

Biodiversity dynamics at a migration stopover site in Western Europe: ecological relevance and implications for conservation

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Abstract

Biodiversity dynamics, i.e. how diversity changes over time at a single site, is a poorly studied subject in bird ecology and conservation. I recorded diversity in terms of species richness and abundance from ringing data obtained in summer and autumn of three successive years at a major migration stopover site located in Uebersyren, Luxembourg. The analysis had three distinct steps: i) defining biological periods, similar in their species composition and identifying which species are responsible for imposing that similarity, ii) comparing mean diversity for those periods using multiple mean comparisons and general linear models and iii) identifying a general pattern of biodiversity change over the considered time frame. The results showed that a “migration calendar” could be constructed with the Reed Warbler *Acrocephalus scirpaceus*, Blackcap *Sylvia atricapilla*, Marsh Warbler *Acrocephalus palustris* and Robin *Erithacus rubecula* as the main drivers of similarity between periods. Diversity was shown to be significantly different between the periods, but not between years. A general pattern emerged with diversity dropping from July to August, then rising steadily until reaching a peak at the end of October before decreasing again in November. The results might convey important information about the extent and change of biotic interactions within a stopover site. Furthermore, they underline the fact that conservation effort in stopover sites should be carried out throughout the whole migratory season.

Résumé : Dynamique de biodiversité sur un site de halte de migration au centre d'Europe: pertinence écologique et implications pour la conservation

La biodiversité dynamique, c'est à dire un changement de diversité à travers le temps, est un sujet peu exploré dans l'écologie et la conservation des oiseaux. Dans cette étude, j'ai interprété la biodiversité en tant que nombre d'espèces et nombre d'individus de chaque espèce en utilisant des données de baguage collectées dans une zone de halte importante à Uebersyren, Luxembourg. L'analyse comportait trois démarches: a) définition de périodes qui sont similaires en composition d'espèces et identification des espèces responsables pour cette similarité, b) comparaison de la diversité moyenne des ces périodes en utilisant des méthodes statistiques et c) identification d'un motif général de changement de biodiversité à travers la période considérée. Les résultats montraient qu'il était possible de créer un “calendrier de migration” et que les espèces les plus importantes pour définir ce calendrier sont la Rousserolle effarvate *Acrocephalus scirpaceus*, la Fauvette à tête noire *Sylvia atricapilla*, la Rousserolle verderolle *Acrocephalus palustris* et le Rouge-gorge *Erithacus rubecula*. Des méthodes statistiques confirmaient qu'il y a des différences de biodiversité considérables entre les périodes nouvellement définies, mais non entre les années. Un motif général a été observé: la diversité diminuait de juillet à août, après elle montait constamment jusqu'à fin octobre avant de décliner de nouveau en novembre. Ces résultats donnent des

informations importantes sur la dynamique des interactions biologiques pendant la migration. En outre, les résultats confirment l'importance de la gestion de biodiversité pendant toute la saison migratoire dans une zone de halte.

Zusammenfassung: Biodiversitätsdynamik an einem Zugrastplatz in Mitteleuropa: ökologische Relevanz und Rückschlüsse für den Naturschutz

Die Biodiversitätsdynamik beschreibt wie sich die Artenvielfalt in einem Gebiet über einen bestimmten Zeitraum verändert. Entsprechende Untersuchungen werden in Vogelökologie und im Vogelschutz eher selten unternommen. In dieser Studie wurde die Biodiversität in Form von Artenreichtum und Individuenzahl pro Art über einen Zeitraum von drei Jahren während des Herbstzuges anhand von Beringungsdaten an einem wichtigen Zugrastplatz in Uebersyren, Luxemburg, gemessen. Die Datenanalyse wurde in drei Schritten durchgeführt: a) Bestimmung von Perioden die sich in ihrer Artenzusammensetzung ähnlich sind und Identifizierung der Arten, die für diese Ähnlichkeit verantwortlich sind, b) Vergleich der Artenvielfalt der Perioden anhand statistischer Mittel und c) Identifizierung eines einheitlichen Musters von Biodiversitätsveränderung über den studierten Zeitraum. Die Resultate zeigten, dass es möglich ist einen allgemeinen "Migrationskalender" aufzustellen, in dem der Teichrohrsänger *Acrocephalus scirpaceus*, die Mönchsgrasmücke *Sylvia atricapilla*, der Sumpfrohrsänger *Acrocephalus palustris*, sowie das Rotkehlchen *Erithacus rubecula* die Hauptarten sind, die die Ähnlichkeit von Perioden bestimmen. Eine statistische Analyse bestätigte, dass es bedeutende Biodiversitätsunterschiede zwischen den neu definierten Perioden gab, aber nicht zwischen den verschiedenen Jahren. Ein jährlich wiederkehrendes Muster der Biodiversität konnte erkannt werden: die Artenvielfalt nahm von Juli bis August ab, stieg dann an und erreichte einen Höhepunkt Ende Oktober, bevor sie im November wieder abnahm. Die Resultate vermitteln wichtige Information über die Dynamik der intra- und interspezifischen Beziehungen der Vogelarten während des Zuges. Zusätzlich bekräftigen die Resultate die Wichtigkeit eines adäquaten Schutzes der Zugrastplätze über die ganze Zugzeit hinweg.

Introduction

The term "biodiversity" has gained increasing importance in the last two decades, a fact supported by an exponential growth of scientific papers on biodiversity analyses (Magurran 2003). This rush of papers is mainly the result of growing concern about environmental change in face of human population growth and the associated consequences of increasing natural resource exploitation and climate change. The term "Biodiversity dynamics" describes how diversity changes over time and has a widespread use in the study of succession (Begon et al. 2009). Depending on the environment, the time frame can span several days (e.g. during decomposition) to several decades or longer (e.g. plant succession). Equally important, and for long ignored in the study of diversity dynamics are environments that are seasonally exploited by a number of species. Bird migration stopover sites i.e. locations that are used by migratory birds to rest and refuel their energy reserves are one example of an environment whose exploitation varies seasonally. All bird species do not migrate simultaneously and each species has particular ecological requirements, often reflected in its choice of a stopover site (Berthold 2008). Measuring how biodiversity changes over time at a stopover site

provides valuable information about the extent of biotic interactions at any particular time point if we choose the measure of diversity carefully. This study recorded the number of species (*species richness*) as well as the number of individuals of each species (*species abundance*) each day in a three-year dataset during autumn migration. Such a measure will be important in quantifying both interspecific and intraspecific interactions. The aim of the study was to identify how diversity of migratory birds at a stopover site changed during autumn migration. More specifically, the investigation aimed at identifying if particular migratory periods could be clustered in terms of similarity in their species composition, if those periods differed significantly in their diversity and if there was any consistent pattern of how diversity changed over the time considered. Besides having ecological relevance, such measures can be relevant for conservation: the tension between human exploitation of stopover sites, be it in agricultural or leisure activities, and its conservation value has been present since early ages. A search on “ISI Web of Knowledge”, a vast database of scientific papers, showed that bird diversity at stopover sites is a poorly studied subject with few papers published. These almost exclusively focussed on species richness and ignored abundance altogether, which limits the predictions that can be made about the ecological and conservational relevance. Thus another aim of this paper was to provide a specific methodology as a guideline to encourage future research in that particular area.

Methods

1. Collecting and selecting the data

The study was carried out during three consecutive years (2007, 2008, 2009) at a migratory stopover site in Uebersyren, Luxembourg, hosting a bird ringing station. This area, known under the local name “Schlammwiss” is part of the Special Protection Area “Vallée de la Syre de Moutfort à Roodt/Syre”. Being part of the conservation area network NATURA 2000, it has been recognized international conservation value. At the national level, it is in the process of being reclassified as “Natural Reserve”. Biver et al. (2010) list 63 species that nationally characterise zones of special “ornithological interest”: 30 of the 63 species use the habitat actively either as a foraging or resting site and four further species have been regularly recorded as breeding locally. The study site, a wetland of 10 ha, is largely covered by *Phragmites australis* and *Carex* species and three large ponds, and, although it is surrounded by agricultural surfaces, a highway, a road and an industrial estate, it proved to be an important resting site for many migratory birds with over 90 species and up to 40'000 individuals caught per year. The data on bird diversity were obtained using mist netting (and ringing) during the autumn migration period, spanning the 10th of July to the 15th of November each year. Nets were opened slightly before sunrise and were generally kept open until noon each day. As mist netting effort was limited by weather conditions and the amount of helpers available, sample sizes turned out to be quite variable, which must be considered in our biodiversity measure. It was important that the sample of birds caught each day reflected the true species richness and abundance present in the reserve. To account for any possible bias, “filtering” the data before use was necessary. This study was limited to diversity dynamics imposed by migrants.

First, to distinguish migrants from local breeders, migratory presence periods were defined for each species, largely based on observations made in the reserve over the last 10 years (Table 1). Birds

caught during breeding time and caught again during the migration period were not included. Furthermore, re-traps (a minority of birds caught each day) were not considered so that true migration dynamics could be reflected. Individuals of all bird species that are known not to breed on the site or in nearby areas were all included in the analysis.

Second, only species with equal “catchability” were considered. Species that were caught using other methods than mist netting (e.g. Water Rails, *Rallus aquaticus*), using the site as a dormitory (like the Barn Swallow, *Hirundo rustica* and the White Wagtail, *Motacilla alba*), or strongly attracted by tape luring (e.g. Wryneck, *Jynx torquilla*, Skylark, *Alauda arvensis*) were excluded from the analysis. This exclusion however cannot completely prevent a potential bias due to tape-lures affecting species diversity and abundance in the migratory season. Tape-lures confer the advantage of attracting all migrants from nearby areas and the disadvantage that only those species whose song is played by tape-luring tend to be attracted, meaning that the strength of the attraction is often species-specific. To minimise this effect, only songs of species that were currently known to migrate were played by the sound traps. For example the song of the Marsh Warbler, *Acrocephalus palustris* was played from beginning of July to mid-August. In addition, a “cocktail” of songs of rare species was played almost continuously in order not to miss any infrequent migrants.

Third, days with less than 10 birds caught were not included as such a small sample size could have disproportionately affected the chosen diversity measure. Forty migrant species were finally retained in the analysis (Table 1). In this article, the term ‘migrant’ species is used in its widest sense i.e. partial migrants are as well considered. Even after extensive filtering, the dataset remained considerable: a total of 30’027 individuals were included in the study.

Table 1: The 40 species collected during the autumn migration 2007, 2008 and 2009 and included in the study (Dates below indicate the periods of consideration for each species. “Young” = birds born in the same year, “Adult” = birds older than one year, “All birds” = all individuals caught are included in the analysis).

1. Acrocephalus arundinaceus All birds	10. Hippolais icterina All birds	19. Oenanthe oenanthe All birds	28. Phylloscopus trochilus After 01.08.	37. Troglodytes troglodytes All after 15.09.
2. Acrocephalus paludicola All birds	11. Hippolais polyglotta All birds	20. Parus ater All after 20.08	29. Prunella modularis All after 05.08.	38. Turdus merula All after 20.08.
3. Acrocephalus palustris Adults: after 10.07. Young: after 25.07.	12. Lanius collurio All birds	21. Parus caeruleus All after 01.09	30. Remiz pendula All birds	39. Turdus iliacus All birds
4. Acrocephalus schoenobaenus All birds	13. Locustella luscinioides All birds	22. Parus major All after 01.09.	31. Saxicola rubetra All birds	40. Turdus philomelos After 05.08.
5. Acrocephalus scirpaceus Adults: after 20.07. Young: after 31.07.	14. Locustella naevia Adults: after 10.07. Young: after 15.07.	23. Parus montanus All after 20.08.	32. Saxicola rubicola All after 20.07.	
6. Anthus pratensis All after 15.07.	15. Luscinia megarhynchos All after 15.07.	24. Parus palustris All after 20.08.	33. Sylvia atricapilla All after 15.07.	
7. Anthus trivialis All after 17.07	16. Luscinia svecica All birds	25. Phoenicurus ochruros All after 05.08.	34. Sylvia borin All after 20.07.	

8. <i>Emberiza schoeniclus</i> All after 20.08.	17. <i>Motacilla flava</i> All after 20.07	26. <i>Phoenicurus</i> <i>Phoenicurus</i> All after 05.08.	35. <i>Sylvia communis</i> All after 20.07.
9. <i>Erithacus rubecula</i> All after 05.08.	18. <i>Muscicapa striata</i> All birds	27. <i>Phylloscopus</i> <i>collybita</i> All after 15.08.	36. <i>Sylvia curruca</i> All after 20.07.

2. Measuring diversity

The diversity analysis had three main components. First, rather than just using the arbitrary measure of “months” as the period of interest, “biological” periods were defined. Second, to see if they differed, the calculated measures of diversity for each period were compared using statistical tests. Third, I tried to identify a general pattern of diversity change that emerged out of the autumn migration period.

In this study I used both, species richness and species abundance data to calculate a diversity index for each sampling day. The measure of diversity used in this study is “Simpson’s 1-D”, the complement of Simpson’s D, a diversity index recommended by many leading ecologists because it is biologically meaningful and especially robust to sample size (Magurran 2003). The formula of Simpson’s D is given by

$$D = \sum \left(\frac{n_i [n_i - 1]}{N [N - 1]} \right)$$

where n_i is the number of individuals in species i and N is the total number of individuals in one sample.

The number of species corresponds to the number of terms in the sum D . If there are 10 species, ten terms are summed together to obtain D . However, D in itself decreases as diversity increases. For the index value and diversity to behave in parallel (i.e. as diversity increases, the index increases) the complement **1-D** was used throughout this study as the diversity measure of choice.

To define the periods of interest for which diversity should be compared, I used cluster analysis, a multivariate method based on the Bray-Curtis similarity measure SBC (Bray & Curtis 1957) which compares species composition in terms of presence and abundance in the defined sampling periods. SBC for two periods is defined as the number of shared species divided by the mean richness of both periods. If two periods have no species in common, SBC equals 0. If two periods have identical species composition, the measure equals 1. Using an appropriate algorithm, the two most similar periods in terms of species composition were combined in a single cluster. Similar periods were successively clustered to form a single dendrogram (a similarity tree). To identify which species were most important in explaining the variation in species composition across the sampling period and hence the clustering, principle component analysis (PCA) was used. To perform PCA and cluster analysis, the pooled species richness and abundance from all three years was combined into pentads (sequences of five days). This means that data of one specific pentad were added together for all three years to eliminate year-specific variation. Choosing the pentad as a unit gave a high resolution of the data as the period was long enough to embrace the species composition of multiple sampling days without compromising the precision of detecting species turnover over time. Based on this

dendrogram, I defined new, biologically more meaningful periods of time. Hence, the outcome of cluster analysis and PCA was the construction of a “migration calendar” (to determine which periods are most similar in their species composition) and the determination of which species were most influential in defining the calendar.

A diversity index for each sampling day was calculated and indices were then averaged over each newly defined period in each year. Mean diversities of each period were compared within each year to see if there were significant differences between them. To do so, a parametric test (ANOVA) was used if the residuals of the data were normally distributed. To test for normality of the residuals, I used the Shapiro-Wilk test. If the residuals were normally distributed, a Tukey-Kramer test identified which means significantly differed. In contrast, if the residual distribution was non-normal (which was the case in two out of three years analysed), a non-parametric alternative of ANOVA, the Kruskal-Wallis test was used to compare the means. Although it is theoretically possible to transform the data to obtain normality, no such transformation could be found. Accordingly, the Mann-Whitney test filled the purpose to see which means significantly differed. All calculations, including diversity measures and statistical analyses were performed using the software package PAST version 2.04 (Hammer & Harper 2001).

ANOVA is part of a type of models called “General Linear Models” (GLM). GLMs are used if there is more than one recorded explanatory variable underlying observations. In this study we had two explanatory variables: years and periods within years to explain the observed levels of diversity. It was thus necessary to assess how much of the variance was due to differences between years and due to the differences between periods. The corresponding equation is thus:

$$\text{Diversity} = \text{Year} + \text{Period} + \text{Year} * \text{Period}$$

where Year*Period represents the interaction factor. This means that, depending on the year, there could be a significant difference between periods or not. The GLM in this study was constructed in JMP (2000).

Results

1. Cluster analysis and PCA

Cluster analysis showed how the various pentads of each month were associated on basis of their species composition. The outcome of the cluster analysis can be seen in Fig. 1. Indeed, as expected, the newly defined sampling periods tended to cluster according to their sequence in time. However, some details would have been missed if we had simply used the unit “month”. The three first pentads of November formed a cluster with the four last pentads of October whereas the first two pentads of October clustered with all pentads of September. All pentads of July were found in one single cluster and so were the pentads of August. Interestingly the sixth pentad of October is clustered with the third and fourth pentad of the same month. Because the Bray-Curtis index accounts for both, abundance and presence of species, this might be due to incoming migration of a northern population of several species.

Overall there is high heterogeneity between pentads, even if they follow each other in time. Measured by the Bray-Curtis similarity index, all pentads of August share a similarity of at least 65 % whereas the heterogeneity is even higher for July, with an average similarity of 45%. As can be seen from Fig.6, the higher the number of species relative to the number of individuals, the more heterogeneous the periods are. Defining the new periods of a “migration calendar” required a compromise between the obtained similarity dendrogram in order to homogenise the comparative units (here: periods) to the maximum extent and the necessity that those new periods must follow each other in time. The newly defined periods are given in Table 2. Those periods turned out to be of different length. This however should not have affected the subsequent analysis because having equal sample sizes is not an assumption of general linear models (Grafen & Hails 2002).

Table 2: The newly defined periods of a “migration calendar” (Those periods were inherently similar in their species composition).

Period	Time Span
July	10 July - 31 July
August	1 August - 31 August
Beginning September	1 September - 15 September
September-October	16 September - 10 October
End October	11 October - 31 October
November	1 November – 15 November

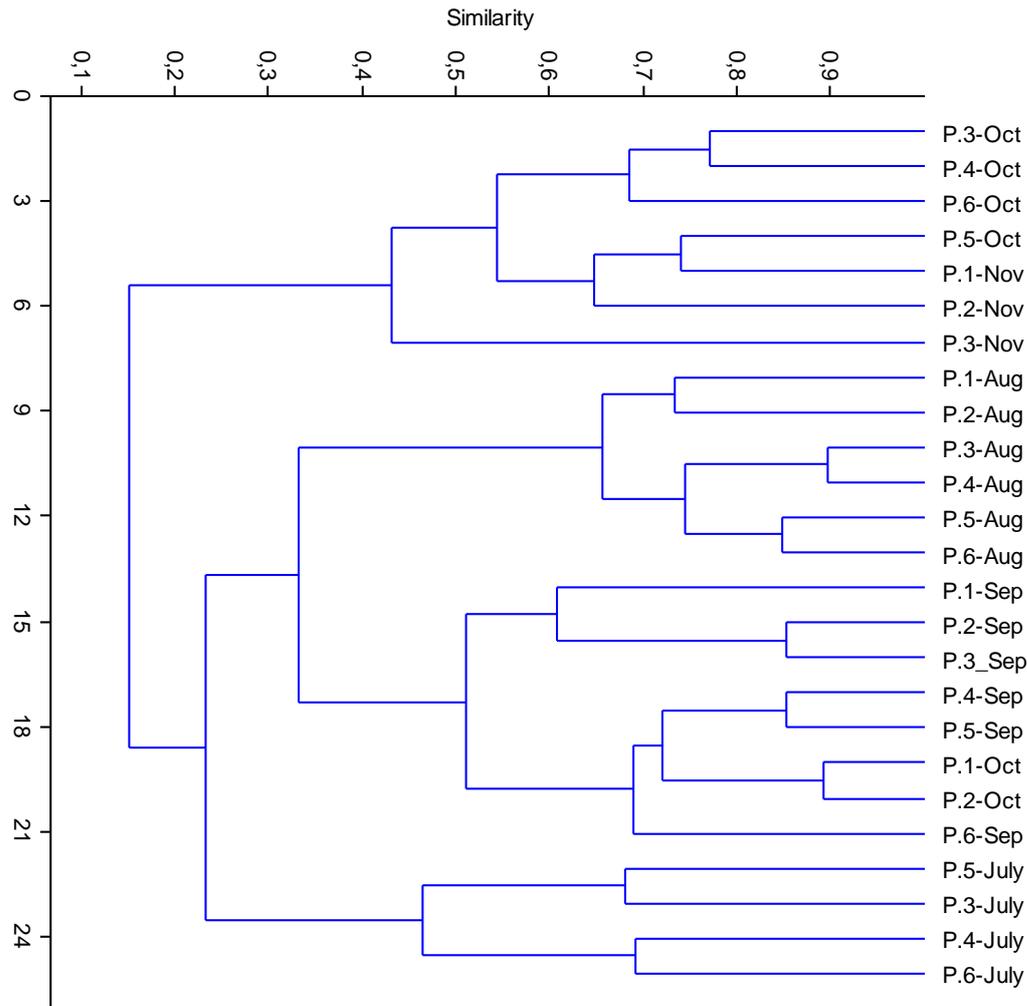


Figure 1: Similarity dendrogram segregating autumn migration into distinct periods that have a similar species composition. The process of clustering two pairs progresses from left to the right and the two most similar periods are always associated in pairs at the tips. The x-axis represents the Bray-Curtis similarity measure ranging from 0 (no species in common) to 1 (all species in common). The y axis simply counts the number of units in the analysis (here pentads). P stands for pentad (for example P.4-July means the fourth pentad of July).

The similarity dendrogram clustered periods in terms of their species composition. The next step was to look which migratory species were most important in defining the similarity between periods. To do so, the Principle component analysis (PCA) was used to capture the complexity of the data. In mathematical terms, each species represents one dimension in the data set. The presences of many species are correlated i.e. there is much redundancy in the data. In essence, PCA reduces these dimensions by defining new axes (called principle components, PC), thus combining the original data in a novel way. Each of the principle components (PC) has a number of bird species associated with it. The PC that explains most of the variance in the data set is called PC1, the second most important is PC2 and so forth. In this study, PC1 explained 55.7% of the total variance, PC2 explained 31.2 %, PC 3 was responsible for 8.3 % and PC4 caused 3.2% of the variance. To find out how those new variables were constructed, the “loadings” of the original species data that were combined to construct those new variables, were consulted. Only the most important species in each PC was considered. The

Reed Warbler *Acrocephalus scirpaceus* turned out to be by far the most important species in defining PC1, followed by the Blackcap *Sylvia atricapilla* in PC2 and the Marsh Warbler *Acrocephalus palustris* together with the Robin *Erithacus rubecula* in PC3. These species were also amongst the most commonly caught on the site. This made intuitive sense: the newly defined periods above largely reflected the migration dynamics of these most common species. However, *Acrocephalus palustris* marked an exception: although the numbers of individuals caught per year were not that high, its presence at the stopover sites in high numbers was limited to July and beginning of August, making it a highly characteristic bird species for that period and, thereby, it explained a disproportionate amount of the variance.

2. Diversity analysis

There were significant differences in diversity between periods, as can be seen in Fig. 2 and Fig. 3. In each year I found significant differences in diversity between periods. However, there was a relatively high heterogeneity between years: sometimes differences between periods were significant in one year but not in another year. Nevertheless, the general trend showed that the periods September-October as well as end October had a significantly higher diversity than other periods. Diversity in October differed significantly from the diversity in August in all three years and in two out of three years it differed significantly from diversity in July and September. In two out of three years, a significant difference between November and August (2009 and 2007) was observed. Moreover, in one out of three years there was a significant difference between September and August (year 2008)/ July (2008), between September-October and July (2008)/ August (2007)/September (2008) as well as between November and August (2008). The comparisons of mean diversity in each year and their associated p-value can be found in Tables 3 and 4.

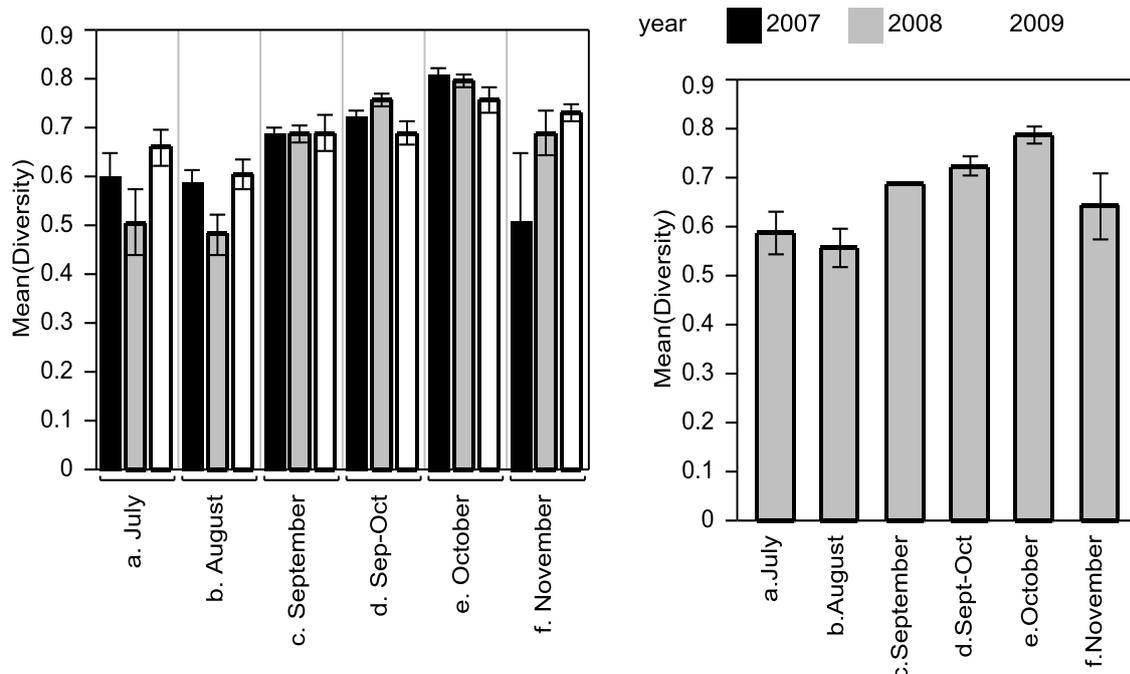


Figure 3 and Figure 4: The histogram on the left (Fig.3) shows the distribution of mean diversity (1-D) within years and defined periods. Error bars represent one unit of standard error from the mean. The year 2007 is marked in black, 2008 in grey and 2009 in white. The histogram on the right (Fig.4) shows the "mean of the

means” for each period by averaging the mean diversity indices found in each year. It gives a general view of how bird diversity changed over time in the reed-bed. One unit of standard error is associated with each mean. (Notice that the standard error for September is too small to be visible on the diagram.)

Table 3: Differences in diversity for 2009. The residuals were not normally distributed, hence a Kruskal-Wallis test was performed which was significant (df=5, H=13.22, p=0.0214). The means were compared with a Mann-Whitney test. Significant p-values are marked in bold.

2009	July	August	September	Sep-Oct	October	November
July	0	0.1296	0.4636	0.7667	0.1023	0.1264
August		0	0.08323	0.06004	0.007643	0.01917
Sept			0	0.7558	0.4208	0.7144
Sep-Oct				0	0.1258	0.2979
Oct					0	0.6761
Nov						0

Table 4: Differences in diversity for 2008. The residuals were distributed normally (Shapiro-Wilk test, W=0.97, p=0.1289). An ANOVA test was performed (df=5 and 59, F=12.35, p<0.01). A Tukey-Kramer test compared the means (with p-value marked in bold if significant).

2008	July	August	September	Sep-Oct	October	November
July	0	0.9989	0.04687	0.001842	0.0003095	0.04405
August		0	0.01658	0.0005941	0.0001749	0.01548
September			0	0.8689	0.4903	1
Sep-Oct				0	0.9868	0.8791
October_					0	0.5058
November						0

Table 5: Differences in diversity in 2007. The residuals were not distributed normally. A Kruskal Wallis test showed high significance (df= 5, H= 28.22, p<0.01). Means were compared with a Mann-Whitney test (p-value is in bold if significant).

2007	July	August	September	Sep-Oct	October	November
July	0	0.3219	0.706	0.08028	0.0001716	0.3191
August		0	0.0771	0.002904	8.11E-05	0.5299
September			0	0.1098	0.0006355	0.0771
Sep-Oct				0	0.002308	0.05523
October					0	0.05019
November						0

It was also possible to construct a general linear model (GLM), but only after the diversity data were square-transformed to meet the assumptions of normality of residuals (Fig. 5). The assumptions were not completely met however (Shapiro-Wilk test, W=0.98, p=0.0451). But due to the symmetry of the residual distribution as well as the robustness (resistance to deviations from assumptions) of GLM, this should not influence the interpretation of the significance values (Schluter & Whitlock 2010).

The GLM showed that the period of migration was most important in explaining variability ($p < 0.001$) and that differences between years were not significant ($p = 0.37$). However, the interaction factor (Year*Period) was significant ($p = 0.0136$), confirming the finding from above that depending on which year we consider, there might be significant differences between periods or not (Table 6 and Table 7). Table 8 shows which periods were significantly different if we controlled for differences between years and hence can be seen as a summary of Tables 3, 4, and 5. Again, there were many significant differences in diversity between periods, with October being different from all other periods. The constructed model explained 43% of the observed variation ($R^2 = 0.43$), the rest of the variation being contained not between years or between periods, but within periods. The fact that there were many significant differences between the sampling periods showed that the periods identified by cluster analysis were biologically meaningful in terms of stopover ecology of migratory birds.

Table 6: ANOVA Table of the general linear model.

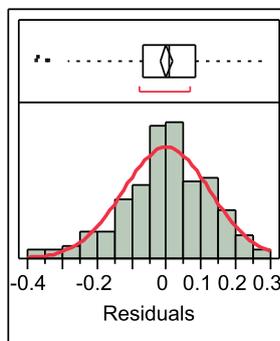


Figure 5: Distribution of residuals of the model. The unbroken line represents the normal distribution for comparison.

Source	DF	Sum of Squares	Mean Square	F Ratio
Model	17	2.3162566	0.136250	7.8587
Error	176	3.0513994	0.017337	Prob > F
C. Total	193	5.3676560		<.0001*

Table 7: Effect tests: the factors “period” and “year*period” had a significant effect on observed differences in diversity. The factor “year” was not significant. Significant values are marked with an asterisk.

Source	Nparm	DF	Sum of Squares	F Ratio	Prob > F
Year	2	2	0.0337739	0.9740	0.3796
Period	5	5	1.7595353	20.2975	<.0001*
Year*Period	10	10	0.4026208	2.3223	0.0136*

Table 8: Differences in diversity between periods, controlling for differences in years. Means were compared with a Tukey-Kramer test. Periods that showed no significant differences in mean diversity are marked with NS (non-significant), periods that differed significantly are marked with $p < 0.05$.

	July	August	September	Sep-Oct	October	November
July	/	NS	NS	p<0.05	p<0.05	NS
August		/	p<0.05	p<0.05	p<0.05	NS
September			/	NS	p<0.05	NS
Sep-Oct				/	NS	NS
October					/	p<0.05
November						/

Another aim of this paper was to look for a consistent pattern of diversity dynamics. When considering Fig. 1 and Fig. 4, a very clear pattern emerged which was consistent across all three years: There was a general increase in diversity starting from the beginning of the migratory season in July, reaching a maximum during end September and the whole of October, but then dropping down again in November. I say “general” increase because there was a slight drop in diversity during August before the increase really took off in September. Although diversity did not differ significantly between those periods, this distinct drop was observed in all three years. An overview how the number of migrating species and migrating individuals (independent of species) are distributed over autumn migration is given in Fig 6.

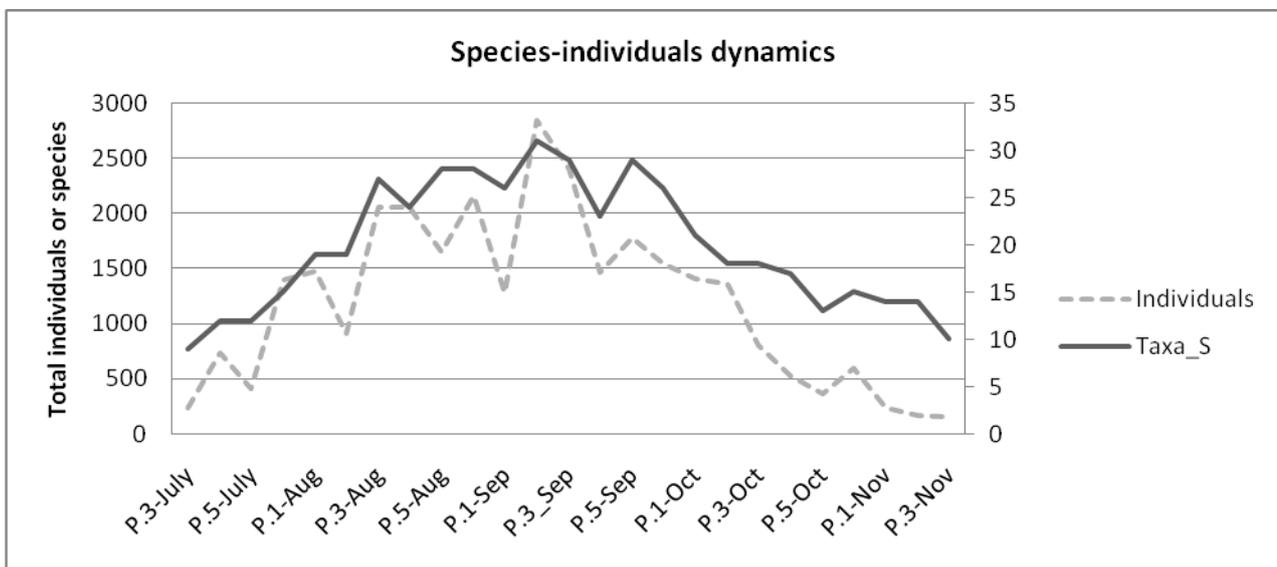


Figure 6: Changes over time in the number of migratory species (unbroken line, Taxa_S) and individuals (broken line) at the stopover site (y-axis, P= pentad; the number of individuals on the left x-axis, number of species on the right x-axis).

Discussion

This study described how diversity of migratory birds changed over time at a stopover site in Luxembourg. Diversity during the migration period was not just measured by species richness, but by an index that took into account the relative abundance of individuals caught of each species. Mist netting birds is a unique way of getting high resolution data that add a quantitative component to the “classical” absence-presence data of species counts. The site where the birds were recorded is fairly small (10ha) and the density of mist nets was relatively high. Although it was certainly not possible to record all individuals present, it remains reasonable to assume that the number of individuals caught each day was a relatively high and constant percentage of the birds present in the reed bed at any particular day. It is thus highly probable that the dynamics observed in this study reflected the true dynamics on the natural site. This conclusion is supported by the fact that the general pattern of diversity dynamics remained fairly constant over all three years: starting at a mean diversity (1-D) of 0.57 in July, there was a slight drop in August, then a distinct rise until

reaching a peak in the second half of October and dropping again in November. Although tape-luring might have had some influence in intercepting nocturnal migration (and thereby might have biased the estimate of the birds that would have used the reserve in the absence of tape-luring), its effect should not be overestimated. Chernetsov (2006) underlines that, unless birds are caught at night (in this study, a minority) or in an atypical habitat (all birds included in this study are known to use wetlands as stopover sites, at least for feeding), one cannot invoke the tape-lures as a reason for flight interception and hence most migrants caught in one day are a subset of the migrant pool that landed in nearby areas (Schwilch & Jenni 2001). One has to remain careful though, as the capture probability of some species was shown to be 3.9 times higher when tape-lures were used than in their absence (Schaub et al. 1999). In this way, this study would rather investigate the composition of (overflying) migratory flocks rather than the diversity of temporary stopover site communities that would naturally use the reserve in the absence of tape-lures. Using tape-lures may increase the number of individuals caught, but as such, the method renders the results more representative for Western European stopover sites in general rather than limiting the conclusions exclusively to the study site in Luxembourg.

In addition, there is a risk that some species that were present, but whose song was not played, were lacking from the samples. This is partly compensated by choosing Simpson's D as an index that is robust to sample size and that does not change overwhelmingly if one species, represented by only a few individuals, is added to the diversity calculation. Furthermore, 29 of the 40 species included in this study were permanently lured by sound during their specific migratory presence, thereby minimizing any potential bias. Nevertheless, it would be of great interest to use the same set-up for studying stopover dynamics in the absence of tape-lures and see if the same patterns emerge.

A last caveat in this study (as in any study of stopover sites) is the problem of distinguishing local breeders (especially concerning partially migrant species) from real migrants: the filtering process (see methods) used here reduced the potential bias as much as possible by choosing the appropriate dates and excluding re-traps known to be locals. However, future studies should consider that there is no inherent reason to exclude local birds as they also play an important role in local community dynamics through competition or other interactions with resting migrants. Again, regarding the low number of locals versus the considerable number of migrants, the relative robustness of Simpson's index would probably leave the conclusions unaltered.

A detailed statistical analysis showed that in most years diversity differed significantly among those periods. However, it is important to consider the underlying biological process in diversity dynamics. This was already partly fulfilled by choosing periods that made intuitive biological sense: the periods in question were inherently similar in their species composition (as revealed by cluster analysis), thereby reflecting the migration activity of the most commonly caught birds (Reed Warbler, Blackcap, Robin and Marsh Warbler). PCA showed that those four species were most important in dictating differences in diversity among periods. I therefore suggest that those four species are equally central in driving other community relationships within a Western European stopover site. The drop in diversity in August was most probably caused by the peak of Reed Warbler inflow into the reserve, together with a sharp drop in Marsh Warbler numbers. Fig. 6 revealed that the number of species was high during August, but so was the number of individuals, the biomass of which is strongly biased towards the Reed Warbler. In mid-September, the Blackcap reached its migration

peak simultaneously with a number of other species, hence the increase in diversity. Once the Blackcap inflow decreased, diversity increased even more because a relatively high number of species tended to be present with equal numbers of individuals. As can be seen from Fig. 6, the number of species in the reserve in end October dropped less sharply than the total number of individuals.

This study was largely descriptive, but it is important to realise that summarising data with diversity indices is of high ecological relevance as this measure catches two of the most important components of a community: the number of species as well as the population size of each species. Although this study was far from being able to infer ecological interactions from the collected data, one can still hypothesise about the extent of intraspecific and interspecific interactions. Intraspecific competition on the stopover site might be especially high when diversity is low and population size is high, e.g. between Reed Warblers during August. Taking account of niche separation between species, the filling of niche space should be maximal when diversity is highest (Tilman 1999). Alternatively, if interspecific interactions are of similar importance, the interspecific competition is highest when diversity reaches a maximum.

Because bird migration is inherently costly (Bairlein 2002), migratory birds should be particularly sensitive to biotic interactions at stopover sites, especially to competition for resources. The main features that have attracted the interest of researchers are the fuelling strategy of individual migrants in terms of time optimisation (Verkuil et al. 2006) and how it will affect predation (e.g. Fransson & Weber 1997). However, stopover sites offer a fascinating model system in which species turnover rate is higher than in any other environment, and where within and among species interactions probably are not the same over time. Interspecific and intraspecific competition on stopover sites has been largely ignored in the scientific literature. The latter is thought to affect species more than the former as members of a species that do indeed share the same traits also have similar resource requirements (Begon et al. 2009). This study showed that diversity was highest at the end of October, suggesting that intraspecific competition reached a low point. Interestingly, many migrants tend to have higher fat reserves at the end of their specific migratory period (Jenni & Schaub 2000) when diversity is low, which might be partly explained by a decrease in intraspecific competition and hence an increase in fuelling efficiency. Taking a community ecology approach to study stopover sites will remain a major challenge for the future: to assess the importance of competition, it is necessary to look at changes in food availability and migrant regime and/or use proxies such as fuelling rate, in addition to recording the relative number of competitors.

Preserving biodiversity is one of the top priorities of international conservation efforts. Too often however, areas are only assessed by their diversity present at a certain time point, meaning that seasonal biodiversity dynamics are ignored altogether. This study showed how variable diversity can be at a single site over the period of a few months. Furthermore, it showed that if we want to preserve biodiversity in wetlands, yearly conservation management efforts should be extended until the end of the migration season, when diversity is highest. The wetland in Uebersyren is a good example of a site that has been recognised as being of crucial importance for seasonal biodiversity dynamics imposed by migrants. It is reassuring that there is an increasing awareness in the Nature Conservation community for assessing the value of a site for migrants in addition to local breeding birds.

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