Conservation credit for plant species diversity of small nature reserves in an agricultural matrix

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Background and aims – Although the effectiveness of protected areas for the conservation of biodiversity is widely accepted, only very little direct scientific evidence exists. For small reserves embedded in hostile agricultural matrix this empirical proof is even lacking all together, although effectiveness can be most questioned here. In this study, we compared the plant species diversity of ten small nature reserves in Flanders, Belgium with the plant species diversity of the adjacent, agricultural landscape matrix.

Methods – Plant species diversity was studied for ten nature reserves in Haspengouw, Belgium using 10×10 m^2 survey plots at a density of one plot/ha. The same sampling density was applied to the direct vicinity of the reserve in the landscape matrix consisting of intensively managed agricultural landscape.

Key results – An overall clear pattern of higher plant species diversity was found for nature reserves compared to landscape matrix at the plot, reserve and regional scale, clearly indicating the effectiveness of nature reserves. This pattern, however, appeared to be influenced by the soil type, with reserves on loamy soils containing higher diversity compared to reserves on sandy loam soils. Also species composition differed between reserves and the landscape matrix, with more threatened, less ruderal species and more stress tolerating species of moist, nitrogen poor soils occurring inside the reserves.

Conclusions – These results provide a clear evidence of the effectiveness of nature reserves in the conservation of plant diversity. Reserves may be considered as having a conservation credit when compared to the agricultural landscape.

Key words – biodiversity, conservation credit, landscape matrix, plant species, protected area, soil type.

INTRODUCTION

We are living in a time of serious diversity decline and species loss (e.g. Scott et al. 2001). Empirical research suggests that the present extinction rate is about one thousand times higher than a few thousand years ago (Novacek 2001, Hermy et al. 2007). Taking the effects of global change into account, this rate could even increase another tenfold (Anonymous 2005). This tremendous decline in species richness is largely the result of the severe human impact on the environment. With human populations, food demands and urbanization still increasing, the pressure on land remains intense and continues eroding the biodiversity of our planet. This clearly illustrates the need for nature conservation.

A key strategy for protecting biodiversity has been the establishment and maintenance of protected areas (Gaston et al. 2008). Although the importance of protected areas for nature conservation is generally accepted, only few studies have actually tried to demonstrate their effectiveness (Par-

rish et al. 2003). Many of the limited studies that did, used a detour approach, which allowed them to test effectiveness without actually looking at the biodiversity as such. Most of these studies looked at protected area characteristics by using gap-analysis: overlaying species distribution maps with protected area maps (Jaffre et al. 1998, Yahnke et al. 1998, Hopkinson et al. 2000, Scott et al. 2001, Oldfield et al. 2004, Rodrigues et al. 2004, Chape et al. 2005, Gaston et al. 2006, Jackson & Gaston 2008). These studies assume that if a species' distribution concurs with a protected area, this species is successfully protected. This kind of assessment likely leads to an overestimation of the degree of species protection, for example because of low resolution of map distribution and absence of any assessment of niche requirements (Rodrigues et al. 1999, Hopkinson et al. 2000).

Another indirect approach quantifies the effects of different types of management, e.g. grazing and mowing on biodiversity. From these results is concluded that since these

practices are used in protected areas, these will yield a higher diversity than their environment (Bruner et al. 2001, Chape et al. 2005, Billeter et al. 2008, Van Calster et al. 2008). Clearly, these studies do not provide any direct, hard evidence for the effectiveness of nature reserves either.

A direct and very straightforward way to quantify the effectiveness of protected areas is comparing species richness between the protected area and its direct unprotected neighbourhood. One could term the expected difference in biodiversity a conservation credit, as it might be expected a consequence of the conservation measures taken in the protected areas. This approach has, apparently never been applied to plant diversity in terrestrial ecosystems (but see for animals Caro et al. 1998, Caro 2003, Rannestad et al. 2006, Setsaas et al. 2007, Gaston et al. 2008).

Effectiveness may be particularly questioned for small protected areas in largely fragmented landscapes, as they are strongly influenced by the surrounding (agricultural) landscape (Green et al. 2005) and implicate only limited population sizes (Honnay et al. 1999). Nevertheless much money and effort is put in their creation and maintenance in many West-European countries. The continuing conflict on land use between urban and rural development and nature conservation has lead to new insight in how conservation could be achieved in these landscapes. Green et al. (2005) suggest that its implementation can be achieved in two ways. On the one hand, agriculture can intensify at the most productive sites, which would leave parts of the land free for exclusive nature conservation through the establishment of protected areas (land sparing). On the other hand, we could also strive

to minimize the degree of intensification, allowing species to survive in the landscape matrix (wildlife-friendly farming) (Bengtsson et al. 2003, Green et al. 2005). Theoretical advantages exist for both alternatives, with the debate on which alternative yields the most efficient way of species conservation continuing (Benton et al. 2003, Tscharntke et al. 2005, Matson & Vitousek 2006, Berkes 2007, Vandermeer & Perfecto 2007, Fischer et al. 2008). Nevertheless without empirical evidence of the effectiveness of small scale protected areas this conflict is potentially based on false assumptions.

In this study we examined to what extent small protected areas (from this point on referred to as 'nature reserves') contribute to the conservation of plant diversity by comparing plant diversity in small protected areas to the diversity of the surrounding rural landscape. Using a standardized sampling design, we surveyed the plant community composition of ten small nature reserves and their direct unprotected surroundings. These nature reserves were all located in the Haspengouw region of Flanders and imbedded in an intensively managed agricultural landscape. More specifically the following questions were answered:

1. What is the difference in plant species richness and community composition when comparing nature reserves with the adjacent agricultural landscape matrix ?
2. Do soil conditions affect differences in species richness and community composition between reserves and their adjacent surroundings?
3. Which plant characteristics are more abundant in nature reserves than in the surrounding landscape matrix?
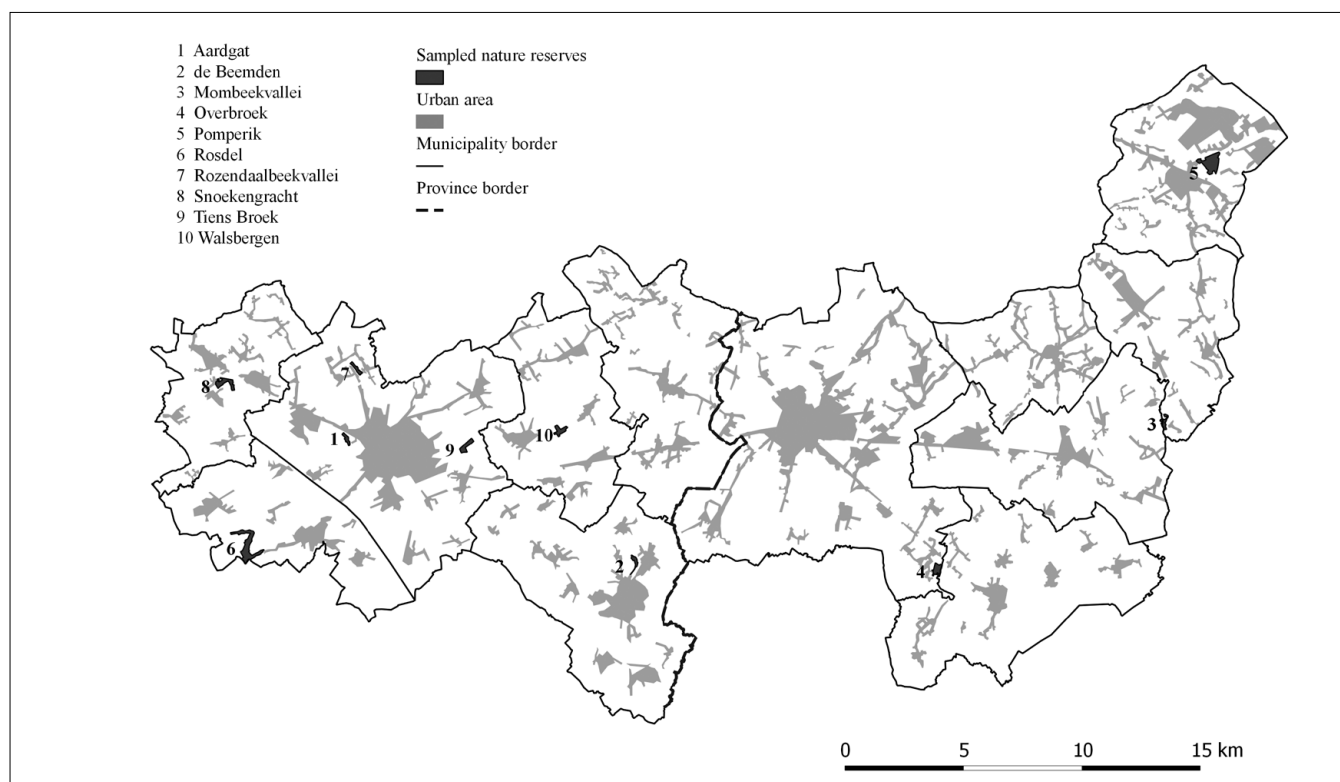

Figure 1 – Location of the ten sampled reserves in the central east part of Belgium. The sampled reserves are indicated in black, urban areas in grey. Remaining area (white) consists of the rural landscape matrix as defined in this text.

MATERIAL AND METHODS

Study area and data collection

This study was performed in the east part of Belgium, the so called Haspengouw region (range: 50°39'06"–50°54'04"N; 4°50'47"–5°19'37"E), which is characterized by sandy loam and loamy soils. Only nature reserves having similar overall soil conditions as the surrounding agricultural land were selected, so that nature reserves only differed with respect to management from their surroundings. However, in some cases, certain management measures taken in the nature reserves and/or the surrounding landscape unavoidably altered soil moisture conditions. Ten reserves, varying in size from 8 to 35 hectares were sampled: seven on loamy soils and three on sandy loam soils (table 1, fig. 1). These reserves consisted mainly of wet and dry grasslands and tall herb communities which all originated from agricultural land, abandoned at some point in the 20th century. During the summer of 2008 the vegetation was surveyed in plots of 10 × 10 m, established at a density of one plot/ha. These plots were randomly positioned within the reserve. Within each plot, the cover (%) of each plant species was recorded. The same sampling technique was applied to the direct vicinity of the reserve within the landscape matrix. This area consisted of a mosaic of intensive arable land and meadows, typical for the intensive agriculture system of North-Western Europe (Billeter et al. 2008). Sampling in the landscape matrix was conducted by creating a buffer around the reserve, of the same size as the reserve itself. Within this buffer the same sampling density was applied as within the reserves. These plots consisted of both arable land and meadows, all under intensive farming practice. In an attempt to avoid edge effects no plots were placed closer than 10 m from the reserve's edge.

Data processing

Species richness and community composition – The α-, β- and γ-diversity was calculated for each reserve and its direct surroundings in the landscape matrix. Mean α-diversity (local diversity) was defined as the mean number of species per plot (Whittaker 1972). The γ-diversity ('regional' diversity) was defined as the total number of species found within the reserve (or within the landscape matrix) (cf. Whittaker 1972). The β-diversity index was defined as γ/α, sensu Whittaker (1972). Diversities were compared between reserves and the landscape matrix using paired t-tests in SPSS 17.0 (Pallant 2007).

Since the different reserves can be interpreted as beeing part of one large regional species pool, we constructed a species-accumulation curve. This was accomplished using the first order jackknife estimator in Biodiversity Pro (McAleece et al. 1997). A χ²-test was conducted to compare the number of neophytes (exotic plant species) (Van Landuyt et al. 2006) between nature reserves and their surroundings, for all ten study areas, using SPSS 17.0 (Pallant 2007). The Dufrêne and Legendre method was used to test for species affinity to nature reserve or landscape matrix, yielding for each species two indicator values. This indicator value (IV) is calculated using the following formula: $IV_{ij} = RA_{ij} \times RF_{ij} \times 100$, in which RA_{ij} is defined as the relative abundance of species j in

Table 1 – Summary of the sampled reserves.

All reserves sampled in the study with municipality, area, plot number, soil type and coordinates. The variable values for the different sampled parts of landscape matrix are identical to their adjacent reserves.

reserve name	municipality	area (ha)	number of plots	soil type
Aardgat	Tienen	7	7	loamy
de Beemden	Landen	4	4	loamy
Rozendaal-beekvallei	Tienen	8	8	loamy
Snoekengracht	Boutersem	13	13	loamy
Tiens broek	Tienen	7	7	loamy
Walsbergen	Linter	12	12	sandy loam
Overbroek	Sint-Truiden	15	15	loamy
Middenloop mombeekvallei	Borgloon	9	9	sandy loam
Rosdel	Hoegaarden	22	22	loamy
Pomperik	Diepenbeek	16	16	sandy loam

group i (reserve or landscape matrix) and RF_{ij} is the relative frequency of species j in group i (Dufrêne & Legendre 1997). Statistical inference of these indicator values was deduced using Monte Carlo randomization in PC-ORD 4.0 (McCune & Mefford 1999).

To analyse differences in community composition a Detrended Correspondence Analysis (DCA) was performed on the arcsinus transformed (plots × species) matrix, using PC-ORD 4.0 (McCune & Mefford 1999). DCA was conducted since gradient length exceeded four times the standard deviation, indicating a unimodel species response model (ter Braak & Šmilauer 1998). It is widely accepted that in the case of unimodel species responses DCA ordination is more appropriate than the more frequently used PCA (Principal Component Analysis) (ter Braak & Prentice 1988). Both are types of statistical methods to reduce large amounts of data variation (plots & species) to a small number of newly derived variables that summarize the original information. Spearman rank correlations (r_s) between DCA scores and the mean Ellenberg indicator values per plot for moisture (F), pH (R) and nitrogen (N) were calculated. These values were obtained from the literature (Ellenberg et al. 1992).

Soil effects – Species richness (S), species diversity (Simpson diversity, D) and Evenness (E_D) were calculated per plot. Linear Mixed Models were run for comparison of these indices between nature reserves and the landscape matrix. We worked with two level models: the plot level (fixed, 1st level) and the reserve level (random, 2nd level) (cf. Singer 1998). The intercept and sampling location (one of ten locations) were included in the random statement. Land use identity (reserve or landscape matrix) was included in the fixed statement. We tested for differences in species diversity in reserves on loamy soils compared to those on sandy loam soils. For this reason the interaction between land use identity and soil type was incorporated in the fixed statement of the model.

Table 2 – Overview of α-, β- and γ- diversity.
Means and standard deviations given for the nature reserves and the parts of landscape matrix.

diversity	nature reserves		landscape matrix	
	mean	st. dev.	mean	st. dev.
α	25.78	3.33	13.90	2.42
β	3.50	0.85	4.46	1.15
γ	90.10	25.92	60.60	13.27

This model design allows us to overcome pseudoreplication by talking into account the clustered structure of ten distinctive groups of our data. Transformations were successfully applied to the diversity indices to obtain normally distributed data (table 3). All Linear Mixed Models were conducted in SAS 9.1.

Plant characteristics – The mean Ellenberg values for moisture, pH and nitrogen were calculated per plot (Ellenberg et al. 1992) and compared between nature reserves and the landscape matrix. Next, the mean position of each plot on the C (competition), S (stress) and R (ruderal) axis of the Grime triangle (the CSR- signature) was calculated according to Hunt et al. (2004). Species were classified using the online BiolFlor database (Klotz et al. 2002). The hemeroby scale, which gives an indication of the human impact on the community (Hill et al. 2002), was used to compare the mean hemeroby value between nature reserves and the landscape matrix. This scale is classified into seven categories ranging from 1 (ahemorobe, natural vegetation unaltered by man) to 7 (metahemerobe, completely altered by man with no natural vegetation remaining). These values were calculated using the hemeroby-class preferences of the observed plants in the online BiolFlor database (Klotz et al. 2002).

Threat status of a species was quantified according to the relative decline of the species in Flanders between two survey periods (1939–1971 and 1972–2004) (Van Landuyt et al. 2006). Using this data, a trend index was calculated, indicating the relative change in occurrence of every species compared to the mean change of all species. A negative trend index for a gives species indicates that the species has had a more severe decline than the mean decline of all species. A positive trend index indicates a less severe decline or even increase between both periods compared to the mean decline. We used this trend index to compare the relative vulnerability of the communities between the nature reserves and the landscape matrix, since this indicator variable is used to classify species in different red list categories for Belgium. All calculated plant characteristics were compared between nature reserves and the landscape matrix using linear mixed models, after transformations to obtain normally distributed data. Model construction was analogous to that of species richness analysis.

RESULTS

Species richness and community composition

In total 326 plant species were observed (23% of all species occurring in Flanders), of which 270 (82.3%) occurred within the reserves and 217 (66.6%) in the landscape matrix. 161 of these species occurred in both nature reserves and the landscape matrix, leaving 110 species occurring exclusively in the reserves and 56 exclusively in the landscape matrix. Both mean α-diversity (t = 8.36; p < 0.001) and γ-diversity (t = 3.65; p < 0.01) were highest in the reserves while β-diversity (t = -3.63; p < 0.01) was found to be highest in the landscape matrix (table 2). The overall species accumulation curve showed that levelling off occurs much sooner for the nature reserves and that the number of species was always higher inside the reserves (fig. 2). Although no significant difference in the number of neophytes exists between nature reserves and the landscape matrix (χ^2 = 1.97, df = 1, p = 0.16), we observed a trend towards more neophytes in the landscape matrix (fig. 3). The Dufrêne and Legendre method showed that 86 species (27%) were positively associated with nature reserves, while only 22 species (7%) were associated with the landscape matrix (electronic appendix). For 218 species (66%) no significant association was found.

The DCA gave a clear separation between nature reserves and the landscape matrix, but no clear separation with respect to soil type (fig. 4). We found a positive correlation between the first ordination axis and the Mean Ellenberg values for pH (r_s = 0.28; p < 0.001) and nitrogen (r_s = 0.68; p < 0.001)

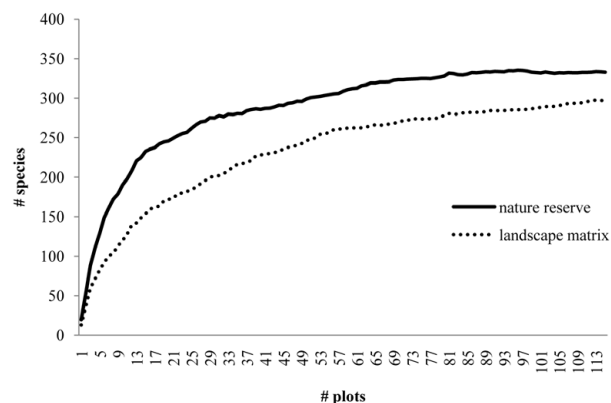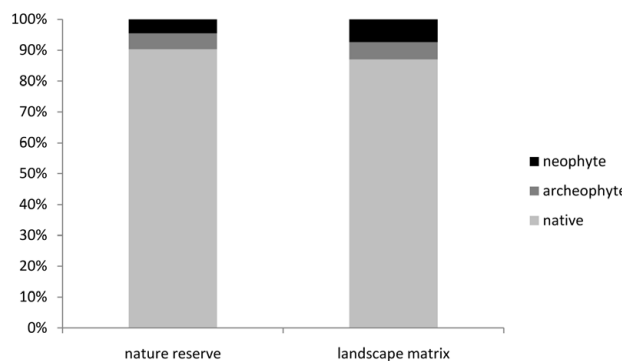**Figure 2** – Synopsis species-accumulation curve over all ten reserves.

Figure 3 – Relation between the share of native species, archeophytes and neophytes in nature reserves and the landscape matrix, for all ten study areas combined.

as well as between the second axis and nitrogen ($r_s = 0.32$; $p < 0.001$). A negative correlation was found between the first axis and the mean Ellenberg values for moisture ($r_s = -0.84$; $p < 0.001$).

Soil effects

Plots inside the reserves had a significantly higher S, D and E_D compared to plots in the landscape matrix (table 3). The difference in species richness was larger on loamy soils compared to sandy loam soils, caused by an overall higher species richness of nature reserves on loamy soil (tables 3 & 4). The same soil effect existed for the Simpson diversity, but was only marginal significant (p-value interaction coefficient is 0.051) (tables 3 & 4).

Plant characteristics

We used several indicators to make a comparison between plant characteristics within reserves and within the landscape matrix. The moist indicator value (F) revealed that reserve plots were characterized by plants of wetter soils. The soil type affected the mean pH indicator value (R). On loamy soils, mean pH preference was equal inside and outside of the reserve. For sandy loam soils however, reserves were characterised by a much lower pH indicator. The nitrogen indicator value (N) was lower inside the reserves, with a larger difference on sandy loam soils (tables 3 & 4).

The CSR-signature between nature reserves and their landscape matrix was dependent upon soil type. Loamy soils showed a lower competition value outside the reserves, while sandy loam soils showed the reverse pattern. The mean position of a plot on the stress axis was higher for nature reserves, but differences between reserves and the landscape matrix were much less pronounced for loamy soils. The mean position on the ruderal axis was highest outside of the reserves, independent of soil type (tables 3 & 4, fig. 5).

As expected reserves had lower mean hemeroby values, independent of soil type. The same pattern was observed for the transformed mean trend index, but with a larger difference for sandy loam soils (tables 3 & 4).

DISCUSSION

Species richness and community composition

Although higher species diversity is observed in nature reserves compared to the landscape matrix at both the plot (α) and landscape scale (γ), variability between plots (β) is higher in the landscape matrix (table 2). This could be explained by a higher degree of abiotic heterogeneity in the landscape matrix (Gough et al. 1994, Honnay et al. 1999, Cox & Moore 2005) or by area effects (Yahnke et al. 1998, Cox & Moore 2005). However, when comparing the mean Ellenberg values between the ten reserves on the one hand and the ten parts of landscape matrix using Kruskal-Wallis ANOVA, we found that only the moisture indicator value was significantly different between the ten different parts of landscape matrix (F-test: 54.01). This unlike the reserves where significant differences were found for all three indicator values (F-test:
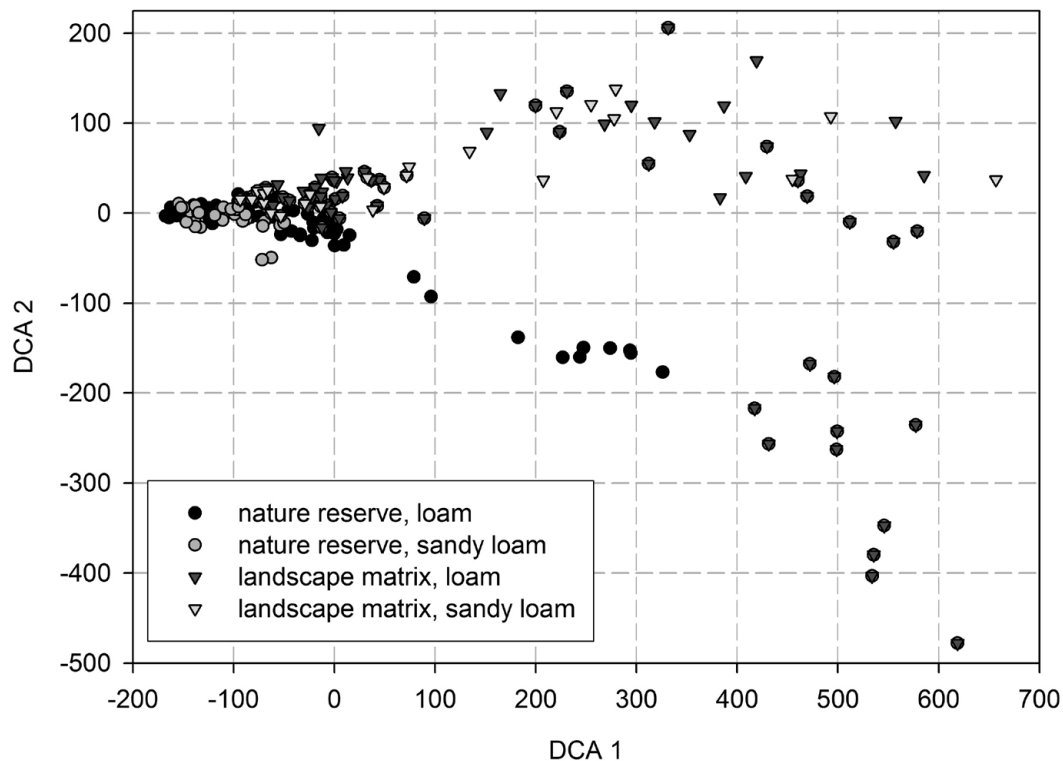

Figure 4 – DCA ordination on the arcsinus transformed data. Grouping within (nature reserve) and outside the reserves (landscape matrix) and loamy and sandy loam soils.

Table 3 – Comparison of the diversity indices and plant characteristics of the ten study areas based on plots inside and outside of the reserves.
Linear mixed models: F-statistic given for comparison between reserves and their adjacent landscape matrix (inout) and the interaction between inout and the reserve soil type (soil) (n = 226, df = 206). Significance: * $0.05 \geq$ p-value > 0.01; ** $0.01 \geq$ p-value > 0.001; *** $0.001 \geq$ p-value. No indication = non-significant correlation.

diversity index	intercept	inout	inout × soil
$\sqrt{S}$ (species richness)	26.30***	243.09***	4.96**
$\sqrt[4]{D}$ (Simpson diversity)	33.73***	197.25***	3.02
E_D (Simpson evenness)	16.29***	33.39***	0.68
plant characteristics	**intercept**	**inout**	**inout × soil**
F (moisture indicator value)	26.08***	78.65***	1.12
R (pH indicator value)	39.79***	37.31***	13.91***
N (nitrogen indicator value)	47.89***	157.65***	7.61***
C (competitive species)	12.31***	0.63	6.09**
S (stress tolerant species)	5.84***	94.96***	9.73***
log(R) (ruderal species)	8.26***	23.20***	1.71
hemeroby	34.30***	78.65***	1.12
log(trend index)	7.31***	40.76***	5.96**

moisture 25.94, pH 51.57 and nitrogen 28.12). This rules out the abiotic heterogeneity hypothesis, with abiotic conditions being more uniform in the landscape matrix, probably as a consequence of a homogenizing agriculture. This leaves only the second hypothesis remaining. Unlike the nature reserves, the surveyed plots in the landscape matrix are part of larger matrix patches. Therefore, more species occur than have been sampled, creating a sampling effect, with every subsample containing different species, accounting for the observed higher variability. This is in line with the shape of the accumulation curve of the landscape matrix, which shows no levelling, therefore suggesting that higher sampling intensity would increase species richness (fig. 2) (Gotelli & Colwell 2001). The somewhat higher than expected diversity in the landscape matrix can partly be explained by a trend towards a higher number of neophytes (fig. 3), which have low nature conservation value (cf. Gordon 1998, Van Landuyt et al. 2006). We also showed that more species are associated with nature reserves (27% associated) than with the landscape matrix (7% associated). Looking at the community composition a clear difference in composition is found between reserves and the landscape matrix (fig. 4). Moreover we see that part of this difference can be explained by differences in abiotic preferences of the species for pH, nitrogen and moisture.

Soil effects

The α- and γ-diversity patterns are confirmed by the significant difference in species richness, diversity and evenness (tables 3 & 4) between reserves and the matrix. Reserves on loamy soils contained more species than reserves on sandy loam soils. Since loamy soils are more alkaline than sandy loam soils (table 4), this may correspond to a more generally observed pattern of high plant diversity on alkaline soils (Pärtel et al. 2004). Although a clear soil effect can be found on the overall diversity patterns, no large differences in community composition are found between communities on loam soils and those on sandy loam soils for neither reserves nor the landscape matrix (fig. 4).

Table 4 – Overview of mean and standard deviation (st. dev.) for all diversity indices and plant characteristics separately for nature reserves and landscape matrix on both loamy (L) and sandy loam (S) soils after Mixed Model analysis.

	reserves L		reserves S		landscape matrix L		landscape matrix S	
diversity index	**mean**	**st. dev.**	**mean**	**st. dev.**	**mean**	**st. dev.**	**mean**	**st. dev.**
S (species richness)	27.45	5.78	23.30	6.21	13.28	5.52	13.65	4.34
D (Simpson diversity)	13.12	5.09	11.49	5.25	4.84	3.31	5.40	3.19
E_D (Simpson evenness)	0.47	0.12	0.48	0.12	0.35	0.14	0.39	0.13
plant characteristics	**mean**	**st. dev.**	**mean**	**st. dev.**	**mean**	**st. dev.**	**mean**	**st. dev.**
F (moisture indicator value)	6.45	1.05	6.81	0.94	5.44	0.47	5.95	0.64
R (pH indicator value)	6.50	0.57	5.73	0.77	6.60	0.53	6.61	0.63
N (nitrogen indicator value)	5.86	0.75	5.21	0.99	6.89	0.69	7.03	0.95
C (competitive species)	0.51	0.09	0.52	0.12	0.43	0.19	0.57	0.21
S (stress tolerant species)	0.17	0.05	0.22	0.09	0.12	0.07	0.09	0.08
R (ruderal species)	0.32	0.09	0.26	0.12	0.45	0.20	0.35	0.21
hemeroby	3.33	0.40	3.10	0.17	3.83	0.76	3.74	0.43
trend index	0.21	0.22	0.04	0.22	0.34	0.28	0.33	0.24

Plant characteristics

Species in nature reserves were characterized by a preference toward higher humidity and lower nitrogen soil content. Both are highly affected by differences in the management between nature reserves and the agricultural matrix. Although separation of the plots according to soil type is not pronounced in the ordination graph, we do see a clear difference in plant preference between both soil types. In nature reserves, plants occurring on sandy loam soils prefer soils of lower pH and lower nitrogen content than those occurring on loamy soils, whereas this difference is not observed for plants from the landscape matrix (table 4). Table 4 clearly demonstrated that reserves on sandy loam soils are characterized by a higher occurrence of acidophilic species than reserves on loamy soils. When comparing the pH profile of species in the landscape matrix this difference between loamy and sandy loam soils disappeared, with the occurrence of species with a similar pH preference to those occurring on loamy soils. These results were expected since it is widely known that sandy loam soils are more nutrient poor and acidic compared to loamy soils (Pärtel et al. 2004). The absence of these plant preferences between soil types in the landscape matrix is probably caused by the alteration of these soils. Here heavy fertilisation will lead to occurrence of more generalist and nitrophilous species, leading to a different pattern in soil preferences.

CSR-signature of species occurring in nature reserves differed from those in the agricultural landscape matrix (tables 3 & 4). The higher number of stress tolerating species in reserves and on sandy loam soils was expected since reserves are known for their lower nutrient availability, which is more severely pronounced on acidic soils (table 4). The higher number of ruderal species in the landscape matrix is due to the high disturbance frequency in these habitats under agricultural use (Hunt et al. 2004). For the competitive species a less consistent pattern appears (tables 3 & 4). This is probably caused by a difference in land use in the matrix. On the fertile loamy soils agriculture will mainly consist of tillage which will support communities of small ruderal species with low competitive strength. On the more acidic sandy loam soils, however, more meadows occurred, because productivity is not always optimal for tillage. These grasslands, however, are characterized by large competitive forbs and grasses, which account for the high mean competition value.

As expected, the mean hemeroby value was lower for reserves compared to the landscape matrix (3; mesohemerobe, semi-natural vegetation compared to 4; b-euhemerobe, ruderal vegetation on strongly altered soils), indicating more natural vegetation inside the reserves. Furthermore the reserves contained more threatened species, indicating the importance of reserves for the conservation of vulnerable and threatened species (lower mean trend index inside reserves, tables 3 & 4). The mean trend index is even lower for sandy loam soils compared to loam soils indicating a larger proportion of threatened species on sandy loam soils. Considering the high
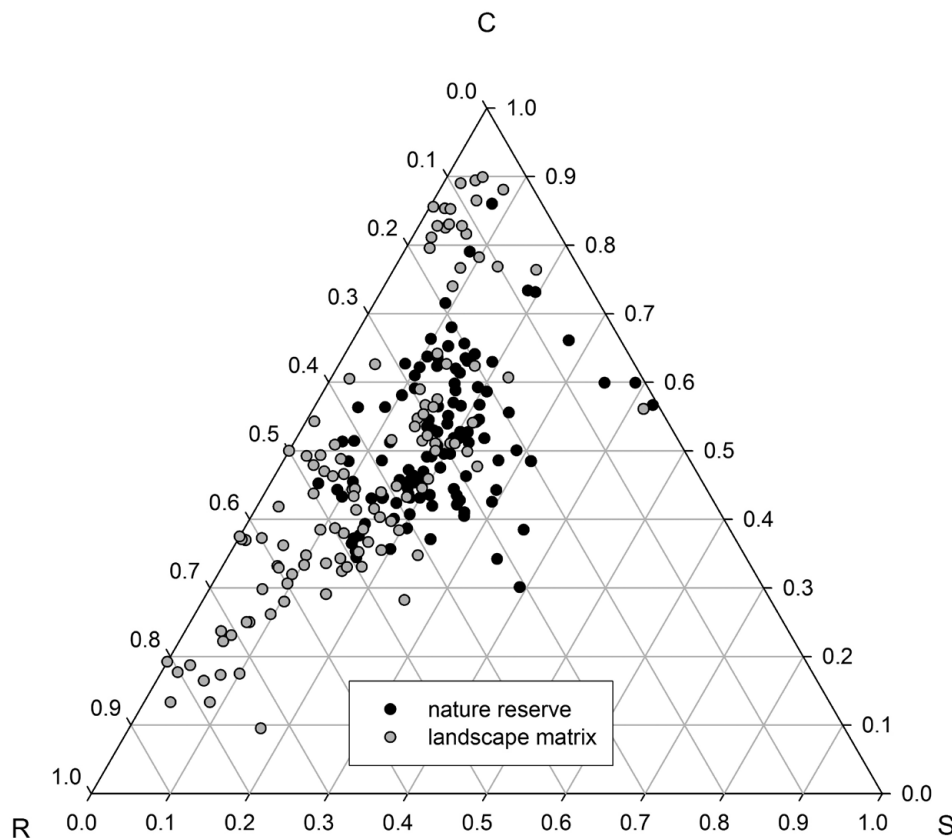

Figure 5 – CSR-signature for the plots inside (nature reserve) and outside (landscape matrix) of the reserves for all ten study areas (C = competitive, R = ruderal, S = stress-tolerant).

variability of abiotic conditions in the landscape matrix on sandy loam soils (R and N Ellenberg values, table 3), we may conclude that species of this soil type are more dependent on nature reserves for their survival, which could help explain their greater decline in Flanders.

Concluding remarks

An overall clear pattern of higher species diversity was found for nature reserves compared to the landscape matrix at plot (S & D), reserve (α) and regional (γ) scale. We cannot exclude that part of this difference may be due to higher initial diversity of habitats upon creation of these reserves. However given the fact that these reserves have been converted from agricultural land, this difference is likely very small and thus not the main reason for the observed pattern, also ruling out the presence of extinction debt. Since 19% of the total species number of Flanders was found within the ten reserves (total area = 113 ha) and a considerable number of these species were positively associated with the reserves, also showing a lower mean rarity trend index value (indicating a higher proportion of vulnerable and threatened species), these results provide clear evidence of the value and effectiveness of small grassland reserves in conserving plant diversity. They confirm the idea of a conservation credit in nature reserves compared to the dominating agricultural landscape matrix.

This proof of the effectiveness of small nature reserves forms in no way an argument in favour of land sparing for being the best strategy (cf. Green et al. 2005). It only proves that land sparing is a valid alternative to conserve at least a part of the local biodiversity in highly fragmented agricultural landscapes. It should however also be noted that the traditional reserves in Belgium mainly focus on communities of pronounced stress regimes (nutrient limitation, shallow soils, wetlands, light limited forests) but often fail to preserve communities of high disturbance regimes, such as arable weeds. We saw that 56 species (17% of all species) in this study only occurred outside of the reserves. This indicates that land sparing alone will not succeed in protecting an area's full biota (unless perhaps creation of high disturbance reserves is achieved).

On the other hand it is important to realize that these observed patterns may be unstable in time. With climate change progressing, many species will be forced to migrate to more suitable habitats further north, which can be problematic, especially for plants (Jackson & Sax 2010). Small nature reserves will only stay sustainable if they become part of a larger network of protected areas, acting as stepping stones. It is in this context that the incorporation of wildlife friendly farming in the matrix around these networks could create sustainable ecosystems resilient enough to overcome current threats (Bengtsson et al. 2003), since much evidence of the effect of landscape matrix configuration on species dispersal exists (Jules & Shahani 2003, Levey et al. 2008, Van Geert et al. 2010).

SUPPLEMENTARY DATA

Supplementary data is available at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect. com/content/botbel/plecevo/supp-data), and consist of a list of species encountered and their distribution between nature reserves and landscape matrix plots (pdf format).

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