

Changes in the species composition of hedgerows in the Westphalian Basin over a thirty-five-year period

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Abstract

In the Westphalian Basin (North-Rhine Westphalia, Germany), 176 relevés of hedgerows first surveyed during the 1970s were reassessed in 2009 and 2010, and the floristic differences between these two time points were compared. The results were used to analyse the impact of exogenous factors on the species community composition using multivariate statistics (non-metric multidimensional scaling). Significant changes were found within all of the communities along the first axis of the ordination, and, in most cases, increasing average temperatures were best correlated with these alterations. However, based on the considerable evidence found, the alterations induced by land-use change and the intensification of agriculture appear to be the inducing factors.

Zusammenfassung: Veränderungen des Artenbestandes von Wallhecken der Westfälischen Bucht – Ergebnisse von Wiederholungsaufnahmen nach fünfunddreißig Jahren

176 Vegetationsaufnahmen von Wallhecken der Westfälischen Bucht (Nordrhein-Westfalen, Deutschland) aus den siebziger Jahren wurden zwischen 2009 und 2010 wiederholt und auf floristische Veränderungen hin untersucht. Die Ergebnisse wurden genutzt, um den Einfluss exogener Faktoren auf die Zusammensetzung der Pflanzengesellschaften mithilfe multivariater Ordinationsverfahren (Nicht-metrische Multidimensionale Skalierung) zu analysieren. In allen Gesellschaften ließen sich signifikante Veränderungen der Zusammensetzung entlang der ersten Achse der Ordinationen feststellen. In den meisten Fällen korrelieren zwar die Durchschnittstemperaturen am besten mit diesen Veränderungen. Allerdings gibt es starke Indizien dafür, dass die aus der Aufgabe der ehemaligen Nutzung und der Intensivierung der Landwirtschaft resultierenden Veränderungen vermutlich die auslösenden Faktoren sind.

Keywords: Ellenberg indicator values, eutrophication, land-use change, climate change, non-metric multidimensional scaling.

1. Introduction

Hedgerows are conspicuous landscape elements in many parts of the world. Except for those rare examples of naturally occurring hedges, they are human-made features, primarily planted to function as limits or boundaries. In addition, hedgerows also have major roles in controlling physical, chemical and biological fluxes at the landscape level (FORMAN & BAUDRY 1984). Hedgerows and associated elements (ditches and earth banks) have been constructed to control drainage or irrigation and to diminish erosion or wind. It is worth examining the function of biodiversity within the context of hedgerow structural diversity and multifunction due to their importance for plant species as habitats (HELLIWELL 1975, HEGARTY et al. 1994, BARR et al. 1995, MCCOLLIN et al. 2000) and their function as important corridors (MARSHALL & ARNOLD 1995, ROY & DE BLOIS 2008, WEHLING & DIEKMANN 2009). Indeed, Central European hedges shelter nearly 10,000 animal species, comprising half of the native mammals and nearly all of the reptiles (STREETER et al. 1984). Due to the importance of hedgerows for the maintenance of ecological diversity, increasing efforts are made to understand the ecological drivers determining their phytodiversity (LE COER et al. 1997, DE BLOIS et al. 2002, DECKERS et al. 2004).

With the homogenisation of the rural landscape through agricultural modernisation and land-consolidation programmes during the post-war period, the previous functions of hedgerows became increasingly unimportant. Mostly regarded as obstacles, their number substantially declined in all of the regions of Europe where they were once characteristic

elements of the landscape (HOOPER 1970, WITTIG 1979a, MCADAM et al. 1994, POINTEREAU & BAZIL 1995, WEBER 2003), although protection by law was ensured as early as 1935 in Germany. Today, hedgerows are highly regarded for their ecological and cultural merits, and the number of conservation groups with an interest in the management of hedgerows continues to expand (BAUDRY et al. 2000). This may be reason that the conservation efforts are enhanced and the laws for their protection are more strictly enforced.

In this study, we focus on a particular type of hedgerow, which is called *Wallhecken* in German. Previously widespread in northwest Germany, these hedges were systematically created between the 17th and 19th centuries. Fast-growing shrubs and trees with good sprouting abilities, such as common hornbeam (*Carpinus betulus*), English oak (*Quercus robur*) or hazel (*Corylus avellana*), were planted (WEBER 2003) in two parallel rows (sometimes only single rows) on hedge banks, usually 1.5 to 4.0 metres wide and 0.5 to 2.0 metres high, with ditches on both sides (mostly as drainage). First of all functioning as living cattle fences throughout Schleswig-Holstein, Lower Saxony and the lowland regions of North Rhine-Westphalia, these hedges were also used to obtain fuel wood (similar to coppices, they were cut every eight to twelve years). Between the years 1973 and 1975, the hedgerows of the Westphalian Basin (North Rhine-Westphalia), previously a typical hedgerow landscape in wide parts (JESSEN 1937), were studied by WITTIG (1976) who identified four associations that he named *Corno-Prunetum*, *Rubo elegantispinosi-Prunetum*, *Poo nemoralis-Rubetum silvatici* and *Rubetum grati*. In 2009 and 2010, a representative number of hedgerows was reinvented to identify possible changes within the communities and their linkage to climate change and eutrophication. It is widely accepted that climate change and its biological consequences are occurring. Changes in the physiology, phenology and distribution of species are evidence of the changes to biodiversity that have occurred within the past few decades (e.g., HUGHES 2000, ROOT et al. 2003, PARMESAN & YOHE 2003). In addition to stresses that individual species may encounter in responding to climate change, the differential rates of responses imply that current communities are disaggregated. With the intensification of agriculture and the increasing amount of vehicle traffic over the past 50 years, both the emission and immission rates of nitrogen rose dramatically, thus changing plant communities toward those compositions that are typical under high N availability (SMITH et al. 1999, BOBBINK et al. 2010). Taking the available climate and land-use data into account, we endeavoured to identify correlations between the environmental changes and the major threats to biodiversity.

2. Material and methods

2.1. Study area

The study was conducted in the Westphalian Basin (North Rhine Westphalia, Germany; Fig. 1), a mostly flat landscape, with an altitude between 40 to 100 metres above sea level and surrounded by low mountain ranges in the north-east, east and south. In some regions, the bedrock of the Cretaceous reaches the surface, partly exceeding 150 metres (*Baumberge*, *Beckumer* and *Stemmer* mountains). The glacial surface cover alternates with moist sands and clays, with loess found at the northern edges of the low mountain ranges.

The notable Atlantic climate regime in the western regions continuously lessens toward the east. The mean annual precipitation in the Westphalian Basin ranges between 700 and 800 millimetres, and the mean annual temperatures are approximately 9–10 °C. Further detailed information can be found in MÜLLER-WILLE (1966).

We studied four distinct hedgerow communities (see Table 1), mainly representing a soil-reaction gradient (in order of decreasing pH): the *Crataego-Prunetum spinosae* Oberdorfer 1957 (“CP”, named *Corno-Prunetum* by WITTIG 1976); the *Pruno-Rubetum elegantispinosi* H. E. Weber 1974 (“Re”, named *Rubo elegantispinosi-Prunetum* by WITTIG 1976); the *Poo nemoralis-Rubetum silvatici* Wittig 1976 (“Rs”), which WEBER (1999) assigns to the *Pruno-Rubetum sprengelii* H. E. Weber 1967; and the *Rubetum grati* R. Tüxen et Neumann ex Wittig 1976 (“Rg”). For these communities, the following affiliations to the units of the

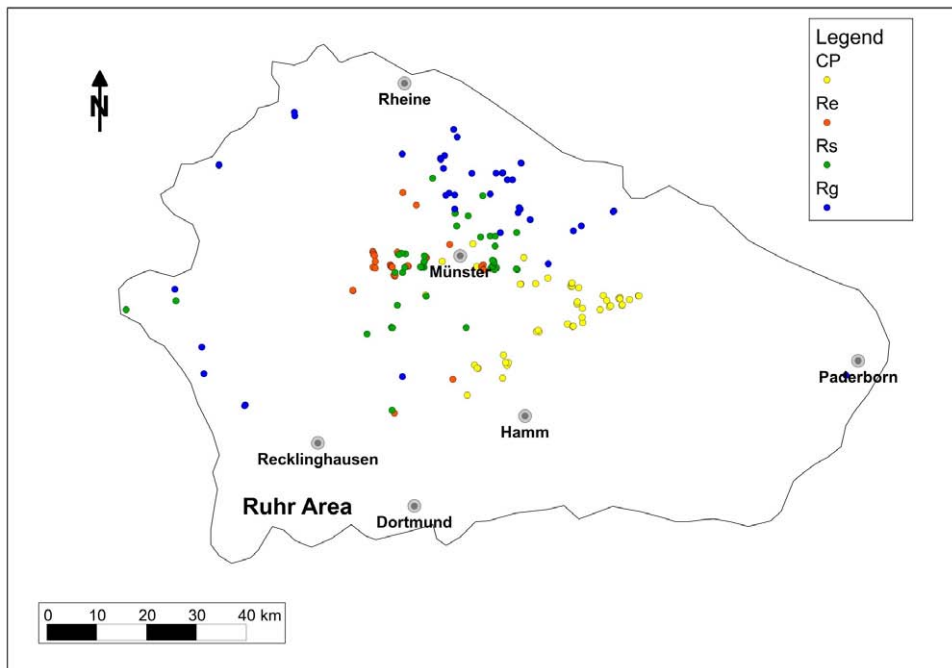


Figure 1: Map of the Westphalian Basin.
Abbildung 1: Karte der Westfälischen Bucht.

potential natural vegetation of the Westphalian Basin used by BURRICHTER (1973) are found: CP mainly grows in the potential area of the *Galio odorati-Fagetum* and of the *Stellario-Carpinetum stachyetosum*, whereas Re mainly occurs in the potential area of the *Milio-Fagetum* (= *Oxali-Fagetum* von Glahn 1981) and the *Stellario-Carpinetum typicum* and *periclymenetosum*. Rs preferentially occurs in the growing area of the *Fago-Quercetum*, and Rg occurs in the area of the *Betulo-Quercetum*. Although the names *Milio-Fagetum* and *Fago-Quercetum* used by BURRICHTER (1973) are no longer accepted, we use these old terms here because it is unclear whether the replacement names have identical meanings. Further details can be found in WITTIG (1976).

2.2. Methods

A total of 176 relevés (CP, 49; Re, 38; Rs, 48; Rg, 41) first surveyed between 1973 and 1975 were repeated in 2009 or 2010. The locations were identified using previously obtained coordinates and comparing old and new topographic maps (there are distinct signatures for *Wallhecken* in German topographic maps). Along a 100 metre length of each hedgerow, the species composition was separately assessed for the tree, shrub and herb layers (the nomenclature of the plant species was according to WISSKIRCHEN & HAEUPLER 1998). In contrast to the first survey, which presented combined relevés of the spring and summer aspects of the *Wallhecken*, the second inventory was restricted to July and August; therefore, the species visible only in early spring (*Anemone nemorosa*, *Adoxa moschatellina*, *Ranunculus ficaria* and *Teesdalia nudicaulis*) were excluded from the analysis.

The reduced list was used to calculate the turnover rates (MÜHLENBERG 1993). The mean cover-weighted Ellenberg indicator values (EIVs) were calculated for the herbaceous layer (ELLENBERG et al. 2001). We also recorded the land-use type of the adjacent area (presence/absence of “grassland” or “cropland”) according to map signatures (first survey) and on-site records (second survey).

The monthly average temperature and precipitation in the study area at 1 km² resolution for the 1960–1974 and 1995–2009 periods were provided by the German Weather Agency (methodological details found in MÜLLER-WESTERMEIER 1995). The different variables (see Table 2) for these periods were derived and spatialised to the vegetation plots.

Table 1: Characteristic species differentiating the four hedgerow communities regarded.

CP = *Crataego-Prunetum spinosae*; Re = *Pruno-Rubetum elegantispinosi*; Rs = *Pruno-Rubetum sprengelii*; Rg = *Rubetum grati*.

Tabelle 1: Bezeichnende Arten der vier betrachteten Wallhecken-Gesellschaften.

CP *Crataego-Prunetum spinosae*; Re *Pruno-Rubetum elegantispinosi*; Rs *Pruno-Rubetum sprengelii*; Rg *Rubetum grati*.

Species	CP	Re	Rs	Rg
<i>Rubus caesius</i>	V			
<i>Cornus sanguinea</i>	V			
<i>Acer campestre</i>	IV			
<i>Rhamnus carthatica</i>	IV			
<i>Stachys sylvatica</i>	IV			
<i>Arum maculatum</i>	III			
<i>Rubus elegantispinosus</i>		V		
<i>Lonicera periclymenum</i>		IV		
<i>Rubus lindleianus</i>		III		
<i>Rubus winteri</i>		III		
<i>Poa nemoralis</i>			V	
<i>Rubus sylvaticus</i>			IV	
<i>Rubus gratus</i>				V
<i>Prunus spinosa</i>	V	IV		
<i>Rosa canina</i>	V	IV		
<i>Crataegus monogyna</i> agg.	V	IV		
<i>Crataegus laevigata</i> agg.	IV			
<i>Euonymus europaea</i>	III			
<i>Carpinus betulus</i> (shrub)	III			
<i>Rubus corylifolius</i> agg.	III	IV		
<i>Hedera helix</i>	IV	IV		
<i>Corylus avellana</i>	V	V	IV	
<i>Quercus robur</i>	IV	IV	V	V
<i>Fraxinus excelsior</i>	III	III		
<i>Moehringia trinervia</i>	III	III		
<i>Alliaria petiolata</i>	IV			
<i>Chaerophyllum temulum</i>	IV			
<i>Galium aparine</i>	IV			
<i>Glechoma hederacea</i>	IV			
<i>Urtica dioica</i>	IV			
<i>Geum urbanum</i>	III			
<i>Viola odorata</i>	III			
<i>Dactylis glomerata</i>	III	III		
<i>Sambucus nigra</i>	III	IV		
<i>Poa nemoralis</i>		V		
<i>Prunus avium</i>		III		
<i>Stellaria holostea</i>		III		
<i>Rubus vigorosus</i>			III	
<i>Galium odoratum</i>			III	
<i>Lonicera periclymenum</i>			IV	III
<i>Rubus plicatus</i>			III	III
<i>Sorbus aucuparia</i>			V	V
<i>Betula pendula</i>			IV	V
<i>Frangula alnus</i>			IV	V
<i>Betula pubescens</i>			III	IV
<i>Populus tremula</i>			III	III
<i>Holcus mollis</i>			IV	IV
<i>Agrostis capillaris</i>			III	IV
<i>Hieracium laevigatum</i>				III
<i>Epilobium angustifolium</i>				III
<i>Festuca rubra</i>				III

V = 100-80 %; IV = 80-60 %; III = 60-40 %

Table 2: Definition of the variables and the abbreviations used.

Tabelle 2: Definition der verwendeten Variablen und Abkürzungen.

Variable	Definition
Climate	
T_mean*	Mean annual temperature
T_veg*	Mean temperature of vegetation period (March-October)
T_wi*	Mean temperature of winter months (November-February)
T_min*	Mean temperature of the coldest month
T_max*	Mean temperature of the warmest month
P_sum*	Mean annual precipitation
P_veg*	Mean precipitation of vegetation period (March-October)
P_wi*	Mean precipitation of winter months (November-February)
Structure	
Rad	Orientation of hedgerow [rad]
Cover_tl	Cover of tree layer [%]
Cover_sl	Cover of shrub layer [%]
Cover_hl	Cover of herb layer [%]
Height_sl	Height of shrub layer [m]
Indicator values (IV)	
L_w	Mean cover-weighted Ellenberg IV for light
T_w	Mean cover-weighted Ellenberg IV for temperature
K_w	Mean cover-weighted Ellenberg IV for continentality
F_w	Mean cover-weighted Ellenberg IV for soil moisture
R_w	Mean cover-weighted Ellenberg IV for soil reaction
N_w	Mean cover-weighted Ellenberg IV for soil nitrogen
* Periods:	1960-1974, 1995-2009

We used non-metric multidimensional scaling (NMS) ordination to evaluate the changes in the vegetation between the sampling periods of each community separately. NMS ordination is an iterative approach for locating species on a plot with k dimensions (axes) that minimises the departure from the monotonicity in the association between the distance (dissimilarity) in the original data and the ordination space (KRUSKAL & WISH 1978). Following the method outlined by MCCUNE & GRACE (2002), we used Sørensen's distances to construct dissimilarity matrices for 50 runs each using random and real data with a random starting configuration. The final instability was tested using 200 iterations.

Multivariate statistics were generated using PC-ORD 5.31 (MCCUNE & MEFFORD 2006). The differences between the two sample periods (Wilcoxon rank sum tests for paired samples) and the comparison of the nominal data (binomial test) were evaluated using R 2.11 (R DEVELOPMENT CORE TEAM).

3. Results

3.1. Non-Metric Multidimensional Scaling

With exception of R_s (two-dimensional), all of the NMS analyses delivered three-dimensional solutions. The final stress of the CP samples was 19.67, with a final instability of less than 0.001 and a cumulative r^2 of 0.678 (axis 1, 0.206; axis 2, 0.210; axis 3, 0.262), and the final stress of the Re samples was 19.40, with a final instability of less than 0.001 and a cumulative r^2 of 0.656 (axis 1, 0.281; axis 2, 0.169; axis 3, 0.206). For the R_s samples, the final stress was 20.22, with a final instability of less than 0.001 and a cumulative r^2 of 0.758 (axis 1, 0.321; axis 2, 0.437), and the final stress was 18.53 for the R_g samples, with a final instability of less than 0.001 and a cumulative r^2 of 0.726 (axis 1, 0.268; axis 2, 0.165; axis 3, 0.294). Using the Monte Carlo test, the final stress values of the real data throughout the communi-

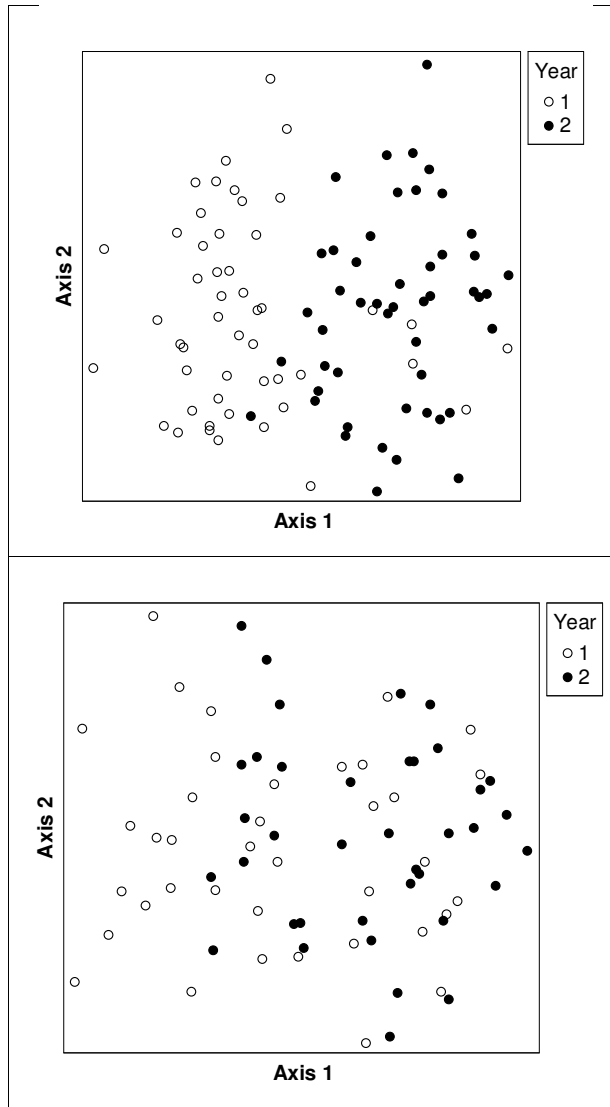


Figure 2: Non-metric multidimensional scaling plot of the relevés (arcsine square root-transformed mean species cover) of the *Crataego-Prunetum* (above) and the *Pruno-Rubetum elegantispinosi* (below) communities.

Abbildung 2: Nicht-metrische multidimensionale Skalierung der Vegetationsaufnahmen (Arkussinus Quadratwurzel transformierte mittlere Deckung der Arten) des *Crataego-Prunetum* (oben) und des *Pruno-Rubetum elegantispinosi* (unten).

ties fell below those values of the random data, proving that the ordination differs significantly ($p < 0.02$) from chance.

Along axis 1 of the ordination, the species composition of all of the communities can be differentiated according to the year they were sampled (Fig. 2, Fig. 3), mostly in association with rising temperature. Testing the sample scores of axes 1 (paired Wilcoxon rank sum tests) on the differences between the sampling years yielded significant results ($p < 0.001$) in all cases, and, except for *Re*, the temperature variable showed good agreement with the sample scores on axis 1 (Table 3). The coefficients of determination of the *Rs* and *Rg* communi-

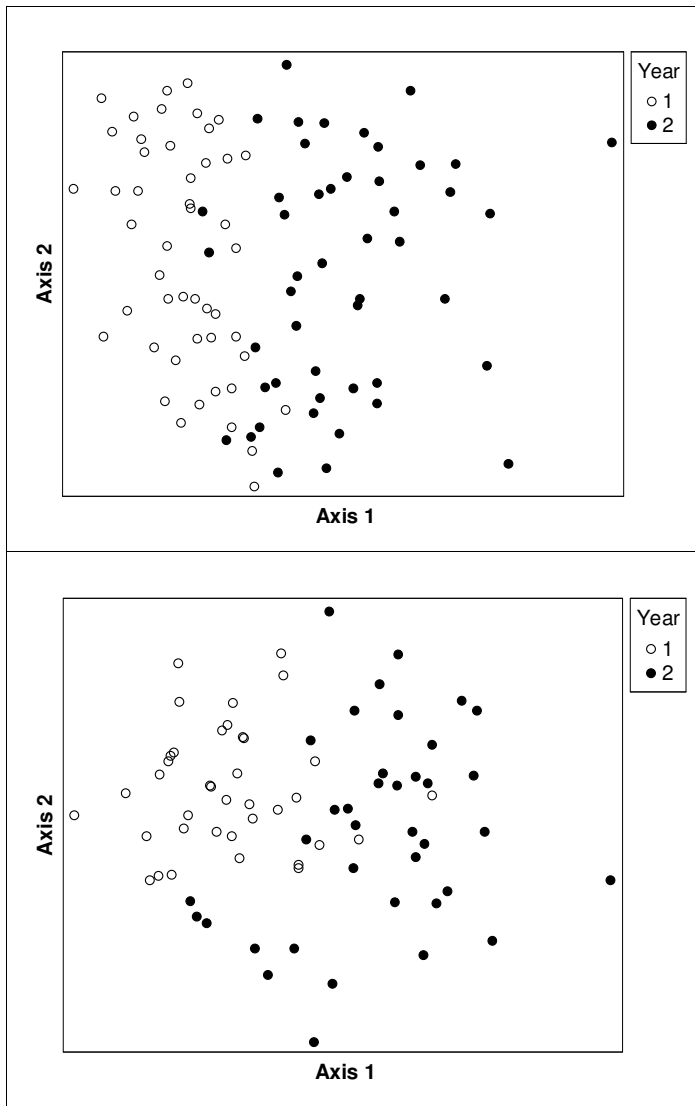


Figure 3: Non-metric multidimensional scaling plot of the relevés (species with > 5% constancy; arcsine square root-transformed mean cover) of the *Pruno-Rubetum sprengelii* (above) and the *Rubetum grati* communities (below).

Abbildung 3: Nicht-metrische multidimensionale Skalierung der Vegetationsaufnahmen (Arkussinus Quadratwurzel transformierte mittlere Deckung der Arten) des *Pruno-Rubetum sprengelii* (oben) und des *Rubetum grati* (unten).

ties exceeded 0.47 in all cases. The changes within the species composition of *Re*, however, seems to be based on different causes, with strong correlations only occurring for the Ellenberg indicator values (temperature and soil reaction). For *Rs* and *Rg*, increasing cover values of the tree layer also play an important part in explaining the alterations with axis 1, whereas the structural variables of the other communities are less important for the ordination. Though not as strongly correlated with axis 1 as the temperature variables, the precipitation, at least for the vegetation period, correlates more strongly when the soil quality is poor, with r^2 scores of the *Rg* samples exceeding 0.4 (Table 3).

Table 3: Correlations (Pearson's r) of variables with ordination axes of the non-metric multidimensional scaling (see Table 2 for abbreviations). Hedgerow communities: $CP = Crataegio-Prunetum spinosae$; $Re = Pruno-Rubetum elegantispinosi$; $Rs = Pruno-Rubetum sprengeii$; $Rg = Rubetum grati$.

Tabelle 3: Korrelation (Pearson r) der Variablen mit den Achsen der Nicht-metrischen multidimensionalen Skalierung (Abkürzungen s. Tab. 2). Pflanzengesellschaften: $CP Crataegio-Prunetum spinosae$; $Re Pruno-Rubetum elegantispinosi$; $Rs Pruno-Rubetum sprengeii$; $Rg Rubetum grati$.

Variables	Axis 1				Axis 2				Axis 3			
	CP	Re	Rs	Rg	CP	Re	Rs	Rg	CP	Re	Rs	Rg
Climate												
T_mean	0.723 ***	0.260 *	0.764 ***	0.702 ***	0.165 ***	0.031	-0.029	0.177	0.196	-0.247 *		0.286 *
T_veg	0.716 ***	0.250 *	0.763 ***	0.700 ***	0.146	0.028	-0.009	0.167	0.205 *	-0.250 *		0.294 *
T_wi	0.732 ***	0.240 *	0.759 ***	0.685 ***	0.204 *	0.030	-0.053	0.185	0.180	-0.247 *		0.249 *
T_min	0.726 ***	0.370 **	0.764 ***	0.724 ***	0.168	0.051	-0.071	0.204	0.194	-0.215		0.357 ***
T_max	0.723 ***	0.356 **	0.762 ***	0.720 ***	0.167	0.050	-0.049	0.214	0.187	-0.213		0.373 ***
P_sum	0.456 ***	0.342 **	0.367 ***	0.545 ***	0.258 *	0.010	-0.276 **	0.035	0.300 **	0.016		0.035
P_veg	0.644 ***	0.485 ***	0.637 ***	0.688 ***	0.213 *	0.021	-0.158	0.119	0.321 **	-0.071		0.187
P_wi	0.533 ***	0.317 **	0.421 ***	0.571 ***	0.294 **	0.035	-0.366 ***	0.045	0.151	0.005		0.094
Structure												
Rad	0.133	-0.119	0.027	0.075	0.053	-0.074	-0.181	0.188	0.002	-0.286 *		0.042
Cover_tl	0.432 ***	0.235 *	0.632 ***	0.587 ***	0.008	-0.198	0.277 **	0.471 ***	0.359 ***	0.211		0.532 ***
Cover_sl	-0.424 ***	0.061	-0.479 ***	-0.398 ***	-0.142	-0.017	-0.170	-0.238 *	0.214 *	-0.187		-0.562 ***
Cover_hl	-0.008	-0.240 *	-0.268 **	-0.298 **	0.190	0.228 *	0.290 **	-0.098	-0.263 **	0.300 **		0.582 ***
Height_sl	-0.204 *	-0.185	-0.192	-0.286 *	0.072	0.036	0.005	-0.245 *	0.004	-0.042		-0.199
Ellenberg IV												
L_w	0.355 ***	0.025	0.181	0.061	-0.394 ***	0.258 *	0.159	0.185	0.116	-0.587 ***		-0.184
T_w	0.076	0.282 *	0.373 ***	0.196	-0.298 **	0.286 *	-0.486 ***	0.216	-0.028	-0.382 ***		-0.243 *
K_w	0.102	-0.199	0.123	0.143	-0.569 ***	0.155	-0.581 ***	0.259 *	-0.379 ***	-0.037		-0.257 *
F_w	0.212 *	0.352 **	0.210 *	0.153	0.072	0.241 *	-0.522 ***	0.208	-0.422 ***	-0.262 *		-0.422 ***
R_w	0.043	0.687 ***	0.280 **	0.366 **	0.215 *	-0.008	-0.733 ***	0.203	0.552 ***	-0.217		-0.377 ***
N_w	-0.093	0.680 ***	0.380 ***	0.585 ***	0.056	0.067	-0.668 ***	-0.092	0.608 ***	-0.390 ***		-0.206

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$

Table 4: Means ($\pm$ SD) of the climate variables (1960–1974 and 1994–2009), structural variables and mean Ellenberg indicator values (1st and 2nd surveys). Hedgerow communities: *CP* = *Crataego-Prunetum spinosae*; *Re* = *Pruno-Rubetum elegantissimos*; *Rs* = *Pruno-Rubetum sprengelii*; *Rg* = *Rubetum grati*. Different letters indicate significant differences ($p < 0.05$, Wilcoxon rank sum tests for paired samples; see Table 2 for abbreviations).

Tabelle 4: Mittelwert ($\pm$ Standardabweichung) der Klimavariablen (1960–1974 und 1994–2009), Strukturvariablen und mittlere Zeigerwerte nach Ellenberg (für die erste und zweite Aufnahme). Pflanzengesellschaften: *CP Crataego-Prunetum spinosae*; *Re Pruno-Rubetum elegantissimos*; *Rs Pruno-Rubetum sprengelii*; *Rg Rubetum grati*. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede ($p < 0.05$, Wilcoxon-Rangsummentest für gepaarte Stichproben; Abkürzungen: s. Tab. 2).

	<i>CP</i>			<i>Re</i>			<i>Rs</i>			<i>Rg</i>		
Climate	1960-1974	1995-2009	1960-1974	1995-2009	1960-1974	1995-2009	1960-1974	1995-2009	1960-1974	1995-2009	1960-1974	1995-2009
T_mean	9.23 $\pm$ 0.08 ^a	10.3 $\pm$ 0.06 ^b	9.09 $\pm$ 0.24 ^a	10.17 $\pm$ 0.19 ^b	9.31 $\pm$ 0.1 ^a	10.32 $\pm$ 0.09 ^b	9.29 $\pm$ 0.2 ^a	10.3 $\pm$ 0.18 ^b				
T_veg	12.42 $\pm$ 0.07 ^a	13.4 $\pm$ 0.06 ^b	12.24 $\pm$ 0.24 ^a	13.23 $\pm$ 0.19 ^b	12.47 $\pm$ 0.1 ^a	13.39 $\pm$ 0.08 ^b	12.47 $\pm$ 0.18 ^a	13.37 $\pm$ 0.17 ^b				
T_wi	2.85 $\pm$ 0.12 ^a	3.84 $\pm$ 0.09 ^b	2.79 $\pm$ 0.24 ^a	3.8 $\pm$ 0.18 ^b	3 $\pm$ 0.11 ^a	3.94 $\pm$ 0.11 ^b	2.93 $\pm$ 0.24 ^a	3.91 $\pm$ 0.21 ^b				
T_min	-6.44 $\pm$ 0.16 ^a	-1.34 $\pm$ 0.11 ^b	-6.49 $\pm$ 0.24 ^a	-1.49 $\pm$ 0.19 ^b	-6.29 $\pm$ 0.23 ^a	-1.41 $\pm$ 0.17 ^b	-6.27 $\pm$ 0.31 ^a	-1.57 $\pm$ 0.24 ^b				
T_max	19.16 $\pm$ 0.09 ^a	22.64 $\pm$ 0.07 ^b	18.95 $\pm$ 0.27 ^a	22.55 $\pm$ 0.22 ^b	19.18 $\pm$ 0.13 ^a	22.76 $\pm$ 0.07 ^b	19.18 $\pm$ 0.2 ^a	22.76 $\pm$ 0.22 ^b				
P_sum	760 $\pm$ 20 ^a	790 $\pm$ 23 ^b	840 $\pm$ 63 ^a	858 $\pm$ 56 ^b	774 $\pm$ 33 ^a	805 $\pm$ 24 ^b	768 $\pm$ 30 ^a	811 $\pm$ 35 ^b				
P_veg	517 $\pm$ 12 ^a	568 $\pm$ 15 ^b	554 $\pm$ 35 ^a	599 $\pm$ 33 ^b	520 $\pm$ 17 ^a	571 $\pm$ 16 ^b	519 $\pm$ 18 ^a	579 $\pm$ 24 ^b				
P_wi	244 $\pm$ 8 ^a	258 $\pm$ 11 ^b	286 $\pm$ 29 ^a	298 $\pm$ 26 ^b	254 $\pm$ 16 ^a	271 $\pm$ 10 ^b	249 $\pm$ 13 ^a	270 $\pm$ 13 ^b				
Structure	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
Cover_tl	0 $\pm$ 0 ^a	29 $\pm$ 26.2 ^b	0 $\pm$ 0 ^a	15 $\pm$ 23.6 ^b	0 $\pm$ 0 ^a	37 $\pm$ 32.9 ^b	0 $\pm$ 0 ^a	54 $\pm$ 36.7 ^b				
Cover_sl	97 $\pm$ 5.5 ^b	93 $\pm$ 9.4 ^a	98 $\pm$ 5.3 ^a	96 $\pm$ 9.2 ^a	95 $\pm$ 3.5 ^b	80 $\pm$ 23.7 ^a	97 $\pm$ 2.7 ^b	72 $\pm$ 24.5 ^a				
Cover_hl	62 $\pm$ 28.3 ^b	44 $\pm$ 25.7 ^a	49 $\pm$ 22 ^b	32 $\pm$ 19.3 ^a	64 $\pm$ 24.5 ^b	43 $\pm$ 24.5 ^a	64 $\pm$ 25.3 ^a	55 $\pm$ 29.3 ^a				
Height_sl	4.3 $\pm$ 1.6 ^a	4.5 $\pm$ 1.6 ^a	4.6 $\pm$ 1.4 ^a	5.5 $\pm$ 1.9 ^b	4.6 $\pm$ 1.8 ^a	4.6 $\pm$ 2.2 ^a	5.1 $\pm$ 1.6 ^b	3.9 $\pm$ 1.6 ^a				
Ellenberg IV	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
L_w	5.1 $\pm$ 0.6 ^a	5.37 $\pm$ 0.53 ^b	5.03 $\pm$ 0.66 ^a	5.48 $\pm$ 0.62 ^b	5.4 $\pm$ 0.48 ^a	5.59 $\pm$ 0.46 ^a	5.99 $\pm$ 0.66 ^a	5.9 $\pm$ 0.46 ^a				
T_w	5.62 $\pm$ 0.28 ^a	5.51 $\pm$ 0.22 ^a	5.29 $\pm$ 0.32 ^a	5.56 $\pm$ 0.29 ^b	5.21 $\pm$ 0.25 ^a	5.41 $\pm$ 0.29 ^b	5.22 $\pm$ 0.24 ^a	5.21 $\pm$ 0.19 ^a				
K_w	3.23 $\pm$ 0.56 ^a	3.16 $\pm$ 0.46 ^a	3.65 $\pm$ 0.66 ^b	3.36 $\pm$ 0.41 ^a	3.41 $\pm$ 0.75 ^a	3.56 $\pm$ 0.52 ^a	2.68 $\pm$ 0.52 ^a	2.84 $\pm$ 0.54 ^b				
F_w	5.29 $\pm$ 0.35 ^a	5.22 $\pm$ 0.35 ^a	5.13 $\pm$ 0.21 ^a	5.36 $\pm$ 0.32 ^b	5.1 $\pm$ 0.24 ^a	5.25 $\pm$ 0.41 ^b	5.22 $\pm$ 0.51 ^a	5.27 $\pm$ 0.53 ^a				
R_w	6.52 $\pm$ 0.52 ^a	6.43 $\pm$ 0.95 ^a	5.04 $\pm$ 0.95 ^a	5.76 $\pm$ 0.9 ^b	4.09 $\pm$ 0.98 ^a	4.71 $\pm$ 1.07 ^b	3.07 $\pm$ 0.9 ^a	3.52 $\pm$ 1.12 ^b				
N_w	7.27 $\pm$ 0.95 ^a	6.99 $\pm$ 1.14 ^a	5.08 $\pm$ 1.21 ^a	6.14 $\pm$ 0.95 ^b	4.25 $\pm$ 0.83 ^a	5.01 $\pm$ 1.02 ^b	3.45 $\pm$ 0.74 ^a	4.26 $\pm$ 1.16 ^b				

3.2. Climate Change

Between the first and the second surveys, all of the 15-year climate variables significantly increased throughout the investigated communities (Table 4). The annual mean temperature increased by approximately 0.88 °C, and the mean temperature of the vegetation period increased by approximately 1.22 °C. The temperature of the warmest month increased by approximately 2.22 °C, and the temperatures of the coldest months increased by approximately 0.14 °C, with the mean temperature of the winter months increasing by approximately 0.45 °C. The annual precipitation increased by approximately 107 mm, the precipitation of the vegetation period increased by approximately 74 mm, and the precipitation of the winter months increased by approximately 38 mm.

3.3. Adjacent Land-use

The relative number of cropland areas adjacent to the *Wallhecken* of the *CP* (61 % and 63 %; $p = 1$) and the *Rg* (79 % in both surveys; $p = 1$) communities did not differ significantly between the surveys. The same is true for the number of neighbouring grassland areas (*CP*, 57 % and 49 %, $p = 0.544$; *Rg*, 39 % and 21 %, $p = 0.134$). In contrast, significant differences were found for the hedgerows of the *Re* and *Rs* communities; in both cases, the number of cropland areas increased (*Re*, 42 % and 97 %, $p < 0.001$; *Rs*, 54 % and 90 %, $p < 0.001$), whereas the number of adjacent grassland areas decreased (*Re*, 76 % and 18 %, $p < 0.001$; *Rs*, 58 % and 19 %, $p < 0.001$). The summation of use types found can be higher than the number of hedges, i.e., can exceed 100 %, because grassland may occur on one side of a hedge and cropland may occur on the other side.

3.4. Species Composition

The number of species did not change over time for three communities. In the first survey, on average, the *CP* community comprised 28.4 (± 4.0) species and 27.9 (± 4.4) in the second ($p = 0.679$), and the *Re* community consisted of 27.8 (± 3.5) species in 1974 and 28.5 (± 4.8) species in 2009 ($p = 0.635$). On average, the *Rs* community had 26.5 (± 4.2 ; 1974) and 27.4 (± 6.8 ; 2009) species ($p = 0.895$). *Rg* is the only community exhibiting a significant change: its species number increased from 22.8 (± 4.6) to 26.9 (± 5.1) ($p < 0.001$). The turnover rates of the communities are 0.22 (*CP*), 0.18 (*Re*), 0.19 (*Rs*) and 0.23 (*Rg*).

Table 5 shows the absolute and relative numbers of species found in the *Wallhecken* communities, which are characteristic of higher-order syntaxa (according to ELLENBERG 1996). Significant changes were only found for the species of the *Artemisietea*, *Quercus-Fagetalia* and *Fagetalia*. The *Artemisietea* species at least doubled in both absolute and relative number between the two sampling years in all communities but the *CP* community. Both absolute and relative number of *Fagetalia* species significantly decreased in the *CP* and *Re* communities. Changes for *Quercus-Fagetalia* species were only found in the *Rg* community, with significant increases of both the absolute and relative number of species. Except of the *Rg*, the number of species bound to closed forests ("1.1" in SCHMIDT et al. 2011) decreased in all hedgerow communities.

Details about the changes of single-species constancies is provided in Tables 6 (increases) and 7 (decreases), which compile all of the species with significantly changing constancies in at least one community. Most of the changes occurred in the *CP* community (17 species increased/9 decreased), followed by the *Rs* (15/8) and the *Rg* (14/8) communities, with the smallest changes occurring in the *Re* community (11/5).

Nearly all of the tree species formerly found as shrubs had grown, building a tree layer that was not previously present. Species that indicate a high soil nitrogen availability, such as *Dactylis glomerata*, *Elymus repens* and *Glechoma hederacea*, increased the most in *Rs* and *Rg*, whereas *Sambucus nigra* and *Urtica dioica* significantly increased in *CP* and *Re*. Climbing individuals of *Hedera helix* and *Humulus lupulus* significantly increased in the *CP* and *Re* communities, although *H. lupulus* did not climb into any of the newly developed tree layers. *Urtica dioica* is the only species that significantly increased in all of the communities.

Table 5: Mean ($\pm$ SD) of the absolute and relative (in italics) species numbers (%) of frequent higher-order syntaxonomic groups. Hedgerow communities: *CP* = *Crataego-Prunetum spinosae*; *Re* = *Pruno-Rubetum elegantissimos*; *Rs* = *Pruno-Rubetum sprengelii*; *Rg* = *Rubetum grati*. Different letters indicate significant differences ($p < 0.05$, Wilcoxon rank sum tests for paired samples).

Tabelle 5: Mittelwert ($\pm$ Standardabweichung) der absoluten und relativen (kursiv) Häufigkeit von Arten (%) übergeordneter syntaxonomischer Einheiten. Pflanzen- gesellschaften: *CP* *Crataego-Prunetum spinosae*; *Re* *Pruno-Rubetum elegantissimos*; *Rs* *Pruno-Rubetum sprengelii*; *Rg* *Rubetum grati*. Unterschiedliche Buchstaben kennzeichnen signifikante Unterschiede ($p < 0.05$, Wilcoxon-Rangsummentest für gepaarte Stichproben).

Syntaxon	CP		Re		Rs		Rg	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
Indifferent	5.2 $\pm$ 1.5 ^a 19 $\pm$ 5 ^a	4.9 $\pm$ 1.6 ^a 18 $\pm$ 6 ^a	7.3 $\pm$ 1.6 ^a 26 $\pm$ 6 ^a	6.9 $\pm$ 2 ^a 24 $\pm$ 6 ^a	7.9 $\pm$ 1.9 ^a 30 $\pm$ 7 ^a	8.1 $\pm$ 2.6 ^a 30 $\pm$ 7 ^a	7.7 $\pm$ 1.7 ^a 34 $\pm$ 7 ^a	8.9 $\pm$ 2.6 ^b 35 $\pm$ 9 ^a
Artemisietea	6.9 $\pm$ 1.8 ^a 26 $\pm$ 7 ^a	7.1 $\pm$ 2.3 ^a 26 $\pm$ 9 ^a	2.4 $\pm$ 2.2 ^a 8 $\pm$ 7 ^a	4.3 $\pm$ 2.1 ^b 15 $\pm$ 8 ^b	1.5 $\pm$ 1.6 ^a 5 $\pm$ 5 ^a	3.3 $\pm$ 1.8 ^b 12 $\pm$ 6 ^b	0.5 $\pm$ 1.1 ^a 2 $\pm$ 4 ^a	2.6 $\pm$ 2.2 ^b 10 $\pm$ 7 ^b
Molinio- Arrhenatheretea	0.2 $\pm$ 0.4 ^a 1 $\pm$ 2 ^a	0.4 $\pm$ 0.7 ^a 1 $\pm$ 2 ^a	0.3 $\pm$ 0.5 ^a 1 $\pm$ 2 ^a	0.3 $\pm$ 0.5 ^a 1 $\pm$ 2 ^a	1 $\pm$ 1 ^a 4 $\pm$ 4 ^a	1 $\pm$ 1.3 ^a 3 $\pm$ 4 ^a	1.6 $\pm$ 0.9 ^a 7 $\pm$ 4 ^a	1.5 $\pm$ 1.1 ^a 6 $\pm$ 5 ^a
Epilobietea	0.1 $\pm$ 0.4 ^a 0 $\pm$ 1 ^a	0.3 $\pm$ 0.6 ^a 1 $\pm$ 3 ^a	1.1 $\pm$ 0.9 ^a 4 $\pm$ 3 ^a	0.9 $\pm$ 1 ^a 3 $\pm$ 3 ^a	1.4 $\pm$ 0.9 ^a 5 $\pm$ 3 ^a	1.4 $\pm$ 1.1 ^a 5 $\pm$ 4 ^a	1.1 $\pm$ 1 ^a 4 $\pm$ 4 ^a	0.8 $\pm$ 1 ^a 3 $\pm$ 4 ^a
Quercu-Fagetea	4.1 $\pm$ 1.3 ^a 15 $\pm$ 5 ^a	3.9 $\pm$ 1.3 ^a 14 $\pm$ 4 ^a	3.8 $\pm$ 0.7 ^a 14 $\pm$ 3 ^a	3.9 $\pm$ 1.1 ^a 13 $\pm$ 4 ^a	3.3 $\pm$ 0.7 ^a 13 $\pm$ 3 ^a	3.5 $\pm$ 1 ^a 13 $\pm$ 4 ^a	1.4 $\pm$ 0.6 ^a 6 $\pm$ 2 ^a	2.6 $\pm$ 1.6 ^b 10 $\pm$ 6 ^b
Fagetalia	4.3 $\pm$ 1.8 ^a 16 $\pm$ 6 ^a	3.6 $\pm$ 1.7 ^b 13 $\pm$ 6 ^b	4.3 $\pm$ 1.8 ^a 15 $\pm$ 6 ^a	3.6 $\pm$ 1.9 ^b 12 $\pm$ 5 ^b	2.2 $\pm$ 1.7 ^a 8 $\pm$ 5 ^a	1.9 $\pm$ 1.4 ^a 7 $\pm$ 5 ^a	0.7 $\pm$ 0.7 ^a 3 $\pm$ 3 ^a	1.1 $\pm$ 1.2 ^a 4 $\pm$ 4 ^a
Prunetalia	5.4 $\pm$ 1.4 ^a 20 $\pm$ 5 ^a	5.5 $\pm$ 1.6 ^a 20 $\pm$ 5 ^a	6 $\pm$ 1.7 ^a 22 $\pm$ 6 ^a	6.5 $\pm$ 1.9 ^a 23 $\pm$ 7 ^a	3.4 $\pm$ 1.9 ^a 13 $\pm$ 7 ^a	3.9 $\pm$ 1.8 ^a 15 $\pm$ 6 ^a	2.2 $\pm$ 1 ^a 10 $\pm$ 5 ^a	2.7 $\pm$ 1.5 ^a 10 $\pm$ 5 ^a
Forest herbs*	4.7 $\pm$ 2 ^a 27 $\pm$ 10 ^a	3.2 $\pm$ 1.5 ^b 19 $\pm$ 7 ^b	4.7 $\pm$ 1.3 ^a 33 $\pm$ 11 ^a	3.2 $\pm$ 1.8 ^b 22 $\pm$ 11 ^b	3.4 $\pm$ 1.6 ^a 21 $\pm$ 8 ^a	2.8 $\pm$ 1.7 ^b 16 $\pm$ 8 ^b	1.3 $\pm$ 0.9 ^a 8 $\pm$ 5 ^a	1.5 $\pm$ 1.5 ^a 8 $\pm$ 7 ^a

* according to SCHMIDT et al. (2011)

Table 6: Species with significantly increasing constancies (%) between the first and second surveys in at least one of the four hedgerow communities investigated. *indicates significant differences ($p < 0.05$; binomial test).

Tabelle 6: Arten, deren Stetigkeit (%) mindestens in einer der vier untersuchten Gesellschaften signifikant zugenommen hat. „*“ kennzeichnet signifikante Unterschiede ($p < 0.05$, Binomialtest).

Species	CP		Re		Rs		Rg	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
Tree layer								
<i>Acer campestre</i>	0	27 *	0	0	0	0	0	0
<i>Alnus glutinosa</i>	0	0	0	3	0	15 *	0	10
<i>Betula pendula</i>	0	0	0	0	0	25 *	0	29 *
<i>Carpinus betulus</i>	0	4	0	16 *	0	4	0	0
<i>Fraxinus excelsior</i>	0	33 *	0	11	0	6	0	2
<i>Hedera helix</i>	0	14 *	0	5	0	4	0	0
<i>Populus tremula</i>	0	4	0	11	0	15 *	0	20 *
<i>Quercus robur</i>	0	78 *	0	34 *	0	67 *	0	83 *
<i>Salix alba</i>	0	16 *	0	0	0	4	0	2
Shrub layer								
<i>Corylus avellana</i>	94	90	89	92	81	85	0	39 *
<i>Hedera helix</i>	12	41 *	8	29 *	4	15	0	10
<i>Humulus lupulus</i>	0	16 *	34	50	31	40	0	10
<i>Populus tremula</i>	20	12	53	55	42	71 *	68	59
<i>Prunus serotina</i>	0	0	0	3	0	8	5	44 *
<i>Rubus elegantispinosus</i>	2	4	97	89	0	15 *	0	0
<i>Sambucus nigra</i>	65	82	76	95	44	63	10	54 *
Herbaceous layer								
<i>Acer campestre</i>	10	37 *	0	0	0	0	0	0
<i>Arrhenatherum elatius</i>	0	16 *	0	0	2	15	2	24 *
<i>Bromus sterilis</i>	0	29 *	0	39 *	0	23 *	0	10
<i>Chaerophyllum temulum</i>	51	67	18	18	0	13 *	0	5
<i>Crataegus monogyna</i> agg.	0	12 *	0	0	0	0	0	0
<i>Dactylis glomerata</i>	65	73	45	79 *	40	63 *	5	59 *
<i>Elymus repens</i>	10	24	18	37	15	33	10	32 *
<i>Euonymus europaea</i>	0	16 *	0	0	0	2	0	0
<i>Fraxinus excelsior</i>	0	16 *	0	3	0	2	0	0
<i>Geranium robertianum</i>	29	12	3	3	0	13 *	0	2
<i>Glechoma hederacea</i>	92	94	37	66 *	4	35 *	0	44 *
<i>Hedera helix</i>	73	82	68	58	19	38	2	27 *
<i>Humulus lupulus</i>	18	24	3	26 *	19	23	5	12
<i>Populus tremula</i>	0	2	0	18 *	4	38 *	2	24 *
<i>Prunus spinosa</i>	51	88 *	29	37	4	8	0	2
<i>Quercus robur</i>	0	12 *	11	26	31	38	51	61
<i>Sambucus nigra</i>	6	33 *	16	45 *	0	19 *	0	10
<i>Sorbus aucuparia</i>	0	0	18	21	29	54 *	27	54 *
<i>Urtica dioica</i>	59	88 *	50	92 *	42	67 *	15	46 *
Number of significant increases	17		10		15		14	

Table 7: Species with significantly decreasing constancies (%) between the first and second surveys in at least one of the four hedgerow communities investigated. *indicates significant differences ($p < 0.05$; binomial test).

Tabelle 7: Arten, deren Stetigkeit (%) mindestens in einer der vier untersuchten Gesellschaften signifikant abgenommen hat. „*“ kennzeichnet signifikante Unterschiede ($p < 0.05$, Binomialtest).

Species	CP		Re		Rs		Rg	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
Shrub layer								
<i>Betula pendula</i>	2	4	37	24	69	38 *	85	59 (*)
<i>Betula pubescens</i>	4	0	8	0	65	13 *	85	32 *
<i>Quercus robur</i>	82	59 (*)	89	53 (*)	92	69 (*)	100	85 (*)
<i>Rubus gratus</i>	0	0	0	0	21	19	100	83 *
<i>Solanum dulcamara</i>	14	0 *	0	0	0	0	0	0
<i>Viburnum opulus</i>	49	22 *	32	8 *	29	25	2	12
Herbaceous layer								
<i>Arum maculatum</i>	55	24 *	0	5	0	0	0	0
<i>Epilobium angustifolium</i>	0	0	16	13	27	8 *	49	12 *
<i>Galium odoratum</i>	4	4	16	0 *	46	4 *	49	20 *
<i>Hieracium laevigatum</i>	0	0	0	0	10	4	56	27 *
<i>Holcus lanatus</i>	2	2	16	24	25	25	44	10 *
<i>Lonicera periclymenum</i>	2	0	13	16	52	29 *	41	51
<i>Luzula multiflora</i>	0	0	0	0	15	0 *	20	5
<i>Moehringia trinervia</i>	59	10 *	79	16 *	63	19 *	27	10
<i>Polygonatum multiflorum</i>	27	6 *	63	13 *	8	10	0	5
<i>Pulmonaria obscura</i>	24	4 *	0	0	0	0	0	0
<i>Solanum dulcamara</i>	35	12 *	8	8	10	10	2	2
<i>Viola reichenbachiana</i>	27	6 *	3	0	0	0	0	0
Number of significant decreases	9		5		8		8	

(*) not significant if those individuals growing to trees are added

The greatest losses in the shrub layer are found for birches (*Betula* species), *Viburnum opulus* and *Quercus robur*; however, in the cases of *B. pendula* and *Q. robur*, the losses were cancelled ((*) in Table 7) by the addition of those individuals to the new tree layer (except for *B. pendula* in the *Rs* community). In the herbaceous layer, *Galium odoratum*, *Moehringia trinervia* and *Polygonatum multiflorum* significantly decreased in nearly all of the communities (partly over 40% losses). In contrast to the two liana species previously mentioned, *Solanum dulcamara* and *Lonicera periclymenum* partly suffered significant decreases (Table 7).

In *CP*, the EIV of light is the only indicator value significantly increasing. In *Re*, all of the EIVs, except that of continentality, increased. The EIVs of light and continentality showed no changes in *Rs*, whereas the values of the remaining EIVs significantly increased. In *Rg*, the EIVs of continentality, soil reaction and soil nitrogen significantly increased (Table 4).

4. Discussion

Our study demonstrates that NMS can be used to detect relationships between derived variables, spatial climate data, and species composition. However, these ordinations do not indicate causality per se because the distribution of the samples in the ordination space solely depends upon the species composition. Thus, it is difficult to determine the influence of single environmental factors on the investigated communities. Although the increasing

temperature and floristic shift along the first axis of the ordinations (Figs. 2 and 3) are by no means proof of an underlying dependency between the two – because the ordinations are derived solely from species data – it is evident that their correlation with axis 1 is strongest in all of the communities except *Re* (Table 3). Increasing constancies of *Hedera helix* also seem to support climate-driven changes, as evergreen-broadleaved species are considered to be the first to gain advantages from rising temperatures in Europe (WALTHER 2002, DIERSCHKE 2005, WALTHER et al. 2005, DIEKMANN 2010).

As the important role that *Wallhecken* formerly played in rural life (e.g., WITTIG 1979b) no longer exists, traditional management was often omitted, as indicated by the increasing tree cover. The role of traditional management is clearly shown in the ordinations of the *Rs* and the *Rg* communities (Fig. 3, Table 3), indicating the importance of this ecological driver, at least in these two communities. The decreased coverage of the shrub layer may be the result of the shade caused by the newly established tree layer, which, in turn, could have led to higher insolation of the hedge bank. This and the intrusion of light-demanding competitors from adjacent fringes may have caused the decline of the typical forest species (*Arum maculatum*, *Galium odoratum*, *Moebringia trinervia*, *Polygonatum multiflorum*, *Pulmonaria obscura* and *Viola reichenbachiana*) which seems to be a possible explanation considering the mean Ellenberg indicator values of light (Table 4). *Epilobium angustifolium*, a species known for its occurrence in forest clearings, i.e., an indicator of disturbances, suffered significant losses in *Rs* and *Rg*. As *E. angustifolium* is also highly regarded as food by roe deer (BERGQUIST et al. 1999), the steady increase in the game population in Germany since 1950 (AMMER et al. 2010) may be the cause of this.

Eutrophication, the third major driver of floristic changes within the hedgerows, is well indicated by the increasing number of nitrogen-indicating species, such as *Dactylis glomerata*, *Elymus repens*, *Glechoma hederacea*, and *Urtica dioica*, in the herbaceous layer and *Sambucus nigra* in the herb and shrub layers. Except for the *CP* community in which no changes were found, the mean cover-weighted EIVs of soil nitrogen also well reflect these changes. Regarding the floristic change along the first axis of the ordinations, the soil nitrogen seems to be one of the most important driver within *Re* and *Rg*, playing a minor role within the two other communities (Table 3), which may be explained by the time the communities “suffered” from the nitrogen inputs of the surrounding cropland. Presuming a steady use of nitrogen fertiliser, significant additional input within recent decades can only be expected in *Re* and *Rs* because the previous high number of adjacent cropland areas, i.e., fertilisation, for *CP* and *Re* did not change (see section 3.3). According to data from the German environmental agency (UBA 2010), the *Re* and the *Rg* plots gained 3 kg more of airborne nitrogen in 2007 than the *CP* and *Rs* plots. Although small, these differences may have enhanced the effects initiated by the fertiliser. Regarding the EIVs of nitrogen, the previously occurring differences between the communities, though still existing, will become more and more equalised. Species, such as *Corylus avellana* or *Rubus elegantispinosus*, newly established in *Rg* and *Rs*, respectively, are good examples of the ongoing species shift toward communities with a higher nutrient demand. Further improved soil nitrogen supplies along with the absence of shading shrubs in the first years after the periodically coppicing will then increase the establishment of fast-growing nitrophytous species. VERHEYEN et al. (2011) discussed this problem of the so-called ‘nitrogen time bomb’ for the understory of deciduous forests.

The increasing constancy of *Bromus sterilis* should be regarded as an indicator of disturbance, though eutrophication also plays a role. Based on a 3-year field experiment, THEAKER et al. (1995) found that native *B. sterilis* populations of hedgebanks do not react to fertiliser addition, suggesting that a positive influence only occurs where disturbances are present. It may be possible that the underlying processes explaining the increase of grasses in the investigated hedgerows can be compared to those found in many previously nitrogen-deficient plant communities in Europe. In particular, nitrogen deposition along with changes in traditional management practices can be regarded as main contributors (SMART et al. 2005, WALKER et al. 2009, BOBBINK et al. 2010).

Taken together, one can conclude that changes occurred mostly at the edges of the ecological gradient of the communities examined, i.e., in the “richer” part (*CP*) and in the “poorer” part (*Rg*), which, in turn, means that the communities between these categories showed less vulnerability to the different stressors evaluated or were more resilient. This is particularly obvious when comparing *CP* with *Re* because the number of significant changes in the species composition is much higher in the *CP* than in the *Re* community (see the last rows of Tables 6 and 7). In contrast, the absolute number of significant changes is almost equal for *Rs* and *Rg*. However, considering the fact that the average species number was much lower for *Rg* than *Rs* in the first survey, one has to state a higher percentage of significant changes for *Rg* than *Rs*. This result is in agreement with the observations of HUWER & WITTIG (2012) who found only little changes over the past 40 years in the species composition of the *Oxali-Fagetum*, a forest community that holds an intermediate ecological position among the forest types existing in Westphalia and, furthermore, represents the potential natural vegetation of the area of the *Re* community.

The hedgerow communities investigated in this study represent another example that illustrates the problems arising from the impact of multiple stressors and their synergistic influences on vegetation in the man-made landscape. Although the identification of the single influences of climate change, eutrophication and land-use change is rather speculative, the following order of decreasing influence seems to be likely: land-use change > eutrophication > climate change. Indeed the temperature variables showed the strongest correlations with the species composition shifts on the first axes. However, the numerous drivers implied in “land-use change” are far more difficult to compile into single variables, thus leaving great uncertainties.

Anthropogenic landscape elements should per se change in the way that the surrounding agricultural area changes (LE COER et al. 1997, BOUTIN & JOBIN 1998, DE BLOIS et al. 2002, DECKERS et al. 2004), especially if their former use became unnecessary, as in the case of the *Wallhecken* in the Westphalian Basin. The rising temperatures, therefore, operated in a subtle manner by enhancing developments that were already initiated. Supporting examples of climate warming-driven changes accompanied with changes in land use or structural alterations are found throughout different ecosystems (e.g., PARTZSCH 2000, DOBBERTIN et al. 2005, VITTOZ et al. 2009).

Acknowledgements

We thank Cornelia Anken, Dr. Ute Becker and Monika Wittig for assistance in surveying the relévés, Martin Diekmann and an unknown reviewer for the valuable critique of the first version of the manuscript and the Hesse Ministry of Higher Education, Research, and Arts *Landes-Offensive zur Entwicklung wissenschaftlich-ökonomischer Exzellenz* (LOEWE) program for its financial support of the Biodiversity and Climate Research Centre (BiK-F) in Frankfurt.

Appendix: List of all of the species exceeding a five percent frequency at least once in one of the four hedgerow communities (*CP* = *Crataego-Prunetum spinosae*; *Re* = *Pruno-Rubetum elegantispinosi*; *Rs* = *Pruno-Rubetum sprengelii*; *Rg* = *Rubetum grati*). Significant changes in the shrub and herbaceous layers are in bold.

Anhang: Tabelle aller Arten mit mindestens fünf Prozent Stetigkeit in einer der vier Pflanzengesellschaften (*CP* *Crataego-Prunetum spinosae*; *Re* *Pruno-Rubetum elegantispinosi*; *Rs* *Pruno-Rubetum sprengelii*; *Rg* *Rubetum grati*). Signifikante Änderungen in Strauch- und Krautschicht sind fett hervorgehoben.

Community Survey	<i>CP</i>		<i>Re</i>		<i>Rs</i>		<i>Rg</i>	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
Nr. of relevés	47	47	38	38	48	48	41	41
Tree layer								
<i>Acer campestre</i>		27						
<i>Alnus glutinosa</i>				3		15		10
<i>Betula pendula</i>						25		29
<i>Betula pubescens</i>						2		12
<i>Carpinus betulus</i>		4		16		4		
<i>Fagus sylvatica</i>				3		10		12
<i>Fraxinus excelsior</i>		33		11		6		2
<i>Hedera helix</i>		14		5		4		
<i>Populus tremula</i>		4		11		15		20
<i>Prunus avium</i>		2		13		2		
<i>Quercus robur</i>		78		34		67		83
<i>Salix alba</i>		16				4		2
<i>Sorbus aucuparia</i>				8		2		
Shrub layer								
<i>Acer campestre</i>	67	65	18	16		2		2
<i>Rhamnus carthartica</i>	45	39	3	3	6	6		2
<i>Salix alba</i>	31	14			6	6		2
<i>Lonicera xylosteum</i>	29	16		5		2		2
<i>Pyrus pyraeaster</i>	16	10						2
<i>Rubus montanus</i>	14	6						
<i>Rosa villosa</i> agg.	8	12		8	2			
<i>Prunus spinosa</i>	94	100	63	68	17	25		2
<i>Crataegus monogyna</i> agg.	88	82	61	79	25	27		10
<i>Cornus sanguinea</i>	80	86	50	32	21	17		2
<i>Crataegus laevigata</i> agg.	61	61	63	42	15	8		2
<i>Fraxinus excelsior</i>	57	63	47	34	19	17		5
<i>Euonymus europaea</i>	45	55	21	32	8	15		2
<i>Carpinus betulus</i>	35	24	74	76	33	23		2
<i>Hedera helix</i>	12	41	8	29	4	15		10
<i>Rosa corymbifera</i> s.l.	12	6	13	8	4	4		
<i>Rubus elegantispinosus</i>	2	4	97	89		15		
<i>Rubus raduloides</i>			47	37				
<i>Rubus lindleianus</i>			45	45	4	13		
<i>Prunus avium</i>	8	6	42	47	10	17	5	10
<i>Rubus winteri</i>		4	29	45	2	4		2
<i>Rubus lindebergii</i>			11	13				

Community Survey	<i>CP</i>		<i>Re</i>		<i>Rs</i>		<i>Rg</i>	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
<i>Rubus pallidus</i>			8	5				
<i>Rubus infestus</i>			5	3				
<i>Humulus lupulus</i>		16	34	50	31	40		10
<i>Rubus macrophyllus</i>	2	6	26	39	17	35	5	5
<i>Rubus rudis</i>			18	11	6	13		2
<i>Rubus schleicheri</i>			3	3	8	10		
<i>Rubus idaeus</i>	4	4	29	26	60	60	27	32
<i>Rubus vigorosus</i>					10	10		
<i>Rubus chloocladus</i>					6	4		
<i>Sorbus aucuparia</i>	8	4	53	53	90	75	80	90
<i>Frangula alnus</i>	14	10	47	34	88	73	95	88
<i>Betula pendula</i>	2	4	37	24	69	38	85	59
<i>Betula pubescens</i>	4		8		65	13	85	32
<i>Alnus glutinosa</i>	6	4	26	29	58	56	44	37
<i>Fagus sylvatica</i>			13	11	40	23	34	27
<i>Rubus nessensis</i>				3	31	21	39	39
<i>Rubus sprengelii</i>	2	2			19	29	10	17
<i>Rubus adspersus</i>	2	2			17	23	10	15
<i>Cytisus scoparius</i>				3	15	13	29	29
<i>Vaccinium myrtillus</i>					6	2	20	7
<i>Rubus gratus</i>					21	19	100	83
<i>Prunus serotina</i>				3		8	5	44
<i>Salix aurita</i>		2					15	10
<i>Calluna vulgaris</i>					2		20	5
<i>Quercus robur</i>	82	59	89	53	92	69	100	85
<i>Rubus corylifolius</i> agg.	57	59	79	76	94	85	93	83
<i>Corylus avellana</i>	94	90	89	92	81	85		39
<i>Sambucus nigra</i>	65	82	76	95	44	63	10	54
<i>Rosa canina</i> s.l.	88	86	76	74	42	42	5	20
<i>Lonicera periclymenum</i>	8	6	58	53	65	58	66	73
<i>Populus tremula</i>	20	12	53	55	42	71	68	59
<i>Salix caprea</i>	8	18	47	37	25	31	27	22
<i>Viburnum opulus</i>	49	22	32	8	29	25	2	12
<i>Rubus plicatus</i> s.l.		2	18	24	56	48	63	78
<i>Rubus silvaticus</i>			13	16	50	44	12	17
<i>Salix cinerea</i>	10	16	13	18	31	23	10	20
<i>Rubus pyramidalis</i>	2		11	13	8	23	10	15
<i>Ribes uva-crispa</i>	12	16		5	2	2	2	5
<i>Ribes rubrum</i> agg.	6	14		11		2		5
<i>Acer pseudoplatanus</i>	6	6		13		2		5
<i>Rubus vestitus</i>			3	11	2	4	2	5
<i>Salix spec.</i>	8	2	5	3	6			
<i>Rubus ammobius</i>				3		2	7	12
<i>Rubus melanoxylon</i>			5	5	6	4		
<i>Rubus radula</i>	2		8	5	2	2		

Community Survey	<i>CP</i>		<i>Re</i>		<i>Rs</i>		<i>Rg</i>	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
<i>Prunus padus</i>		4		3	2			10
<i>Rubus divaricatus</i>					4	2	7	5
<i>Tilia cordata</i>				3	6	8		
<i>Ulmus minor</i>	2	8		3		4		
<i>Rubus buhnensis</i>			8	3	4	2		
<i>Ilex aquifolium</i>				3	2	2	2	7
<i>Solanum dulcamara</i>	14	0						
<i>Salix fragilis</i>		2		5		6		
<i>Rubus senticosus</i>			3	5	2		2	
<i>Rubus platyacanthus</i>								10
<i>Salix repens</i>							10	
<i>Rubus armeniacus</i>		2		5				2
<i>Fallopia japonica</i>				5				
Herbaceous layer								
<i>Acer campestre</i>	10	37						
<i>Rubus caesius</i>	92	94	5	8	4			2
<i>Alliaria petiolata</i>	80	88	8	18		4		5
<i>Arctium lappa</i>	14	16		3		2		2
<i>Arctium minus/nemorosus</i>	8	4						
<i>Arum maculatum</i>	55	24		5				
<i>Cirsium arvense</i>	20	20		5	2	4		2
<i>Cirsium vulgare</i>	8	10		3				
<i>Clematis vitalba</i>	12	14				2		
<i>Cornus sanguinea</i>	20	24	5	3				
<i>Geranium robertianum</i>	29	12	3	3		13		2
<i>Geum urbanum</i>	45	41	5	8	4	10		2
<i>Heracleum sphondylium</i>	10	4	3					
<i>Lapsana communis</i>	37	43	5	11		8		2
<i>Pulmonaria obscura</i>	24	4						
<i>Rumex sanguineus</i>	29	14				2		2
<i>Viola odorata</i>	47	41						
<i>Viola reichenbachiana</i>	27	6	3					
<i>Campanula trachelium</i>	10	10	5	5	2			
<i>Chaerophyllum temulum</i>	51	67	18	18		13		5
<i>Glechoma hederacea</i>	92	94	37	66	4	35		44
<i>Polygonatum multiflorum</i>	27	6	63	13	8	10		5
<i>Prunus spinosa</i> agg.	51	88	29	37	4	8		2
<i>Stachys sylvatica</i>	65	73	24	13		2		2
<i>Lamium galeobdolon</i>	4		18	18				
<i>Poa nemoralis</i>	45	51	100	100	98	94		12
<i>Teucrium scorodonia</i>			13	13	21	17	7	7
<i>Galium album</i>					10	4		
<i>Deschampsia flexuosa</i>					10	4	39	29
<i>Betula pubescens</i>					6		10	5
<i>Epilobium angustifolium</i>			16	13	27	8	49	12

Community Survey	CP		Re		Rs		Rg	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
<i>Festuca rubra</i> agg.			8		23	19	73	61
<i>Frangula alnus</i>					19	15	39	39
<i>Galeopsis bifida</i>	2				23	17	41	41
<i>Galium odoratum</i>	4	4	16	0	46	4	49	20
<i>Hieracium lachenalii</i>			3		15	2	12	2
<i>Hieracium sabaudum</i>			8		10	8	24	29
<i>Lonicera periclymenum</i>	2		13	16	52	29	41	51
<i>Luzula multiflora</i>					15	0	20	5
<i>Lysimachia vulgaris</i>	6		16	3	29	15	29	17
<i>Maianthemum bifolium</i>					10	6	5	5
<i>Poa pratensis</i> agg.					17	4	20	20
<i>Rumex acetosella</i>					10	4	24	17
<i>Cytisus scoparius</i>					4	4	10	7
<i>Epipactis helleborine</i>							7	5
<i>Festuca capillata</i>					4	2	32	12
<i>Hieracium laevigatum</i>					10	4	56	27
<i>Hypochoeris radicata</i>							10	
<i>Luzula campestris</i>							7	
<i>Melampyrum pratense</i>					6	2	22	15
<i>Molinia caerulea</i>					2		49	32
<i>Urtica dioica</i>	59	88	50	92	42	67	15	46
<i>Galium aparine</i>	84	84	58	68	52	56	10	27
<i>Dactylis glomerata</i>	65	73	45	79	40	63	5	59
<i>Galeopsis tetrahit</i>	45	53	68	84	56	63	24	27
<i>Holcus mollis</i>	2	2	42	32	83	79	85	88
<i>Hedera helix</i>	73	82	68	58	19	38	2	27
<i>Agrostis capillaris</i>			37	24	56	54	95	85
<i>Moehringia trinervia</i>	59	10	79	16	63	19	27	10
<i>Quercus robur</i>		12	11	26	31	38	51	61
<i>Stellaria holostea</i>	22	10	50	42	42	40		2
<i>Sorbus aucuparia</i>			18	21	29	54	27	54
<i>Elymus repens</i>	10	24	18	37	15	33	10	32
<i>Holcus lanatus</i>	2	2	16	24	25	25	44	10
<i>Humulus lupulus</i>	18	24	3	26	19	23	5	12
<i>Sambucus nigra</i>	6	33	16	45		19		10
<i>Dryopteris filix-mas</i>	2	6	32	29	19	23	7	10
<i>Bromus sterilis</i>		29		39		23		10
<i>Scrophularia nodosa</i>	20	14	21	13	17	10		2
<i>Silene dioica</i>	2	8	18	18	13	15	7	15
<i>Populus tremula</i>		2		18	4	38	2	24
<i>Solanum dulcamara</i>	35	12	8	8	10	10	2	2
<i>Aegopodium podagraria</i>	12	22	3	5	6	17	2	17
<i>Arrhenatherum elatius</i>		16			2	15	2	24
<i>Equisetum arvense</i>			11	8	15	8	5	10
<i>Dryopteris carthusiana</i>			8		6	21	7	10

Community Survey	<i>CP</i>		<i>Re</i>		<i>Rs</i>		<i>Rg</i>	
	1 st	2 nd	1 st	2 nd	1 st	2 nd	1 st	2 nd
<i>Fallopia dumetorum</i>		8	11	16		6		7
<i>Fallopia convolvulus</i>		2		5	2	8	7	17
<i>Milium effusum</i>	4	2	8	8	8	8		
<i>Juncus effusus</i>		2		3	10	8	7	7
<i>Polypodium vulgare</i>		2	5		4	4	10	10
<i>Agrostis stolonifera</i>						2	17	15
<i>Anthriscus sylvestris</i>	4	8	3	5		6		7
<i>Tanacetum vulgare</i>					6	10		12
<i>Stellaria media</i>	2	4	3	3	2	10	2	
<i>Impatiens parviflora</i>			3	8	2	8		5
<i>Senecio sylvaticus</i>				5		4	10	5
<i>Artemisia vulgaris</i>		2				10		10
<i>Lamium album</i>	8	2			2			10
<i>Eupatorium cannabinum</i>	2	2		5		2	2	7
<i>Fraxinus excelsior</i>		16		3		2		
<i>Vinca minor</i>	2	6	5	5	2			
<i>Prunus serotina</i>						6		12
<i>Euonymus europaea</i>		16				2		
<i>Pteridium aquilinum</i>					6	6		5
<i>Poa trivialis</i>	4				6	4		2
<i>Hieracium umbellatum</i>			5		2	2		7
<i>Prunus avium</i>	4	2				2		7
<i>Hypericum perforatum</i>				5		4	2	2
<i>Stellaria graminea</i>					4		2	7
<i>Lamium argentatum</i>		2		5		4		2
<i>Fagus sylvatica</i>						6		7
<i>Phalaris arundinacea</i>					4	6		2
<i>Crataegus monogyna</i> agg.		12						
<i>Rumex acetosa</i>					2		2	7
<i>Galium album</i>						4		7
<i>Vaccinium vitis-idaea</i>					4		7	
<i>Poa annua</i>	2				6			
<i>Torilis japonica</i>		8						
<i>Potentilla erecta</i>							7	
<i>Aethusa cynapium</i>		6						
<i>Allium vineale</i>			5					

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Manuscript received: 03.01.2012; accepted: 16.03.2012

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Jahr/Year: 2012

Band/Volume: [NS_32](#)

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Artikel/Article: [Changes in the species composition of hedgerows in the Westphalian Basin over a thirty-five-year period 31-53](#)