

Research Article

Respective roles of recent hedges and forest patch remnants in the maintenance of ground-beetle (Coleoptera: Carabidae) diversity in an agricultural landscape

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Abstract

We compared three kinds of habitats: small remnants of native forests, recent hedges and barley crops, in order to investigate their respective roles in the maintenance of carabid-beetle diversity in a 950-ha area of an intensive agricultural landscape. Carabid faunas in remnants differed weakly from those found in hedges and crops. In particular, small remnants had few typical forest carabid species and a large number of open-area or ubiquitous species. Different approaches in the measurement of α and β -diversity (classical indices, and additive partitioning of Simpson's index) showed similar results: hedges supported a high α -diversity but habitat types were quite similar overall, with weak differences between open and closed or disturbed and undisturbed habitats.

A comparison of species dispersal powers in the various habitat types showed that species with a low dispersal power were rare in all habitats. However, wing development measured on two dimorphic species revealed, surprisingly, that brachypterous individuals were mainly present in hedges, which were expected *a priori* to be more disturbed, than remnants hence less suitable for the establishment of populations with a low dispersal power.

These results suggest that small remnants do not behave as 'climax' habitats in this intensive agricultural landscape, probably because of their small size and strong isolation. We discuss the interest of new undisturbed habitats, such as recent hedges, for the maintenance of carabid diversity at both the local and landscape scale.

Introduction

During the past decades, agricultural practices have led to landscape simplification and fragmentation in many industrialized countries. As a result, ancestral habitats are reduced to small remnants. Recently, management efforts promote or enhance more recent habitats that are less disturbed than cultivated areas, such as set-asides or field boundaries. In agricultural regions, these two trends result in mosaic landscapes, consisting of patchy undisturbed habitats distributed across the fields in varying densities and connectivity levels (Webb 1989; Saunders et al. 1992).

In some European regions where very intensive crop culture is conducted, such as in our study in Beauce (France), the process of landscape fragmentation has been very strong and rapid, producing extremely damaged open landscapes. In addition to physical and microclimatic changes (through modification of radiation and water fluxes or wind profiles), ecological processes are strongly modified by habitat fragmentation (Dunning et al. 1992; Davis 1994). Undisturbed habitats are often considered refuges for a number of species, hence reservoirs for regional diversity, and the interest of their conservation in open landscapes is generally recognized. However, patch

features such as shape, age, size, connectivity, or distance from other patches, appear to be critical for the survival of organisms and populations, hence community diversity (Fahrig 1985; Burel 1989; Webb 1989; Saunders et al. 1992; Davis 1994; Gruttko 1994; Gilbert et al. 1998). Dispersal behavior and demography determine the response of individual species to fragmentation.

Ground beetles (*Coleoptera: Carabidae*) have been widely used to study the effect of fragmentation (Den Boer 1987; Burel 1992; De Vries 1996; Luff 1996; Tischendorf 1998), because of their rapid response to environmental changes, their well-known biology, and their easy sampling. Just as for other organisms, the positive role of remnants of native forests in the establishment and survival of carabid populations have been emphasized: as 'climax' environments, they allow the survival of typical forest species in patchy landscapes, especially when they are connected by corridors (Fahrig 1985; De Vries 1996; Tischendorf 1998). The Kellerberrin project conducted in western Australia (Hobbs et al. 1993; Saunders et al. 1994; Hobbs and Humphries 1995; Yates and Hobbs 1997) aimed to study the various effects of drastic habitat fragmentation and restoration of undisturbed habitats. In Europe however, most of the studies have been limited to only moderately damaged areas. In intensive agricultural regions where remnants are very small, strongly isolated and possibly more disturbed by human activities, do they really behave as more continuous habitats? What are their respective roles, as compared with other habitat types, in the maintenance of local carabid populations and regional species diversity? The role of more recent habitats, such as young hedges, is also interesting to consider. We previously showed (Fournier and Loreau 1999) that these habitats have a strong influence on carabid species diversity at a local scale (100 m around the hedges), thus confirming other work on the importance of field margins for predaceous arthropods (Desender et al. 1989; Chiverton and Sotherton 1991; Sotherton 1992; Thomas et al. 1992; Kiss et al. 1994). What may be the role of such hedges at the landscape scale, as compared especially with small forest remnants?

In order to address these questions, we sampled carabids in two forest remnants, two recent hedges and two barley crops. Hedges (recent, undisturbed and open habitats) were in a young successional stage, intermediate between crops (periodic, disturbed habitats) and remnants (old, permanent, undisturbed habi-

tats). After the examination of the faunas sampled in the three habitat types, we compared the results given by classical measures of α - and β -diversity (Simpson's diversity and species richness for α -diversity, Kendall's coefficient of correlation for β -diversity), to those given by an innovative and unifying approach proposed by Lande (Lande 1996). To better assess the disturbance level of the three habitat types, we also compared the dispersal power of carabids. Carabid species can be classified in three groups according to their wing development: (1) monomorphic brachypterous species disperse by walking only, hence have a low dispersal power; (2) monomorphic macropterous species mainly disperse by flight, thus have a high dispersal power; (3) in dimorphic species both macropterous and brachypterous individuals coexist in the same populations, so that the total dispersal power decreases with the percentage of macropterous individuals in the population. Now, several authors have shown that dispersal power also depends on the stability and degree of openness of the habitat (Den Boer 1977, 1987; Roff 1994; Gutierrez and Menendez 1997). Indeed ancient, stable and closed habitats are mainly inhabited by species with a low dispersal power (i.e., either monomorphic brachypterous species, or dimorphic species with a majority of brachypterous individuals). In our case, small forest remnants belong *a priori* to this category. On the contrary, more recent, open and disturbed habitats are mainly inhabited by species with a high dispersal power (i.e., monomorphic macropterous species, or dimorphic species with a majority of macropterous individuals). In our case, hedges and crops belong to this category. Hence we compared the numbers of species with low/high dispersal power in the three habitat types. We also directly compared the percentage of macropterous individuals in populations of two dimorphic species, *Notiophilus biguttatus* and *Bembidion lampros*, from the three habitat types.

Thus, considering the characteristics (age, degree of openness, disturbance levels) of the three habitat types, we aimed to test the following hypotheses :

- (1) The carabid fauna in remnants should be different from the carabid fauna in hedges and crops.
- (2) Because of their intermediate stage of succession, hedges should exhibit a higher α diversity than crops and remnants. Indeed, new habitats often support a high α -diversity, at least in the beginning of succession (Ranta and As 1982; Niemelä et al. 1993).
- (3) Because hedges and crops are both recent and open habitats, whereas remnants are ancient and

closed habitat, similarity between hedges and crops (hedge/crop similarity) should be greater than hedge/remnant similarity, or crop/remnant similarity.

- (4) The number of species with low dispersal power should be higher in remnants than in hedges and crops.
- (5) In the dimorphic species *N. biguttatus* and *B. lampros*, the percentage of macropterous individuals should be smaller in populations from remnants than in populations from hedges and crops.

Materials and methods

Study area

We conducted this study in Ouarville (100 km southwest of Paris) (Figure 1) in a region of intensive crop culture.

Hedges were planted during the winter 1994–1995 and are described in detail in Fournier and Loreau (1999). They consisted of shrubs that were not higher than 3 m. The area of one hedge was 3000 m² (500 m × 6 m). Each hedge was separated from the adjacent crop culture by a 5000 m² transition zone (500 m × 10 m) planted on each side. There were no connections between the different hedges. Hedges remained totally undisturbed. They can therefore be qualified as recent, open, isolated and undisturbed habitats.

Crops were planted with spring barley at the time of the study (1996). The area of each plot was 250,000 m² (1000 m × 250 m). During the sampling period (March 24–August 1), barley crops were subjected to irrigation and usual chemical treatments. These habitats can be qualified as periodic, open, continuous and disturbed.

The farm was surrounded by a few small woody patches (from 0.75 to 2.03 ha) and two larger woods (14 and 19 ha) (Figure 1). All of them are remnants of ancestral forests, dominated by beech and chestnut-tree. Their minimum age is two centuries, thus they are in a late successional stage. These habitats can therefore be qualified as old, closed, isolated and undisturbed.

We sampled ground beetles in six sites: two hedges (hereafter ‘Hedge $\frac{1}{2}$ ’), two crops (‘Barley $\frac{1}{2}$ ’ and two forest remnants (‘Wood $\frac{1}{2}$ ’) (Figure 1). The two hedges were identical in size, shape, orientation and floristic composition, as were the two crops. Wood 1 had a

surface of 2.03 ha and was close to two larger remnants. Wood 2 was smaller (0.75 ha) and completely isolated. The shortest distance between a hedge and a remnant was 400 m, the longest 1125 m. The six sites were classified according to habitat type, and together represent a gradient in size, age, disturbance level and degree of openness (Table 1). In addition, sample sites have different shapes.

Sampling design and method

Beetles were sampled using pitfall traps that were plastic bottles buried in the soil, filled with a 4% formalin solution and a drop of detergent. In hedges and crops, we used traps that were already in place for another study (Fournier and Loreau 1999). In crops, we considered only the 4 traps situated far enough from the hedge (100 m apart). Hence, there were unequal numbers of traps: 15 in each hedge versus 4 in each crop. We added 10 traps in each remnant. Traps were spaced out 5 m in hedges and remnants, 15 m in crops. They were emptied every 2 to 4 weeks. Sampling began on March 24 1996, and stopped on August 1 in barley crops (date of harvesting) and October 9 elsewhere. We used the 131-days sampling period from March 24 to August 1 for all the comparisons involving crops.

Carabid faunas in the three habitat types

Because remnants are closed, ancient and undisturbed habitats, we expected their faunas to differ greatly from those found in hedges and crops, both open and young habitats; in particular, closed-habitat species were expected in majority in remnants (hypothesis 1). To test this hypothesis, we compared the mean catch per species according to their habitat preferences. We distinguished 3 kinds of species: open-habitats species, closed-habitat species and ubiquitous species (Jeannel 1941, 1942; Lindroth 1974, 1992; Den Boer 1977; Den Boer et al. 1980). For 3 species we did not find any habitat preferences; they were removed from the analysis. The null hypothesis was that the number of individuals in each category of habitat preference does not depend on habitat type. Contingency tables were analyzed using χ^2 -tests of independence. Sites from the same habitat were pooled.

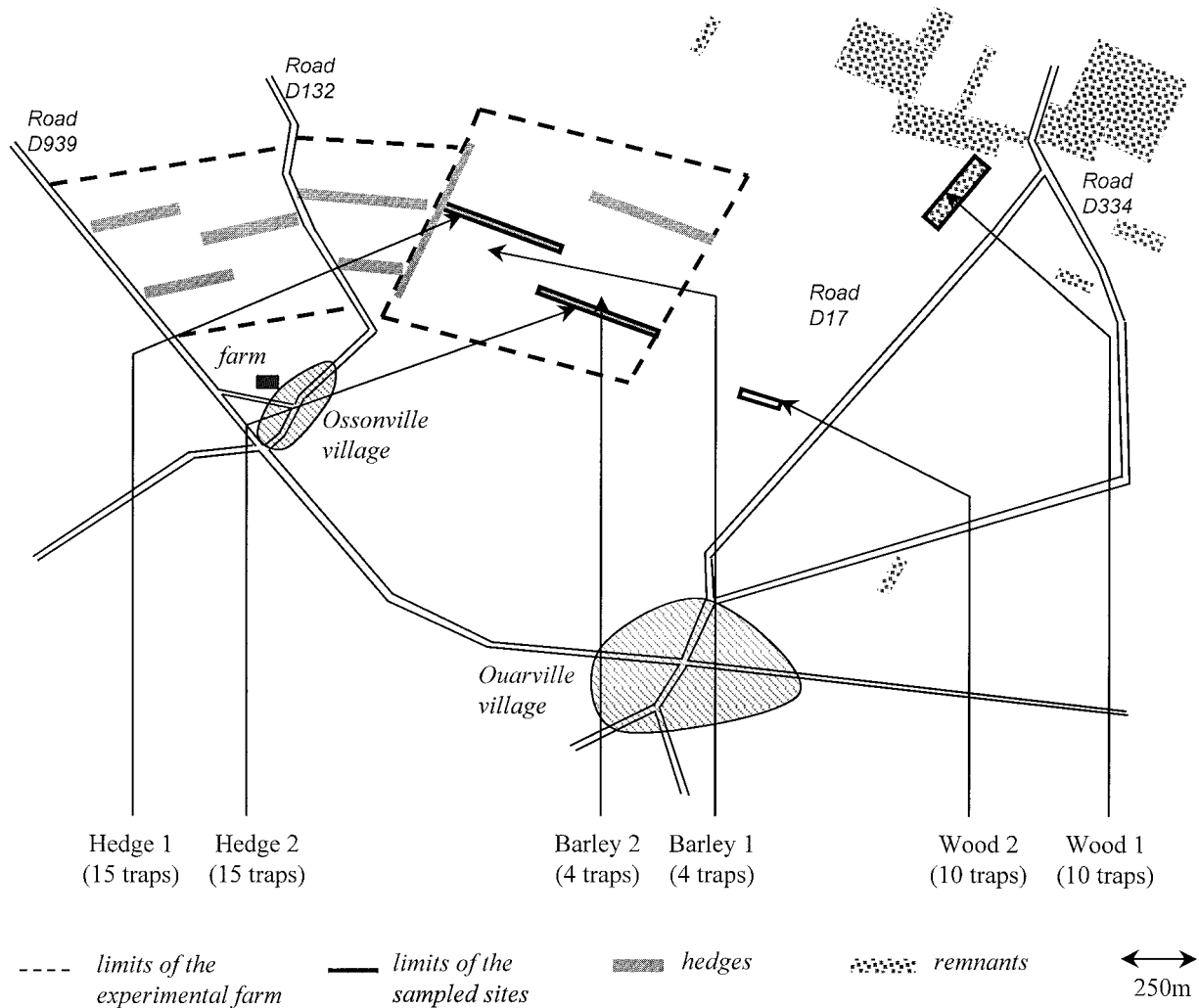


Figure 1. Map of the study area and sampled sites (with numbers of pitfall traps in brackets).

Table 1. Characteristics of sampled sites.

	Name of site					
	Wood 1	Wood 2	Hedge 1	Hedge 2	Barley 1	Barley 2
Size	2.03 ha	0.75 ha	0.3 ha	0.3 ha	20 ha	20 ha
Habitat type	wood	wood	hedge	hedge	crop	crop
Age	ancient	ancient	recent (1.5 year)	recent (1.5 year)	very recent (a few months)	very recent (a few months)
Permanence level	permanent	permanent	permanent	permanent	periodic (9 months at most)	periodic (9 months at most)
Disturbance level	undisturbed	undisturbed	undisturbed	undisturbed	disturbed	disturbed
Opening level	closed	closed	open	open	open	open

Diversity α and β and similarity

Classical α - and β -diversity indices

Hypotheses 2 (high species richness and diversity in hedges) and 3 (high β -diversity and similarity between hedges and crops) can be tested separately using the classical indices of α and β -diversity widely used in ecology to address these questions (Cancela da Fonseca 1969; Southwood 1978; Taylor 1978).

To describe α -diversity, we calculated species richness S and Simpson's index D at the trap level. They were chosen for their simplicity in calculation and interpretation, and also because they are complementary in giving different importances to rare species (Hill 1972; Fournier and Loreau 1999). In each trap k , we recorded :

S_k : the total number of species,

N_k : the total number of individuals of species i , and

$p_{i,k} = \frac{N_{i,k}}{\sum_{i=1}^{S_k} p_{i,k}^2}$: the relative abundance of species i .

Simpson's (1949) diversity index, was calculated as :

$$D_k = 1 - \sum_{i=1}^{S_k} p_{i,k}^2.$$

Statistical analysis of α -diversity was performed using a nested ANOVA model (with 'site' effect nested into 'habitat' effect).

To describe β -diversity we calculated Kendall's (1962) coefficient of rank correlation (τ) between the ranks of species in two sample sites. In each site, species were ranked by order of decreasing abundance. All pairs of sites were considered in this analysis.

Additive partitioning of diversity

The former approach presents two major disadvantages. First, α - and β -diversity classical measures do not have the same functional forms, and are thus generally interpreted separately. Second it is often difficult with such measures to integrate several spatial scales.

We thus tried a new approach to test hypotheses 2 and 3, following Lande's (1996) method, derived from the partitioning of genetic diversity within and among populations. This author pointed out that Simpson's diversity index as defined above can be expressed as a variance. The total diversity of a set of communities can then be partitioned into non-negative, additive components within and among communities :

$$\overline{D}_{\text{within}} + D_{\text{among}} = D_T. \quad (1)$$

The three terms of Equation (1) are defined as follows:

$$\begin{aligned} \overline{D}_{\text{within}} &= 1 - \sum_j q_j \sum_i p_{ij}^2, \\ D_{\text{among}} &= \sum_j q_j \sum_i (p_{ij} - \overline{p}_i)^2, \\ D_T &= 1 - \sum_i \overline{p}_i^2 \quad \text{where } \overline{p}_i = \sum_j q_j p_{ij}, \end{aligned}$$

where p_{ij} represents the frequency of species i in community j , and q_j the proportional weight associated to community j (because sample importance, i.e. number of traps, can differ among communities). For Simpson's index, this partitioning is equivalent to an analysis of variance. $\overline{D}_{\text{within}}$ is a measure of the average α -diversity within communities, D_{among} a measure of β -diversity among communities, and D_T , a measure of γ -diversity in the total set of communities. Thus, the three dimensions of diversity are expressed under the same functional form (a variance) and can be compared directly. As a consequence, a measure of similarity among communities is

$$\Psi_D = \frac{\overline{D}_{\text{within}}}{D_T}$$

Another benefit of this method is that it allows partitioning at more than two hierarchical levels (Patil and Taillie 1973); for example, a set of traps from the same site, a set of sites from the same habitat type, and a set of habitat types from the same landscape. In our study, diversity within and among communities were basically assessed at the trap level, but we also considered three other hierarchical levels: site, habitat type, landscape (Figure 2). The equations at each levels are as follows (where k names the trap, j the site, and h the habitat type):

$$D_{\text{Total}} = \overline{D}_{\text{within habitats}} + D_{\text{among habitats}} = \sum_h q_h D_{\text{within habitat } h} + D_{\text{among habitats}},$$

$$D_{\text{within habitat } h} = D_{\text{total in habitats } h} = \overline{D}_{\text{within sites } h} + D_{\text{among sites } h} = \sum_j q_j D_{\text{within site } j,h} + D_{\text{among sites } h},$$

$$D_{\text{within site } j,h} = D_{\text{total in site } j,h} = \overline{D}_{\text{within traps } j,h} + D_{\text{among traps } j,h} = \sum_k q_k \overline{D}_{\text{within trap } k,j,h} + D_{\text{among traps } j,h}.$$

This partitioning is analogous to a nested ANOVA.

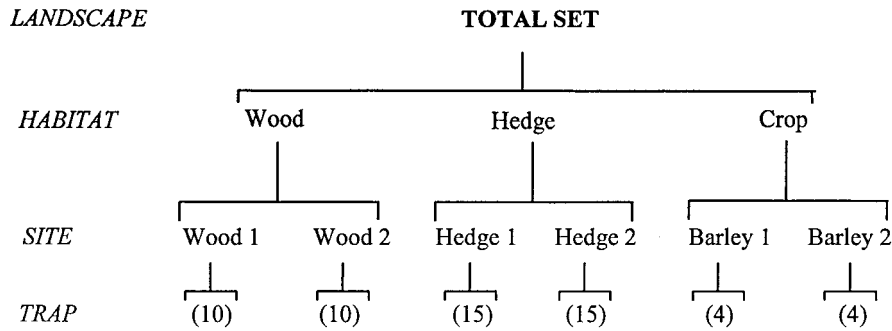


Figure 2. The four nested levels of diversity considered in the additive partitioning of species diversity.

Dispersal powers

Dispersal powers of all species

We hypothesized (hypothesis 4) that remnants should be richer in species with low dispersal power than hedges and crops, because they are *a priori* closed and undisturbed habitats. The dispersal powers of carabid species were obtained from the literature (Jeannel 1941, 1942; Lindroth 1974, 1992; Den Boer 1977; Den Boer et al. 1980). When data were not available, species were removed from the analysis (8 species). We distinguished three categories of species: species with a high dispersal power (mainly macropterous), species with an uncertain or medium dispersal power (mainly dimorphic), and species with a low dispersal power (mainly brachypterous, or with non-functional flight muscles). In order to test if the number of insects in each category depended on habitat type, we analyzed the contingency tables with χ^2 -tests of independence. Sites from the same habitat type were pooled.

Dispersal power of two dimorphic species:

Notiophilus biguttatus and *Bembidion lampros*

Dimorphic carabid species are of particular interest to examine the relationship between dispersal power and habitat. In these species, both macropterous and brachypterous morphs are found. The dispersal power in a population depends on the percentage of macropterous individuals. In our case (hypothesis 5), we expected more brachypterous species in remnants than in hedges and crops.

We measured wing development in two dimorphic species, *N. biguttatus* and *B. lampros*. *N. biguttatus* is a small species (5 to 5.5 mm), inhabiting all kinds of forest habitats, with a preference for borders and clearings (Den Boer 1977; Ernsting and Isaaks 1987). Its life cycle seems to be very irregular. *B. lampros*

is also small (3.4 to 4.4 mm); it prefers exposed soil with sparse vegetation, including agricultural fields, and breeds in the spring (Mitchell 1963a,b). Individuals caught in pitfall traps were dissected for both species. For *B. lampros*, there were too few captures in the crops; therefore the comparison was restricted to hedges and remnants.

Wing development (*WD*) was calculated for each individual as the ratio between wing area and elytron area. Wing or elytron area was approximated by the product of the greatest width and the greatest of length of wing or elytron (Den Boer 1977; Desender et al. 1986).

Individuals were classified as macropterous when *WD* was higher than 1.5, and brachypterous otherwise (Den Boer 1977). After pooling samples from sites of the same habitat type, frequencies of macropterous and brachypterous individuals were compared using χ^2 -tests of independence.

Results

Carabid faunas in the different habitat types

In total, 41 species were found over the study area between March and August ('Period 1') (Table 2). They were mainly open-area or ubiquitous species (34 species). The second part of Table 2 lists the species caught in hedges and remnants over the whole period from March to October ('Periods 1 + 2'); only 3 species, all from open habitats, were added in hedges compared with the first period. Hereafter, all tests will be realized with the data from the first sampling period.

Seven species were found only in remnants (Tables 2 and 6): *Abax ater*, *Badister bipustulatus*, *Calathus piceus*, *Leistus fulvibarbis*, *L. rufimarginatus*,

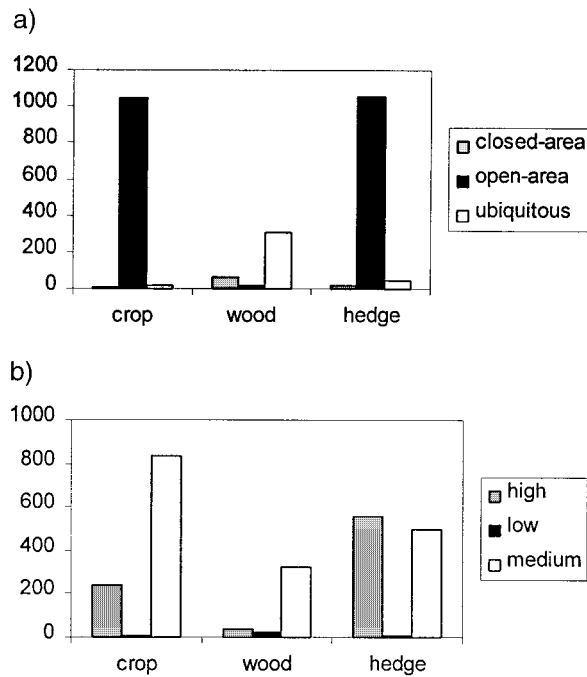


Figure 3. Distribution of species mean catch per trap across the various habitat types, with species grouped according to their habitat preferences (a) and dispersal powers (b).

Metabletus foveatus and *Stomis pumicatus*. Except *M. foveatus*, they are all closed habitat species. The 21 remaining species found in remnants are also found in the other habitat types. Among them, only *Notiophilus biguttatus* is a closed-habitat species: the 20 remaining are ubiquitous or open-area species. Eight species were found only in hedges, some of them in very low numbers (Tables 2 and 6): *Acupalplus brunripes* (one specimen), *Brachinus sclopeta* (one specimen), *Calathus melanocephalus*, *Diachromus germanus*, *Harpalus ardosiacus* (one specimen), *H. azureus* (2 specimens), *Leistus ferrugineus*, and *Notiophilus germinyi*. Almost all species found in hedges (33 species) are ubiquitous or open-area species, except *N. biguttatus*.

The species found in crops were a subset of those found in hedges (Table 2). However, we verified elsewhere (data not shown) that the faunas sampled in crops 100 m apart from hedges, are identical to the faunas sampled in similar crops not bordered with hedges. Hence, it can be considered that the influence of the hedge is reduced at such a distance.

Closed-habitat species were rare overall, but they were more rare in hedges and crops than in remnants. The χ^2 analyses on mean catches per trap

confirmed that habitat preferences of species depended significantly of habitats ($\chi^2 = 1863$, $df = 4$, $P < 0.0001$). Open-area species were less numerous in remnants than in hedges and crops, whereas closed-habitat and ubiquitous species were more numerous in remnants (Figure 3a). However it can be noticed that the dominant category in remnants is not closed-habitat species, but ubiquitous ones.

Species diversity within and between communities

Classical α and β -diversity indices

α -diversity. The nested ANOVA showed similar results for species richness and Simpson's index assessed at the trap level (Table 3). The effect of site was not significant for S , but was significant for D . The Bonferoni classification of means showed that for both indices there were no significant difference between sites from the same habitat type. The effect of the habitat type was significant for S and D . The Bonferoni classification of means showed that α -diversity in hedges was significantly higher than in crops and remnants, the last two being not significantly different.

β -diversity. A cluster analysis of Kendall's τ calculated for pairs of sites, showed two levels of grouping (Figure 4a). First, the six sites could be grouped by pairs of sites belonging to the same habitat type. Second, the remnant group was the most distant in similarity. Surprisingly, the correlation coefficients (Table 4) were high overall.

Additive partitioning of diversity

The partitioning of species diversity at four nested levels first showed that the α -diversity in hedges was higher than in crops or remnants (Table 5): at the site level, the values of diversity within 'Hedge 1' and 'Hedge 2' are higher than all other sites, and the same is true at the level of the habitat type. Also, whatever the level considered (trap, site, habitat), the average diversity within items was always much higher than the diversity among items (Figure 5). As a consequence, the different sites can be considered very similar to each other: the similarity coefficient Ψ_D was 0.749 at the site level. The same conclusion can be drawn at the habitat type level: the similarity coefficient was 0.752 at this level.

Table 3. Effects of site and habitat type on classical α -diversity indices (species richness S and Simpson's index D). Effects were analysed using a nested ANOVA model ('site' nested into 'habitat type'). The total sample size was 58. Means (\pm standard deviation) were classified with Bonferroni's method: values with the same letter are not significantly different.

Dependent variable	effect	d.f.	F	P	Mean (\pm std. dev.)		
S	Site	3	1.99	0.13	Hedge 1	17.53 (\pm 2.03)	A
					Hedge 2	17.67 (\pm 2.82)	A
					Barley 1	11.5 (\pm 1.29)	B
					Barley 2	14.25 (\pm 0.96)	B
					Wood 1	10.5 (\pm 2.07)	B
					Wood 2	12.2 (\pm 2.20)	B
	Habitat type	2	25.39	0.0132	Hedge	17.60 (\pm 2.25)	A
					Barley	12.87 (\pm 1.81)	B
Wood					11.35 (\pm 2.25)	B	
D	Site	3	4.60	0.0062	Hedge 1	0.73 (\pm 0.05)	A
					Hedge 2	0.79 (\pm 0.04)	A
					Barley 1	0.42 (\pm 0.09)	B
					Barley 2	0.47 (\pm 0.03)	B
					Wood 1	0.36 (\pm 0.13)	B
					Wood 2	0.45 (\pm 0.07)	B
	Habitat type	2	33.60	0.0088	Hedge	0.76 (\pm 0.05)	A
					Barley	0.45 (\pm 0.07)	B
					Wood	0.40 (\pm 0.11)	B

Dispersal power

Comparisons of species dispersal powers in the three habitat

Species with a low dispersal power were rare overall: only 7 species with a low dispersal power were found in the whole area (Tables 2 and 6): *Abax ater*, *Badister sodalis*, *C. melanocephalus*, *L. ferrugineus*, *L. fulvibarbis*, *M. obscuroguttatus* and *Stomis pumicatus*. Five of them were present in remnants (17.8% of remnant species) and 4 in hedges (12% of hedges species).

χ^2 tests showed that species dispersal power depended significantly on habitat types ($\chi^2 = 401$, $df = 4$, $P < 0.0001$) (Figure 3b). Species with high dispersal powers were less numerous in remnants than in hedges and crops. Species with intermediate dispersal powers were especially found in crops. There were few species with low dispersal power in all habitats, but this category was significantly more numerous in remnants ($\chi^2 = 22$, $df = 2$, $P < 0.0001$). However, this habitat type is significantly dominated by species with intermediate dispersal powers.

Dispersal power of dimorphic species

From the 6 sites a total of 230 individuals were examined for *N. biguttatus*, but only 59 for *Bembidion lampros* (Table 7). For both species, sites from the same habitats types presented almost identical distributions (Figures 6 and 7). Dispersal power for *N. biguttatus* was high overall: 89.5% of individuals were macropterous. In this species brachypterous individuals were found only in hedges and crops (Table 7a; tests on pooled samples: $\chi^2 = 23.25$, $df = 2$, $P < 0.0001$). For *B. lampros* we limited the comparison to hedges and remnants because of the too low numbers of specimens in crops. Again brachypterous individuals were mainly found in hedges (Table 7b; tests on pooled samples: $\chi^2 = 32.22$, $df = 1$, $P < 0.0001$).

Discussion

Because of the harvesting date (beginning of August), it was not possible to sample in barley crops during the whole season. Thus the sampling period (March 24–August 1) used for the comparison between the three habitat types only covers the beginning of the activity

Table 4. Correlation values for Kendall's rank correlation coefficient, calculated for pairs of sites.

	Hedge 1	Hedge 2	Barley 1	Barley 2	Wood 1	Wood 2
Hedge 1	1	0.783**	0.711**	0.731**	0.228	-0.007
Hedge 2		1	0.612**	0.732**	0.204	-0.020
Barley 1			1	0.825**	0.355	0.123
Barley 2				1	0.364	0.081
Wood 1					1	0.529**
Wood 2						1

Table 5. Additive partitioning of species diversity using Simpson's index D : values of total diversity in each site ($D_{\text{total in site}} = \overline{D}_{\text{within traps}} + D_{\text{amongtraps}}$), and in each habitat type ($D_{\text{total in habitat}} = \overline{D}_{\text{within sites}} + D_{\text{among sites}}$). (Values at the trap level are not presented).

Level	Item	$D_{\text{total in item}}$
Site	Hedge 1	0.746
	Hedge 2	0.813
	Barley 1	0.429
	Barley 2	0.475
	Wood 1	0.374
	Wood 2	0.455
Habitat type	Hedge	0.783
	Crop	0.453
	Wood	0.417

period of carabid species; 'autumn breeders', which are mainly active in the second part of the year, were thus missed or little captured (Table 2). Typical forest carabid species are known to be autumn breeders. Hence, our diagnosis concerning the high similarity between remnants and open habitats might have been biased by the absence of these late-active species in our samples. However, comparing the species composition between hedges and remnants over the whole season (March 24–October 9, 'Periods 1 + 2, Table 2) shows that no new forest species were added in the second period. We also applied additive partitioning of species diversity between hedges and remnants with enlarged samples covering the second period (results not presented), and again the similarity between hedges and remnants was very high ($\Psi_D = 0.748$). Thus our results are not due to too short a sampling period.

The eventual bias induced by the unequal sampling effort is reduced by the length of the sampling period. This bias mainly influences the calculation of the species richness at the site level; therefore we avoided the recourse to this index: as regard α -diversity, we performed the comparisons at the trap level, and as regard β -diversity, we preferred the Kendall's τ to the Sorensen's index because the first does not require the biased species richness.

The study of carabid faunas in the various sites (Table 2) showed a rarity of typical forest species in remnants. Only 7 species preferring closed habitats were found, all of them present in remnants. They represent a very small subset of the typical forest species usually found in old growth temperate forests (Den Boer 1977; Loreau 1984a,b; Guillemain et al. 1997): numerous typical forest species are entirely lacking. Except 7 species found exclusively in remnants, carabid faunas were rather similar in remnants and in hedges and crops. In particular open-area or ubiquitous species remained important in remnants. Remnants differ from hedges and crops more in species abundances than in species composition, as will be discussed further. Hence, the difference in faunas is less important than expected, but hypothesis 1 cannot be entirely disproved.

As expected (hypothesis 2) α -diversity was significantly higher in hedges than in remnants and crops; this was true for both S and D (Table 3). However, it is not possible to conclude, from these results only, that hedges are more suitable habitats for carabid communities than the other habitat types. Recent habitats in early succession stages are often found to support a high species diversity (Ranta and As 1982; Thomas et al. 1992; Niemelä et al. 1993; Lys 1994; Kinnunen et al. 1996), mainly because of colonisation by open-area species, but also because of changes in species evenness: many species tend to be equally abundant in

Table 6a. Species distributions in the six sites according to their habitat preferences (C = Closed-habitat species; U = Ubiquitous species; O = Open-area species).

Site	Habitat preferences			Habitat type	Habitat preferences		
	C	U	O		C	U	O
Wood 1	6	7	9	Wood	7	9	12
Wood 2	6	8	9				
Hedge 1	1	8	17	Hedge	1	10	20
Hedge 2	1	9	20				
Crop 1	1	4	11	Crop	1	7	13
Crop 2	1	7	12				

Table 6b. Species distributions in the six sites according to their dispersal power (L = Low; M = Medium; and H = High dispersal power).

Site	Habitat preferences			Habitat type	Habitat preferences		
	L	M	H		L	M	H
Wood 1	3	10	8	Wood	5	12	9
Wood 2	5	9	8				
Hedge 1	3	12	8	Hedge	4	13	10
Hedge 2	3	13	10				
Crop 1	1	9	5	Crop	1	10	8
Crop 2	1	9	8				

early-successional habitats, whereas communities are strongly dominated by a few species in climax forests (Loreau 1984b). The high species diversity in recent habitats tends to decrease as succession progresses.

The measurement of β -diversity was also necessary in order to evaluate the role of habitat type on community structure. Here our aim was simply to compare community structure among a few habitats. The Kendall's coefficient of rank correlation is interesting because it takes into account species richness and abundances; it is less biased than other measures of similarity by the unequal sampling effort in the different habitat types. The sites from the same habitat types presented high similarities (Figure 4, Table 4). This result, added to those concerning faunas and α -

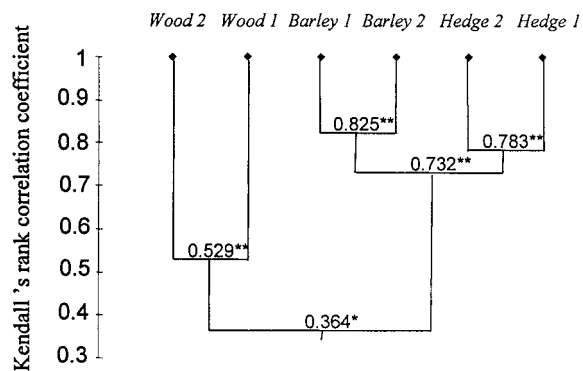


Figure 4. Cluster analysis for Kendall's rank correlation coefficient, calculated for pairs of 10 sites. Probability levels are indicated by ** when $P \leq 0.0001$, * when $P \leq 0.05$, and no sign when $P > 0.05$.

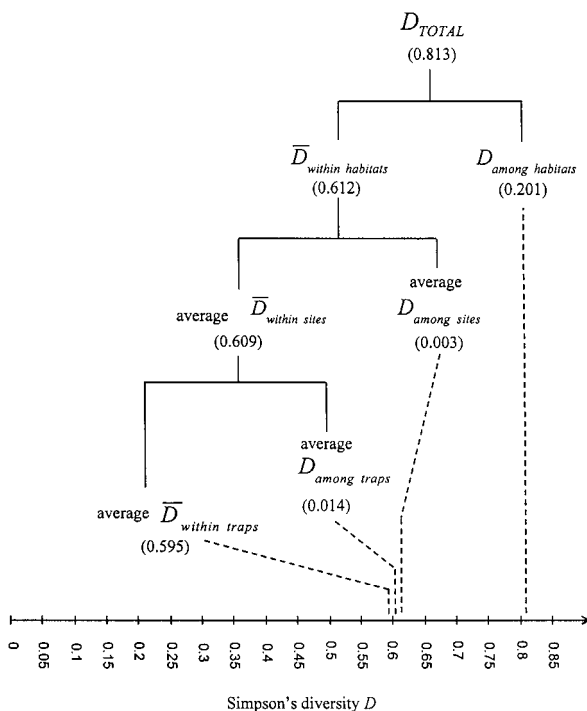


Figure 5. Results of the additive partitioning of Simpson's diversity index within and among the four nested levels (traps, sites, habitats, landscape).

diversity, lead to the conclusion that sites from the same habitat type can be considered as true replicates. Remnants were separated from the other habitat types (non significant correlations between species ranks). However this difference was weak: we expected lower, or even negative, correlation values (hypothesis 3).

Classical indices of α - and β -diversity are unrelated mathematically, hence are generally interpreted separately. This is an important limitation of these

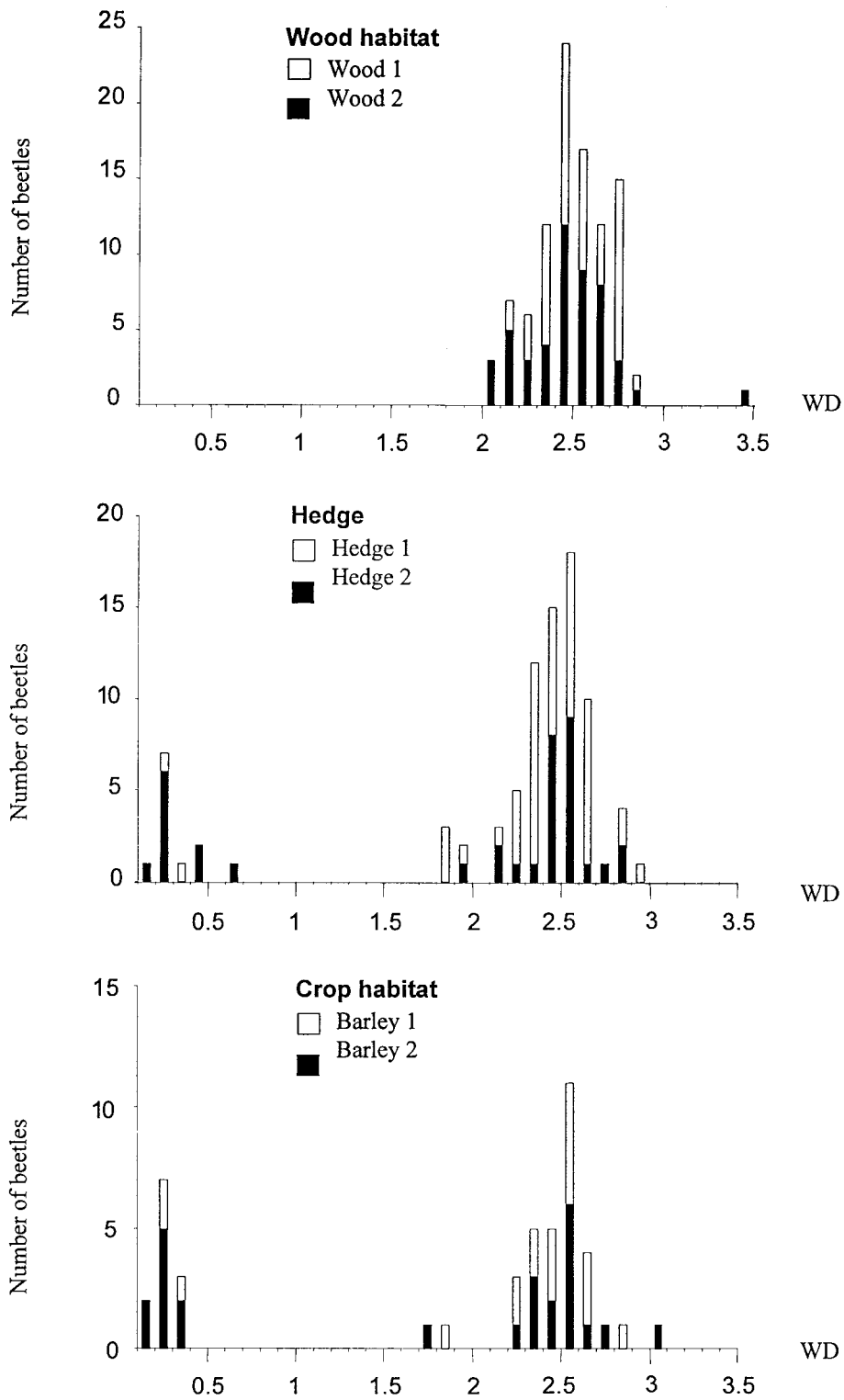


Figure 6. Frequency distributions of wing development (WD) units in the various sites for the dimorphic species *N. biguttatus*.

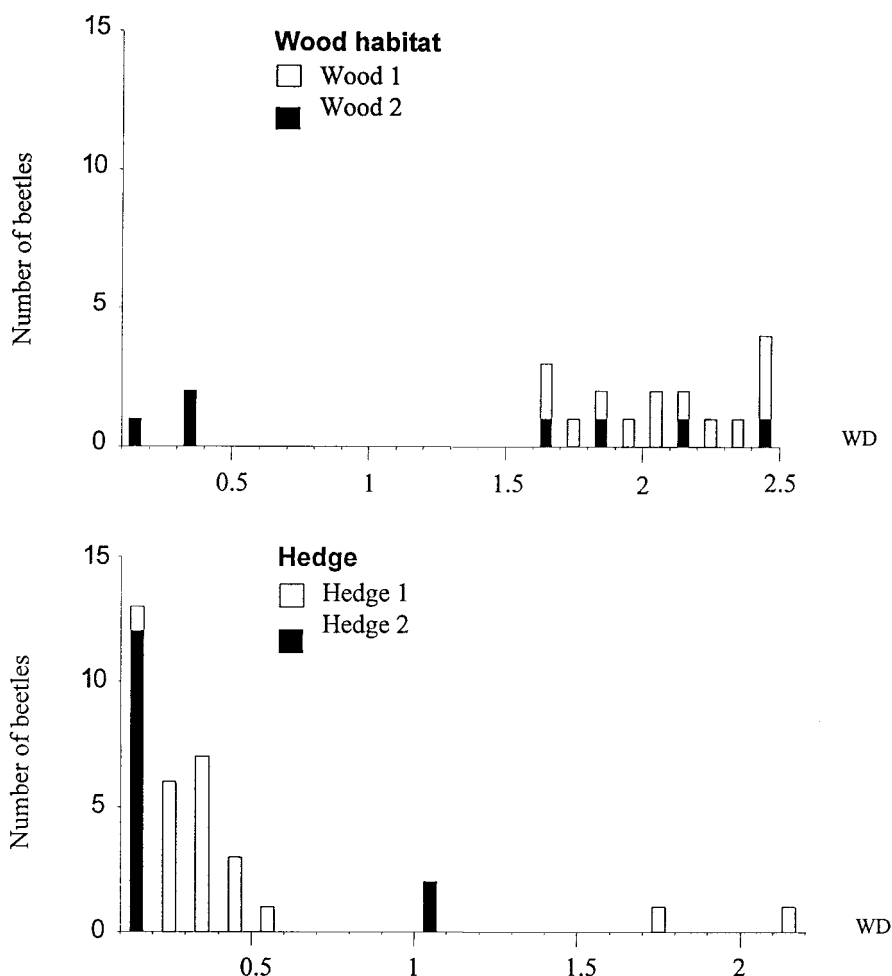


Figure 7. Frequency distributions of wing development (WD) in hedges and remnants for the dimorphic species *Bembidion lampros*.

approaches. Therefore, we applied Lande's (1996) method of additive partitioning of species diversity. This conformed to the results obtained with the classical approaches (Figure 5): the average diversity within communities or habitat types was high (especially in hedges), and the diversity among sites or habitat types was low, yielding a high level of similarity between sites or habitat types (around 75%). More generally, this new approach opens interesting perspectives in the study of general patterns of community structure, because it offers the possibility of reunifying the three dimensions of within (α), among (β), and total (γ) diversity in a set of communities.

Thus, contrary to expectation, remnants differed only slightly from the other habitats in their carabid-beetle community composition, diversity and structure. Our study lacks a sampling of carabid communities in larger forest patches surrounding the study area.

However, data from the literature (Den Boer 1977; Thiele 1977; Loreau 1984a,b; Burel 1989; Guillemain et al. 1997) showed important differences between faunas in old-growth temperate forests and results obtained in the small remnants of the study. The study of species dispersal powers provided a tool to understand this unexpected result.

In carabid beetles, dispersal power has both a genetic and an environmental basis (Aukema 1986; Desender et al. 1986; Desender 1987). Moreover, a trade-off between dispersal ability and several life-history traits (reproductive success, establishment ability) has been reported several times (Roff 1984). Hence, environmental as well as historical factors affect dispersal power (Roff 1994). In particular, dispersal power is related to habitat stability. Several studies showed that ancient, stable, closed habitats are mainly inhabited by species with a low dispersal power (Den Boer 1977;

Table 7. Frequencies of wing morphs (macropterous or brachypterous) in the various sites for the dimorphic species *N. biguttatus* (a), and in hedges and woods for the dimorphic species *B. lampros* (7b).

Habitat	Site	Wing morphs		Total
		Brachypterous	Macropterous	
<i>(a) N. biguttatus</i>				
	Wood 1	0	49	49
	Wood 2	0	50	50
Wood		0	99	99
<i>(Wood 1 + 2)</i>				
	Hedge 1	2	48	50
	Hedge 2	10	26	36
Hedge		12	74	86
<i>(Hedges 1 + 2)</i>				
	Barley 1	9	16	25
	Barley 2	3	17	20
Crop		12	33	45
<i>(Barleys 1 + 2)</i>				
<i>(b) B. lampros</i>				
	Wood 1	0	13	13
	Wood 2	3	4	7
Wood		3	17	20
<i>(Wood 1 + 2)</i>				
	Hedge 1	17	2	19
	Hedge 2	18	2	20
Hedge		35	4	39
<i>(Hedges 1 + 2)</i>				

Ranta and As 1982 ; Den Boer 1987; Roff 1994; Gutierrez and Menendez 1997). This is a general trend in patchy landscapes (Dunning et al. 1992; Kinnunen et al. 1996): individuals that have found a suitable habitat may invest less in dispersal. Hence, our predictions were that dispersal power should be lower in remnants than in recent hedges and crops (hypotheses 4 and 5).

In fact we found exactly the contrary. If species with low dispersal power were more numerous in remnants than in hedges and crops (Figure 3 and test of independence), however, remnants were dominated by species with rather high dispersal power. More surprisingly, data on wing development for the two dimorphic species showed that dispersal power was higher in remnants than in hedges and crops (Figures 6 and 7). For *N. biguttatus*, the high overall wing development confirms previous observations (Den Boer 1977). In this species as well as in *B. lampros* brachypterous individuals were mainly found in hedges and crops.

Hence, remnants seem to be unsuitable for the colonization by species with a low dispersal power. Note, however, that, although a forest generalist species, *N. biguttatus* prefers clearings or sparse forests (Den Boer 1977; Ernsting and Isaaks 1987). Therefore recent hedges, which may be similar to clearings, may be suitable enough for the establishment of *N. biguttatus* populations with a low dispersal power. The same explanation may also be valid for *B. lampros*, an open-area species. Nevertheless our results confirm that even recent, relatively open and isolated hedges may represent suitable habitats for a number of carabid species.

According to Den Boer (Den Boer 1970, 1987; Den Boer et al. 1980), a high dispersal power may be selected either in populations living in unstable environments (high environmental stochasticity) or in suitable but too small environments (high demographic stochasticity). Both processes tend to increase extinction risks: according to this point of view dispersal power is interpreted as a long-term, selective response for facing the extinction risks. Another explanation is found in the 'source-sink habitats' literature (Dias 1996; Eriksson 1996; Loreau and DeAngelis 1997): in species with a high dispersal power, macropterous individuals may be found even in adverse habitats ('sink habitats') as vagrants coming from the suitable colonized 'source' habitats; on the contrary, species with a low dispersal power are confined to 'source' habitats (Gutierrez and Menendez 1997; Petit and Burel 1998).

A last explanation for the presence of brachypterous individuals in hedges and crops and not in remnants, is that, macropterous individuals may be able to escape the adverse conditions they have to face in agricultural habitats by flying to woody habitats, whereas brachypterous individuals are able to reach only hedges because they must walk. This would mean that the observed difference is due to a short-term 'refuge effect'. Choosing between the different hypotheses would require a more detailed study of temporal changes in wing development in these populations.

All these results indicate that in this agricultural landscape patchy remnants of ancestral habitats do not act as climax habitats like old forests for the maintenance of carabid diversity. Since they are not early successional forests, two other factors may be responsible for this pattern: (1) remnants may be too small and isolated to allow the survival of typical forest species, and (2) remnants may be highly disturbed due to edge effect (Dunning et al. 1992; Saunders

et al. 1992). In addition, the remnants may be periodically disturbed by wood-cuttings or other human perturbations. Recently planted hedges appear to provide suitable habitats for carabids at a local scale by inducing a strong spatial reorganization around the hedge (Wallin 1987; Desender et al. 1989; Lys 1994; Wissinger 1997; Fournier and Loreau 1999). Our present study showed that such habitats are also interesting at a larger scale, in a perspective of maintenance of carabid diversity, because they may host populations that cannot establish either in remnants nor in crops. However, the examination of the literature (Burel 1992; Gilbert et al. 1998; Tischendorf 1998) lead us to think that such a mosaic of unconnected small woody remnants and young open hedges will never be sufficient to replace true large forests. Specialized forest species that are characteristic of climax environments need a strong connectivity between suitable habitats (Burel 1992) and will probably remain absent from such a landscape.

Conclusion

In very intensive agricultural landscapes such as the French Beauce region, remnants of ancestral forest habitats are very small, isolated, and perhaps more disturbed than expected. Our results show that these remnants are only moderately different from hedges and crops in their carabid faunas, and that they do not allow the survival of typical carabid forest species. Their role as reservoirs of carabid diversity is thus probably reduced compared with larger old-growth forests. The creation of hedges appears to elevate carabid species diversity, at both local and landscape scales. However, the lack of connectivity, within and between patchy remnants and hedges may limit their beneficial role at the landscape scale. Such habitats cannot replace true large forests for the conservation of specialized forest species.

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