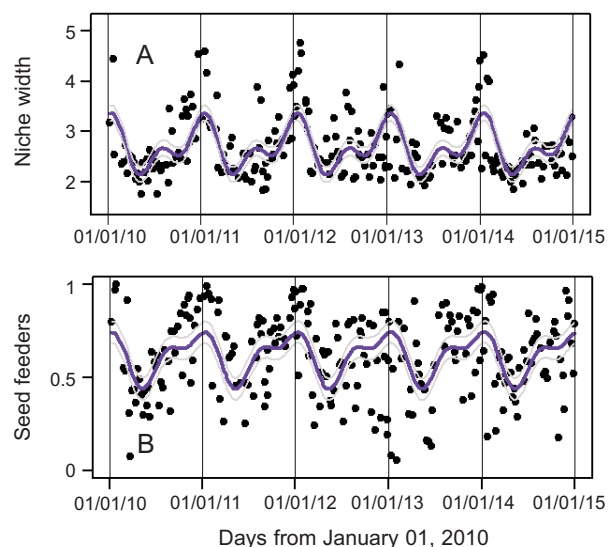


Fig. 5. Variation of the niche breadth across individuals (A) as well as relative portion of individuals belonging to species, which feed also on seeds (B), for the five years of bird sampling. The blue lines are the predicted values (± 2 standard deviations — grey lines) using a cosinor-approach with two cycles: one with 360 days and one with 180 days (for a test of the significance of the two cycles for niche breadth see Table 1). Note that winter is characterized by species with a broad niche and species that are able to feed on seeds.

and exploit food sources. They are able to locate hidden food, to unroll leaves which are infested by insect larvae and, in the best known example, to open the metal foil tops of milk bottles (Glutz & Bauer 1993). Second, some species are able to bypass bottlenecks of food availability by food hoarding, which is found in some tit species (especially Marsh Tits *Poecile palustris*, for an overview see Sherry 1989), corvids (Grodzinski & Clayton 2010), but also in the Great Grey Shrike *Lanius excubitor* (Glutz & Bauer 1993). Third, many overwintering small birds minimize energy losses during cold winter conditions by utilizing natural and artificial cavities as roost sites (e.g. Great Tits *Parus major*, Pauritsch 1982) or sleeping in close body contact (e.g. Long-tailed Tits *Aegithalos caudatus*, Riehm 1970; Goldcrests, Reinertsen et al. 1988; Eurasian Wrens *Troglodytes troglodytes*, Ammermann 1975). Some of them are also able to fall into hypothermia (Reinertsen 1983) and are so able to survive the long dark period during winter nights without food intake.

Despite our reasonable results, one must be careful in generalizing from one single observational study with several methodological shortcomings to a general pattern. For example, the number of individuals used in our analysis is a biased metric for abundance, because detectability varies between species and seasons. In general, the detectability of most species is higher in summer than in winter, because of the singing, displaying and foraging activities. Therefore, our counts are lower estimates of real densities during winter. Furthermore, one might argue that some migrating individuals do not consume energy in the area. This is undoubtedly the case of those detected as flying above the transect and is also much lower for those birds staying for short stopovers than for those breeding in the area. In this respect, the number of individuals is not an accurate measure of consumed energy.

Overall, our results showed that the structure of bird assemblages varies considerably across the seasons of a year and that endogenous rhythms appear to be the main factors for this variation. Weather conditions have only a marginal influence on the seasonal pattern. So far these results are not really new, although comprehensive analyses are rare. More important is the conclusion that the 'energy availability hypothesis' in its narrow interpretation is not able to explain the annual cycles in the bird assemblages. The traits of species also play important roles in structuring bird assemblages across seasons. Generalists in

respect to diet dominate during winter and these species use obviously resource produced during summer (e.g. seeds). We expect that these "left-overs" from the summer season will show a latitudinal pattern. However, presently the available data do not allow to explore such patterns to put our local study into a broader context. Nevertheless our analyses suggests that macroecological hypotheses provide heuristic ideas ('energy availability hypotheses', 'niche breadth hypothesis') to understand the seasonal variation of bird communities.

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STRESZCZENIE

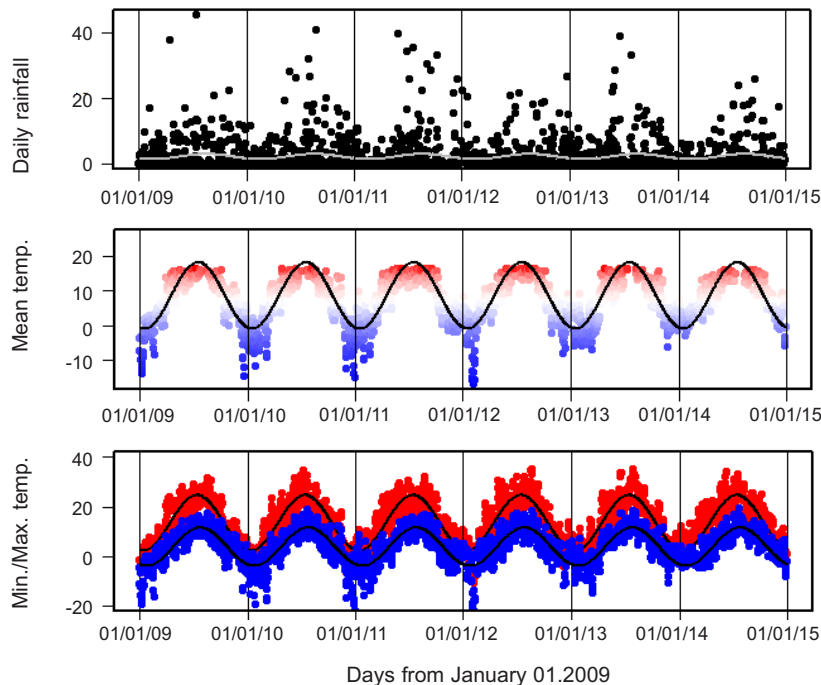
[Czy sezonowa zmienność liczby gatunków oraz liczebności ptaków jest tłumaczona ilością dostępnej energii]

Dostępność energii wyjaśnia przestrzenną zmienność bogactwa gatunkowego, z obserwowanym spadkiem liczby gatunków od tropików do biegunów. Poza zróżnicowaniem przestrzennym, bogactwo gatunkowe ptaków wykazuje również wyraźną zmienność sezonową z wysoką liczbą gatunków latem i niską w zimie. W pracy badano, czy taki wzorzec wynika z wysokiej dostępności energii w lecie i niskiej dostępności w zimie, biorąc pod uwagę, że 'hipoteza dostępności energii' zakłada dodatnią korelację między liczebnością osobników a bogactwem gatunkowym.

Analizy wykonano na danych zebranych w ciągu pięciu lat (2010–2014) podczas cotygodniowych liczeń prowadzonych wzdłuż transektu w północnej Bawarii (Fig. 1), uwzględniając także dane pogodowe (Apendyks 1, 3). Podczas 232 liczeń zaobserwowano łącznie 108 gatunków, najliczniej występowały szpaki, zaś najczęściej podczas liczeń spotykano wrony siwe (Fig. 2). Zgodnie z przewidywaniami w przypadku liczby gatunków potwierdzono zarówno ogólną roczną zmienność, jak i zmienność związaną z wiosennym i jesiennym okresem wędrówkowym (Tab. 1, Fig. 3, Apendyks 2). Natomiast w przypadku liczebności osobników potwierdzono zmienność związaną z okresem wędrówkowym, ale stwierdzono brak sezonowych zmian z niską liczebnością osobników w zimie i wysoką latem (Tab. 1, Fig. 3, Apendyks 2). Warunki pogodowe miały niewielki wpływ na liczbę osobników i bogactwo gatunków. (Tab. 1). Dla tej samej liczby osobników więcej gatunków stwierdzano latem, jednak liczba osobników nie jest wystarczająca, aby wyjaśnić

cykliczną zmienność liczby gatunków (Fig. 4). Zespoły ptaków obserwowane podczas lata wykazywały się niższą szerokością niszy pokarmowej niż zimą (Fig. 4, 5).

Autorzy konkludują, że hipoteza dostępności energii nie jest w stanie wyjaśnić sezonowej zmienności bogactwa gatunkowego w regionach klimatu umiarkowanego.



APPENDIX 1.

Fig. S1. Records of daily rainfall, mean temperature (°C) as well as minimum (blue symbols) and maximum temperature (red symbols) between January 1st 2009 and December 31st 2014. The grey and black lines are predicted values from a cosinor-regression implementing a cycle with a period of one year. The data were recorded at the Ecological Botanical Garden of the University of Bayreuth (Micrometeorology, Prof. Dr. Thomas, BayCEER, University of Bayreuth).

APPENDIX 2. AN ALTERNATIVE APPROACH TO TEST FOR BIENNIAL AND ANNUAL CYCLES.

Another method for the analysis of cyclic variation within data sets would be the Fourier analysis (Chatfield 1975). However, the algorithms implementing a Fourier analysis like the fast Fourier transform for computing the constituent frequencies of a signal require data sampled at equal intervals (e.g. daily, weekly). Although we made considerable efforts to make weekly counts, it was not always possible to follow such a regular schedule. Thus a direct application of the fast Fourier transform was not possible. Therefore, we first fitted general additive models (gam; ad-on package mgvcin R using a cubic regression with $k = 25$; Wood 2006) of the response variables using the date of sampling as an independent variable. The difference of the approach using gam models to the cosinor-approach is that gam models also capture differences in the frequencies (cycles) between years (caused e.g. by the weather conditions of a particular year) whereas for the cosinor-approach the frequency and amplitude of the cycles is constant across years. Thus for estimating the importance of weather conditions for the annual variation of abundance or richness the use of the cosinor is conservative.

In a next step we used these gam models to predict the response variables on a daily basis. These predicted values were then submitted to a fast Fourier transform to estimate the “importance” of the various cycles (Barnett & Dobson 2010; formula 1.7) using the function `peri` within the add-on package `season` (Barnett & Dobson 2010). As the predicted daily values are not independent due to the underlying model, a statistical evaluation of importance is not straight forward. We implemented a simple approach: First we randomized the response variables across the dates of the transect counts. Second we fitted gam models to the randomized data sets (100 randomizations) and generated predicted values on a daily basis. Third we submitted these predicted values to a fast Fourier transform and estimated the importance of the various cycles. Only cycles of the original data sets that had a clearly higher importance than expected from the randomizations were considered significant.

Note that in Fig. S2 the predicted values for species richness using a gam model showed clear biennial and annual cycles. The analyses of the importance of cycles with different frequencies also shows the significance of a biennial and annual cycle: the values of the importance estimates from the original data set is much higher than the expectations from the 100 randomized data sets. For the number of individuals, the predicted values show a more complex pattern compared to the predicted values of the cosinor-approach (compare Fig. 3 with Fig. S2). Nevertheless, our heuristic statistical test indicates a biennial cycle. Furthermore, the analysis of the niche breadth in respect to diet was also consistent between the approach using a gam model and the fast Fourier transform. Overall both approaches generated very similar results and we decided to present in the main text the much simpler cosinor-analyses.

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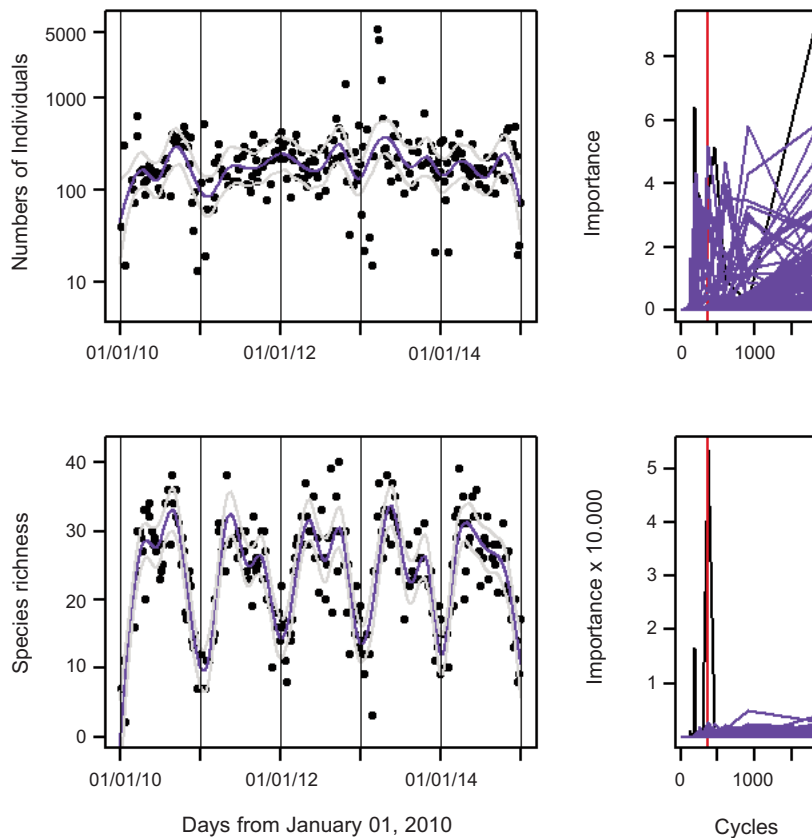


Fig. S2. Variation of the number of individuals (\log_{10} -transformed) and species richness across the five years of bird observations (right panels), with predicted values (± 2 standard deviations — grey lines) using a generalized additive model. The left panels show the importance of the various cycles for the respective response variable. The black line shows the importance for the actual data set, the blue lines the importance for 100 randomizations. The red vertical line indicates an annual cycle. The absolute values of the importance are not comparable between the analysis of the number of individuals and species richness.

APPENDIX 3. SELECTING AN APPROPRIATE TEMPORAL RANGE FOR WEATHER VARIABLES.

The correct selection of the temporal range of explanatory weather variables is essential to the correct assessment of weather impact on the number of individuals as well species richness in the study area (see also Stenseth & Mysterud 2005). Furthermore, temperature in particular shows clear temporal autocorrelation. Therefore, we did not use the temperature or rainfall on the actual day of the count for analysis but rather a mean (or in the case of rainfall the sum) across a time window of 10 days starting with the actual day of the transect count. Of course, there are numerous options and therefore we evaluated various scenarios of possible time lags and number of days for the window (Fig. S3a). First we considered the temperature and rainfall data of a single day with an increasing time lag between the transect count and the measurement of the climate data. In the second and third scenario we used a moving window (5 days and 10 days) with an increasing time lag to the actual day of the transect count. Across each window we calculated the mean temperature and the sum of the rainfall. Fourth, as we increased the window we averaged or summed the weather variables accordingly. All scenarios gave more or less similar results (Fig. S3b), the highest t-values being those for the regression coefficients for small time lags. Of course, the details of such plots varied between variables and after considering graphs for all response variables we decided to use a window of 10 days with no time lag.

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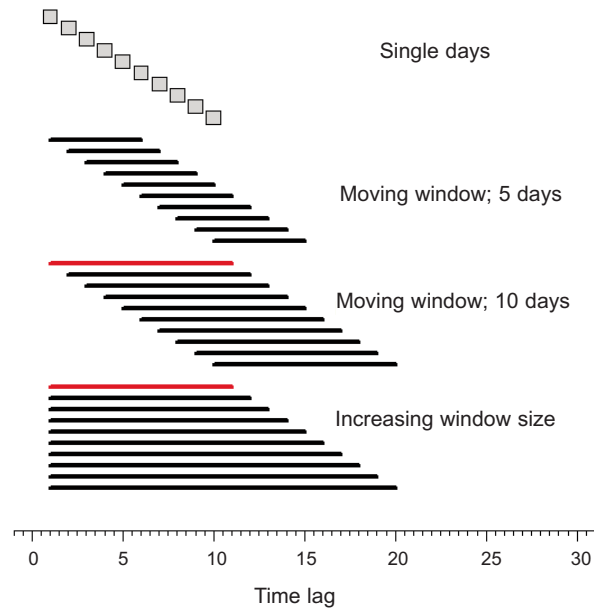


Fig. S3a. Sketch of the scenarios evaluated in Fig. S3b (we show only the first 10 steps in each scenario). We considered single days with increasing time lags for modelling our response variables, moving windows of 5 and 10 days and a scenario with increasing window size. In red we indicate the selection used during our analysis (first step in the third and fourth scenario).

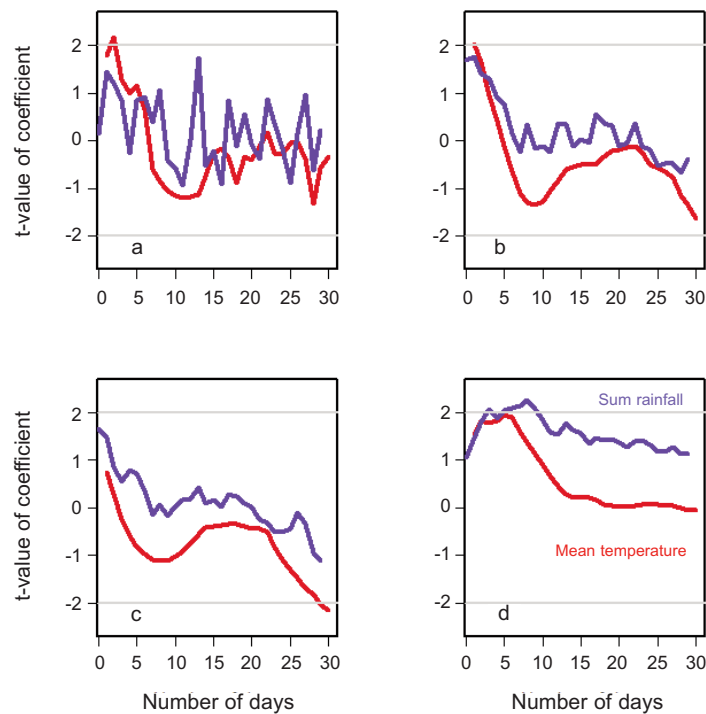


Fig. S3b. Example of our exploration to select meaningful weather characteristics. We present the results of the four scenarios outlined in Fig. 3a for the response variable $\log_{10}(\text{number of individuals})$. We evaluated the importance of temperature and rainfall (t-values of the regression coefficients; grey lines indicate significance at $p = 0.05$) in models that included the cosinor-terms for an annual as well as a biannual cycle as well as the two weather variables. Note that all four scenarios (Fig. S3a) suggest that we should use the weather variables with no time lag. Furthermore, averaging or summing the values across a window of several days decreases the variability of the results.