Do species abundance distributions respond to landscape properties?

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Running headline: SAD and landscape properties

Summary

1. We investigated the relationships between species abundance distribution (SAD) and landscape properties (habitat extent, landscape composition and structure). First, the relationship between community evenness and SAD models was investigated using simulated communities. Then, the following hypothesis were tested on three data sets (birds, hoverflies and butterflies) in two French LTER sites: i) Landscape heterogeneity and low aggregation of resource patches in a landscape lead to a SAD fitting LogNormal distribution ii) The SAD and the resources abundance distribution in a landscape fit the same theoretical model.

2. Relationships between community evenness and SAD model should be used carefully for high value of J.

3. No consistent relationships were found between landscape properties and SAD in bird, butterfly and hoverfly community.

4. Increasing landscape heterogeneity was linked to low deviance to LogNormal model for butterfly, but it exhibited different pattern depending on the context (open versus wooded landscape) for birds and no relationship was found for the hoverflies.

5. Resources aggregation promoted dominance by few species and lead to high deviance to LogNormal model.

6. SAD of butterflies and hoverflies fitted partially or poorly to resources patch size distribution in the landscape.

Key-words: community, birds, butterflies, hoverflies, landscape heterogeneity, resource aggregation.

Introduction

According to Huston , the causes of variation in species diversity may act at local scale (competition, predation, mutualism, resources productivity and diversity) as well as regional scale (differences in age, rates of speciation, migration and extinction). Landscape scale could be considered as an intermediate one, where most of the local processes acted and some of the regional one can be perceived (e.g. metapopulation dynamics, . Landscape composition and structure control some of the processes involved in the relative abundance of species in animal communities. Bennett, Radford and Haslem (2006) in their review about the effect of landscape properties (the extent of habitat, the composition of mosaic and spatial configuration) on biodiversity in rural environment, pointed out that many studies have demonstrated that landscape heterogeneity promoted biodiversity as a whole. Extent and spatial configuration of suitable habitat patches influence butterfly species richness . However, most of these studies relied on diversity indices and did not investigate the mechanisms by which landscape properties affect species diversity.

Here, we used the Species Abundance Distributions (SAD) because i) they are in an intermediate position on a spectrum of increasingly complex description of a community and allows for comparison of communities that have no species in common and ii) it exists a strong literature about their relationships with ecological processes . Since the 1970s, SAD models and interpretations have proliferated; Mc Gill et *al.* (2007) identified 5 families of SAD models with over 40 members.

Five main models have been proposed along a gradient of evenness between species in the community. First, the geometric series or pre-emption model where a few species are dominant (has pre-empted most of the resources) with the remainder fairly uncommon . In this model, the most successful species is able to appropriate a fraction k of the environmental resources and each succeeding species utilizes the same fraction of the resources not appropriated by more successful species (Whittaker 1965). Then, the Zipf and Zipf-

Mandelbrot models relate originally to information systems . They are closely related and presume that the presence of a species can be seen as dependant on previous physical conditions and previous species presences. Pioneer species have thus low cost requiring few prior conditions and late successional species have a high cost and will thus be rare . Log normal distributions where species of intermediate abundance become more and more common . They were described for even community in undisturbed environment . Finally, the broken stick model which reflects a case of minimal pre-emption, individuals are randomly distributed among observed .

First, we examined the relationship between community evenness and SAD models because many ecological assumptions rely on that relationship. Then, we tested the following hypothesis about landscape properties and biodiversity: i) SAD will better fit a LogNormal model in heterogeneous landscapes (landscape composition), because it should offer high resources diversity and thus more ecological niches ii) SAD will better fit a LogNormal model in landscape where resources are not aggregated (landscape structure) because competition should be limited by spatial segregation. Finally, we tested Huston hypothesis stating that "… *If species are not actually competing, but rather represent different functional types using the environment in different ways, the lognormal distribution of resources in the environment, rather than ecological subdivisions of resources by organisms may be the underlying cause of the ubiquitous lognormal distribution of species abundances"*. In that particular case, the extent of habitat is not considered as a whole but depending one resource patch size distribution. Even if this hypothesis is new and ambitious, it has never yet been investigated. One reason for this discrepancy may be the difficulty to define and qualify well delimited resource patches in "natural" ecosystems. Agricultural practices lead to a highly heterogeneous and contrasted mosaic of crops and permanent elements (woods, hedges, field margins, road verge, green lanes) constituting for animals well delimited resource patches. In this study, we defined resource patches as discrete portion of the space providing resources (food, reproduction) for all the life cycle of the studied animals (hoverflies, birds and butterflies).

Methods

The three data sets considered in this study come from French Long Term Ecological Research sites (AlterNet network) investigating the relationships between rural landscape organizations and biodiversity . Butterflies were studied in herbaceous elements of hedgerow network landscape in western France and birds and hoverflies in small woods of a hilly landscape in South western France .

Study regions

The two study regions are located in two rural regions of France (Figure 1), they differed by their topographical characteristics and agronomic systems.

The first one, called “Brittany Bocage”, is a hedgerow network landscape in plain dominated by dairy production (Table 1). It is situated in western France (lat: 48°50’, long: 1°66’). Sample meadows and linear herbaceous element were distributed in five landscapes (abbreviated B. B. 1, 2, 3, 4, 5) (Table 2).

The second one, “Gascon Hills”, is situated in the south west Pyrenean mountains foot-hills (lat: 43°, long: 1°) where the main agricultural activity was cattle rearing (grazed meadows and fodder crops), now replace by cereals and oleaginous in valleys and weak slopes. Sampled woods for the hoverflies were distributed in four landscapes (abbreviated G.H. 1, 2, 3, 4) (Table 2). Bird counts took place in the whole agricultural mosaic.

Land covers in both regions were determined by different ways. Brittany Bocage landscape maps were based on land survey maps (1/5000 scale), land use was determined by aerial photographs and field observations. Gascon Hills landscape was analysed by remote sensing images since it was a larger study area. Four SpotView images (pixel resolution: 20 meters)

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were used to map the study sites. Images in Multiband mode were taken on April 14, 2001; July 21, 2001; October 30, 2001 and January 12, 2002.

For butterfly and hoverfly studies, landscapes were delimited by the smallest polygon convex encompassing all the recorded patches. Only, herbaceous patches and woodlands, were taken into account as resource patches in the aggregation index respectively for butterflies and hoverflies.For bird surveys, the whole landscape was taken into account to calculate the heterogeneity index. Land cover around each point count (in a 250 length side square) was determined manually using aerial photographs.

Insects recording

The two insect communities were chosen to be linked to specific resource types. Both larvae forms fed on more species-specific substrates (plants for butterflies, plants or animals for hoverflies), than adults which feed on nectar and need flower plants. Butterflies depend on resources patches constituted of herbaceous areas (grasslands, field margins, hedge banks) , while the studied hoverfly species were linked to wood habitats . Both insect families are flying and one year generation species.

Butterflies were recorded in the Brittany Bocage landscapes between May and August 1998, on transect routes passing through herbaceous patches: meadows, and along hedges, road verges. A total of 746 individuals spread in 20 species were recorded (Ouin & Burel, 2002a).

One hundred and one Malaise traps were laid between May and October 2000 in 61 woods to trap hoverflies. In this study, we considered the 28 forest species (N=738) which larvae depend only upon forest habitat (Ouin et al., 2002b).

Birds recording

For each of the 256 point counts (cells of 250m wide), experienced observers recorded all bird species contacted visually or by their vocalizations during 20 minutes between sunrise and 4h maximum after sunrise. 5405 individuals belonging to 72 species were contacted (Balent & Courtiade, 1992).

Rank abundance models and community simulations

The best model fitting to the animal communities and resource patches in the landscape was determined by Akaike Information Criteria (AIC) calculated by the rad.fit function of the R Vegan Package . For each formula below: Ai = the abundance of the species at rank i; S = number of species and N = total number of individuals.

The five models considered were (see Wilson, 1991):

- Broken-Stick model (MacArthur 1957) with no fitted parameters.

$$Ai = \frac{N}{S}\sum_{x=i}^{S}\frac{1}{x}$$

- Geometric series or **Premption model** (Motomura 1932) with only one estimated parameter k which gives the decay rate of abundance per rank.

$$A_i = A_1.k^{(i-1)}$$

- Lognormal model (Preston 1948), with two ajusted parameters : μ (fitted mean of the logarithmic abundance) and σ (fitted standard deviation of logarithmic abundance).

$$A_i = \mu + \sigma\, \Phi^{-1} \cdot \frac{(S - i + 0.5)}{S}$$

Where Φ^{-1}= the inverse cumulative distribution function of normal distribution (i.e. the logarithmic abundance at which the area under the normal curve is the value indicated).

- Zipf model (Zipf 1949) with two adjusted parameters: A_1 adjusted abundance of the most abundant species; γ (a constant which represent the average probability of the appearance of a species).

$$A_i = A_1.i^{-\gamma}$$

- Zipf-Mandelbrot model (Mandelbrot 1977, 1982) with a third parameter: β (Ecologically it can be seen as the potential diversity of the environment, i.e. niche diversity).

$$A_i = A_1(i + \beta)^{-\gamma}$$

Simulated communities for given value of S and N were calculated using a specific program developed under Matlab (Gergaud, 2007). According to our data set and available calculation power, communities were simulated for N=90 (the maximum reached by the available computing calculus centre) and S=30 (realistic regarding our data set, Birds: 45, Butterflies:

17, Hoverflies: 21).

Landscape heterogeneity

Landscape heterogeneity was calculated using all the land cover types present in the landscape (habitat and non habitat patches were considered). A Shannon Index was calculated (Burel and Baudry 1999).

For bird communities, data from the 256 point counts were ordered along a gradient of landscape openness following findings by Balent et Courtiade (1992). In order to investigate the relationship between community structure and landscape heterogeneity in different part of this gradient, a Pearson's product moment correlation coefficient was calculated between the deviance to the Lognormal model and the landscape heterogeneity in two sections of this gradient: (1) wooded areas (wood and hedge), (2) open areas (crops and meadows)

The aggregation of resource patch was evaluated using the aggregation index for butterfly and hoverfly studies (He, et al. 2000). It calculates the proportion of adjacent cells having the same land cover compared to the total possible pairs, it varies from 0 (no aggregation) to 100 (complete aggregation).

Data concerning quality and quantity of resource patches in terms of nectariferous plant and host plant abundance on such large area are not logistically easily recordable. As suggested by Huston (1994), "*the environment is viewed as a heterogeneous mosaic of resources, which may be patches of different sizes and successional ages, or plants of different types and sizes* ". We used the diversity in size (surface area) of the resource patches as a surrogate of the patch diversity in term of resource quantity and quality. Indeed, differences in the management of small patches (linear herbaceous elements: hedges, field margins) and large patches (meadows) lead to different plant composition and insect diversity . We considered each herbaceous resource patch as a species and its surface area as its abundance. The same relationships could be put forward for woodlands; the smallest are owned by farmers or abandoned with unknown owners and the largest one are managed by Forest National Office or private forest companies. Such differences in their owners and managers conducted to difference in tree composition and structure as well as undergrowth vegetation . Because woods were numerous, classes of surface area were considered as the species and the abundance in each class as the number of individuals for one species.

Results

Relationship between SAD model and community evenness

The evenness range of the 943 442 simulated communities (N=90, S=30) started from 0.5. 88 communities were extracted to determine their deviance to each model for eleven values of J ± 0.01 with a step of 0.05 (Figure 2). Overall, deviance to all models decreased with increasing J. Models selected by AIC for the simulated communities showed a consistent pattern from Zipf model to Lognormal model for the three communities with J=1 (Figure 2). However, the thirty models around 0.9 and 0.95 demonstrated opposite trends matching to Geometric, Zipf as well as LogNormal models.

In real communities, four of the five butterfly communities showed the same evenness value (0.6) but each of them fit to a different model. Butterfly SAD demonstrating the lowest evenness (0.5) fitted best to Zipf model (Table 3). Two of the three hoverfly communities showing the same evenness value (0.8) fitted best to Geometric model. The hoverfly SAD fitting the best to LogNormal was also the one showing the lowest evenness (0.7) (Table 4).

Landscape heterogeneity and SAD

Landscape heterogeneity and deviance to lognormal demonstrated significant correlations in open and wooded landscapes (Figure 3). However, deviance to LogNormal is negatively correlated with landscape heterogeneity in wooded areas ($N = 57$, $r = -0.454$, $p < 0.001$) and positively correlated with landscape heterogeneity in open areas ($N = 57$, $r = 0.865$, $p < 0.001$)

Along a gradient of landscape heterogeneity, birds SAD in wooded landscapes demonstrated low deviance to LogNormal for homogeneous landscape (forest), then increasing landscape heterogeneity was positevely correlated to higher deviance to LogNormal model up to H=0.15. Then, increasing heterogeneity in wooded landscapes (woods surrounded by hedges, meadows and crops) sheltered birds community showing low deviance to LogNormal model.

In open landscapess (dominated by crops and meadows), low landscape heterogeneity was also correlated to low deviance to LogNormal, however, increasing heterogeneity was steadily correlated to higher deviance to LogNormal up to H= 0.5 (Figure 3). In the same landscape context, hoverfly communities better fitted to a LogNormal model for intermediate value of heterogeneity (H = 1.4, G.H.3) (Table 4).

In Brittany bocage landscapes, the lowest landscape heterogeneity (H =1.2, B.B.3) lead to high deviance to LogNormal model for butterfly communities. The community best fitted to a LogNormal model in landscape exhibiting intermediate heterogeneity value (H = 1.4, B.B.4).

Resource patches aggregation and SAD

Forest hoverfly and butterfly communities SAD showed lowest deviance to LogNormal model in landscapes where resource patches were not aggregated (Figure 4).

Similarity between resources patches distribution in the landscape and SAD

Most of the butterfly communities did not fit to the same model than the resource patches distribution except in B.B. 3 (Figure 5). Nevertheless, in two of the four other landscapes, SAD and resources distribution models were of the same family (Zipf and Zipf-Mandelbrot). Most of the landscapes exhibited a Zipf or Zipf-Mandelbrot models for resources patches distribution. In contrast, three of the four forest hoverfly SAD fitted different models from the resource patches distribution in the landscape (Figure 6). Resource patches distribution in the landscapes fitted to broken stick or geometric models.

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Discussion

Relationship between SAD model and evenness

Simulations exhibited a general trend Zipf and Zipf-Mandelbrot models to Geometric and finally LogNormal model. This gradient was already describes in many reference books (. According to the simulated communities, butterfly communities ($0.6<J<0.5$) mainly fitted Zipf or Zipf Mandelbrodt models. However, for high value of J ($J>0.9$) for the simulated communities, all the models are chosen equally by AIC (except the Broken stick model). Hoverfly communities ($0.7<J<0.8$) exhibited this similar switch between all models for high J values. Consequently, this “fuzzy” relationships between J and SAD models for high J values should be kept in mind when interpreting SAD model in term of even or uneven resource partitioning between species.

Landscape heterogeneity and SAD

The relationship between bird SAD and resources heterogeneity did not remain constant along the gradient of landscape openness. Indeed, increasing heterogeneity in wooded area and decreasing heterogeneity in open areas both lead to LogNormal SAD.

In open and wooded landscapes, homogeneous landscapes (respectively crops or woods) sheltered few species (down to 8 for open landscape and 27 in wooded landscape) with similar ecological traits and no or few spatial niche seggregation leading to a strong competition with no or few dominance of one species on the other. This phenomenon of better fitting to a lognormal distribution consecutive to the lost of rare species have already been reported in plant community .

In open landscapes, most of the landscape was still dominated by crops, thus the landscape elements adding heterogeneity (hedges, pastures) increase species richness by adding new habitat and resources but they may not be large enough to support large populations. Consequently, present species may have showed different ecological traits but communities were still dominated by the few ones able to use crops, increasing deviance to LogNormal curve.

In wooded areas, the deviance to LogNormal model wass also low for heterogenous landscapes (up to H=1.5) and the same mechanism could have applied (addition of few elements, bringing new, strongly dominated species) . Nevertheless, in wooded landscapes the general pattern exhibit a negative relationship between deviance to LogNormal and landscape heterogeneity which contrasted to the one described in open landscapes. In wooded area, species richness remained high (always above 27 species). It is therefore likely that the present species exhibit more different ecological requirements and niche seggregation could occured thanks to wood intra-heterogeneity (not taken into account in the landscape heterogeneity measure). Consequently, rare species were present but strongly dominated by others, which lead to a high deviance to a LogNormal model (even with a slice increase in landscape heterogeneity, up to 0.15). In contrast, with increasing heterogeneity , the addition of crop and pasture provided to the dominated species complementary resources, their abundances thus increase and contributed to the "table" of species with intermediate abundance characterising LogNormal model. In wooded landscapes,less competition and the distribution of resources in the environment could explained the fit of SAD to LogNormal corroborating Huston's hypotheses.

Few studies have already reported similar SAD patterns for different landscape structures Mac Nally pointed out that the same SAD models could be exhibited by two landscapes differing by their fragmentation level. He developed the abundance spectra which use ordered lists of species ranked by species commonness in a reference system, and showed dramatic changes using abundance spectra. In the Australian context, the reference system or "pre-impact" condition was defined as the landscape before its extensive and rapid conversion to agricultural landscape: large woodland areas. However, in our European context such reference landscape is very difficult to define. A study of skylark (*Alauda arvensis*) density over 600 randomly selected 1-km squares throughout Britain showed that skylark density increased with habitat diversity across the whole sample. However, some lowland farmland plots showed a significant decrease with increasing habitat diversity. The authors concluded to the effect of crop type rather than habitat diversity *per se*.

Bird SAD along a gradient of landscape openness validated our first hypothesis (SAD will better fit a LogNormal model in landscape offering a high resources diversity) only in wooded landscapes. Similar results were found for butterflies. However forest hoverflies SAD deviance to LogNormal did not decrease with landscape heterogeneity. The selected hoverfly species may have been too restricted to woody habitats to be able to use other habitat provided by an increase in landscape heterogeneity.

Resource patches aggregation and SAD

Our second hypothesis (SAD will better fit a LogNormal model in landscape where resource are not aggregated) was validated by our results on both butterfly and hoverfly communities. Few studies in the real world and at landscape scale were able to tease apart the effect of aggregation from the effect of the extent of suitable habitat. Most of the literature at landscape scale concluded to a weak or positive effect of aggregation on fauna diversity. Bird diversity was positively related to aggregation when the extent of suitable habitat was below 15% but above that threshold no more relationship still exist .

Because habitat fragmentation interferes with organism movement abilities, species will not necessarily be present in all suitable habitat patches . In a landscape where resources are not aggregated, less competitive species but with high dispersal abilities will maintain high population in suitable patches for other species which were not able to reach them because of limited dispersal abilities . Therefore, within a landscape with dispersed resources, a generalist species with bad dispersal abilities could not dominate all the patches.

Similarity between species and resource patches rank abundance curves

Three of the five butterfly communities and only one of the hoverfly communities fitted the same or nearly the same SAD model than resource patches distribution in the landscape. The Huston hypothesis was only partially validated for the butterfly communities in Brittany Bocage landscape. The converse of Huston hypothesis would argue that if species and resource patches followed the same distribution, competition is not the main processes driven species assemblages. In heterogeneous, changing environment such as agricultural landscape; spatial segregation of species niche could be strong enough to delete or at least minor inter-specific competition. Although few butterfly species are territorial such as some Nymphalinae exhibiting inter-specific competition, the studied butterfly species were not described to exhibit strong direct competitive interactions. Moreover, butterfly are, known to use different host plants at their larval stage . The partial similarity between butterfly SAD models and resource patches distribution could be attributed to their use of other patches than herbaceous one. The absence of relationship for the hoverflies could not be imputed to competition. Indeed, Gilbert *et al.* studying hoverfly community in urban environment concluded that there was little evidence of competitive interactions, except between species with predatory larvae which is not the case of most of forest hoverflies.

The way we tested Huston's hypothesis did not consider distance between patches because we were not able to enter it in a SAD model perspective. Yet, the recent unified neutral theory assuming that species are ecologically identical, considered that local community is a subset of a meta-community and could be helpful to tackle this gap. The immigration rate, m, is the proportion of individuals in a local community that are replaced by individuals from the meta-community . Because we postulated that our community is more a “taxonomically” and geographically delimited set of organisms than the “*group of trophically simiar, sympatric species that actually or potentially compete in a local area for the same or similar resources*”, we did not investigate the zero-sum polynomial distribution or the dispersal limited multinomial distribution . The challenge now could be to integrate immigration rate between resource patches before testing for resource patches distribution model.

Conclusion

Relationships between community evenness and SAD model should be used carefully for high value of J. No consistent relationships were found between landscape properties and SAD in bird, butterfly and hoverfly community. Yet, an increase in landscape heterogeneity was linked to low deviance to LogNormal model for butterfly, but it exhibited different pattern depending on the context (open versus wooded landscape) for birds, no relationship was found for the hoverflies. Resources aggregation promoted dominance by few species and lead to high deviance to LogNormal model. SAD of butterflies and hoverflies fitted partially or poorly to resources patch size distribution in the landscape.

Magurran reminded the fact that “*a natural community displays a species abundance relationship in line with the one predicted with the one predicted by a specific model does not itself vindicate the* [biological] *assumptions on which the model is based*.” She advocated for direct experimental tests of the processes involved. At landscape scale, only comparisons of landscapes differing by their heterogeneity or resource patches aggregation are conceivable as an indirect method.

Acknowledgements

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References

Table 1. The two LTER sites main characteristics. Values given for the proportion of woods and meadows are an average of the studied "sub-landscapes" for butterflies and hoverflies.

	Brittany Bocage (B.B.)	**Gascon Hills (G.H.)**
Location	Western France in typical hedgerow network landscape	South west France
Slope	No	Slopes and plains before the Pyrenean Mountains
Type of agriculture	Extensive dairy farming in a gradient of hedgerow network density	Beef production on slopes and cereals in plains
Surface area (ha)	9500 ha	19 000ha
Proportion of woods and average size (Km^2)	No woods	25.5% 0.057±0.01
Proportion of meadows and average size (Km^2)	45.5% 0.006±0.005	10.7% 0.00849±0.0153
Type of recorded patches for the present study	Meadow, hedge, road verge	Woods (hoverflies) and the whole mosaic (birds)

Table 2. Characteristics of the 10 landscapes investigated: area, suitable habitat extent and number of suitable patches (number of recorded patches).

	Land.	Area (ha)	Extent of suitable habitat (%)	Nb. of suitable habitat patches*	Resources	Tested hypothesis
B.B.	1	40.5	40.4	17 (11)		
	2	16.5	41	14 (13)		Heterogeneity
	3	110	22.2	10 (12)*	Meadows, Hedges	Aggregation
	4	9	76.4	27 (10)	Field margins	Resource patches
	5	53.3	47.6	11 (9)		distribution
G.H.	1	8509.3	18.8	129 (13)		heterogeneity
	2	5538.7	17.7	72 (14)		Aggregation
	3	6563.5	11.2	59 (14)	Woodland	Resource patches
	4	8289.9	14.7	49 (20)		distribution
	Whole landscape	19 000 ha		The whole mosaic (256 point counts)		Heterogeneity Resource patches distribution

*Only grasslands are counted here fro B. B., in the case where road verges were sampled too, the number of recorded patches could be > to the number of suitable patches.

Table 3: Deviance to the 5 SAD models, Diversity, Evenness, Richness and abundance of butterfly communities and landscape heterogeneity of land cover in Brittany Bocage (B.B.) (in italic). (The models selected by AIC are in bold and underlined).

		B.B. 1	**B.B.2**	**B.B. 3**	**B.B 4**	**B.B 5**
Models	Geometric	94.0466	133.8595	53.3322	57.242	203.5318
	Lognormal	16.2497	32.3153	17.4173	**16.6995**	58.9126
	Zipf	**13.4096**	**6.4728**	28.2883	25.0006	**23.376**
	Zipf –Mandelbrot	13.4096	6.4728	**14.561**	16.218	23.376
	Broken-Stick	227.3317	324.2243	204.3242	212.0106	457.6111
Diversity	Shannon	1.7	1.6	1.8	1.8	1.3
Evenness	Shannon	0.6	0.6	0.6	0.6	0.5
Richness	S	16	16	16	17	16
Abundance		423	453	474	420	408
Landscape Heterogeneity (Shannon)		*2*	*1.3*	*1.2*	*1.4*	*1.9*

Table 4: Deviance to the 5 SAD models, Diversity, Eveness, Richness and abundance of hoverfly communities and landscape heterogeneity of land cover in Gascon Hills (in italic). (The models selected by AIC are in bold and underlined).

		G.H. 1	**G.H. 2**	**G.H. 3**	**G.H. 4**
Models	Geometric	**4.4779**	16.2033	15.8313	**9.3363**
	Lognormal	8.0263	13.1733	**9.9569**	15.5447
	Zipf	13.0751	13.5409	20.003	43.6223
	Zipf-Mandelbrot	3.8743	**7.0733**	9.5582	9.1014
	Broken-Stick	8.5761	29.2835	49.9891	21.8185
Diversity	Shannon	2.5	2.2	2.2	2.5
Evenness	Shannon	0.8	0.8	0.7	0.8
Richness	S	20	18	20	21
Abundance	N	94	126	201	317
Landscape Heterogeneity (Shannon)		*1.4*	*0.9*	*1.4*	*1.7*

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Fig. 1. Situation of the two LTER sites in France, western Europe.

Fig. 2. Relationships between the deviance to the four theoretical models (LogNormal, Preemption, Mandelbrodt, zipf) and evenness in 88 simulated communities. The models selected by AIC and the number of replicates (numbers in brackets) are given.

Fig. 3. Deviance to the LogNormal model for the start (wooded areas) and the end (open areas) of the gradient for the birds in Gascon Hills in relation to landscape heterogeneity. (Wooded area, N = 57, r = 0.454, P<0.01; Open area, N = 50, r = 0.865, P<0.01)

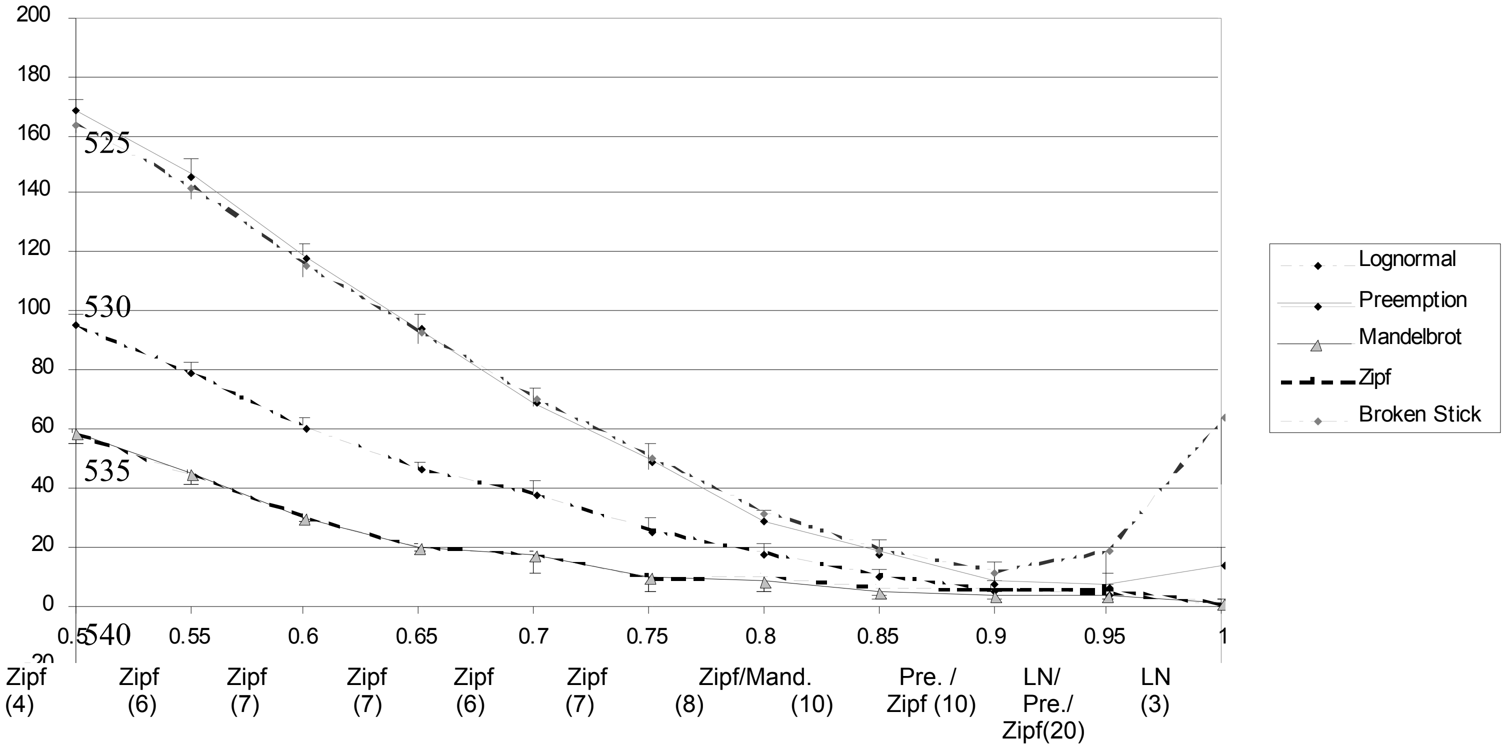
Fig. 4. Deviance to LogNornal for butterfly and hoverfly SAD in relation to aggregation index of resource patches.

Fig. 5. The best model fitting the butterfly SAD and the best model fitting resource patch distribution in the Britany Bocage landscapes.

Fig. 6. The best model fitting the forest hoverfly SAD and the best model fitting resource patch distribution in the Gascon Hills landscapes.


UNITED KINGDOM
NETHERLANDS
BELG.
GERMANY
Dunkerque
LUX.
Brittany Bocage
FRANCE
SWITZ.
Gascon Hills
ITALY
Barcelona
PORTUGAL
SPAIN
MOROCCO
ALGERIA
TUNISIA

Fig. 1.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100
80
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40
20
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Zipf (4)
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Zipf/Mand. (8) (10)
Pre. / Zipf (10)
LN/ Pre./ Zipf(20)
LN (3)
Lognormal
Preemption
Mandelbrot
Zipf
Broken Stick

Fig. 2.

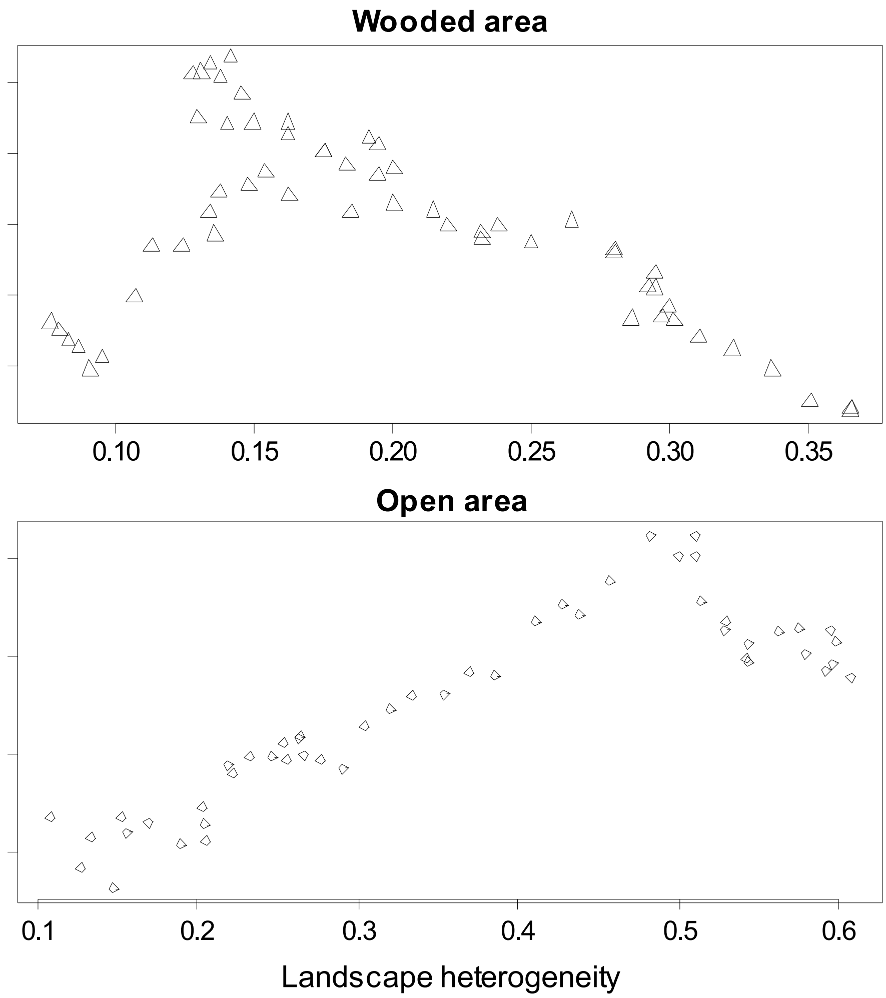

Wooded area
0.10
0.15
0.20
0.25
0.30
0.35
Open area
0.1
0.2
0.3
0.4
0.5
0.6
Landscape heterogeneity

Fig. 3.

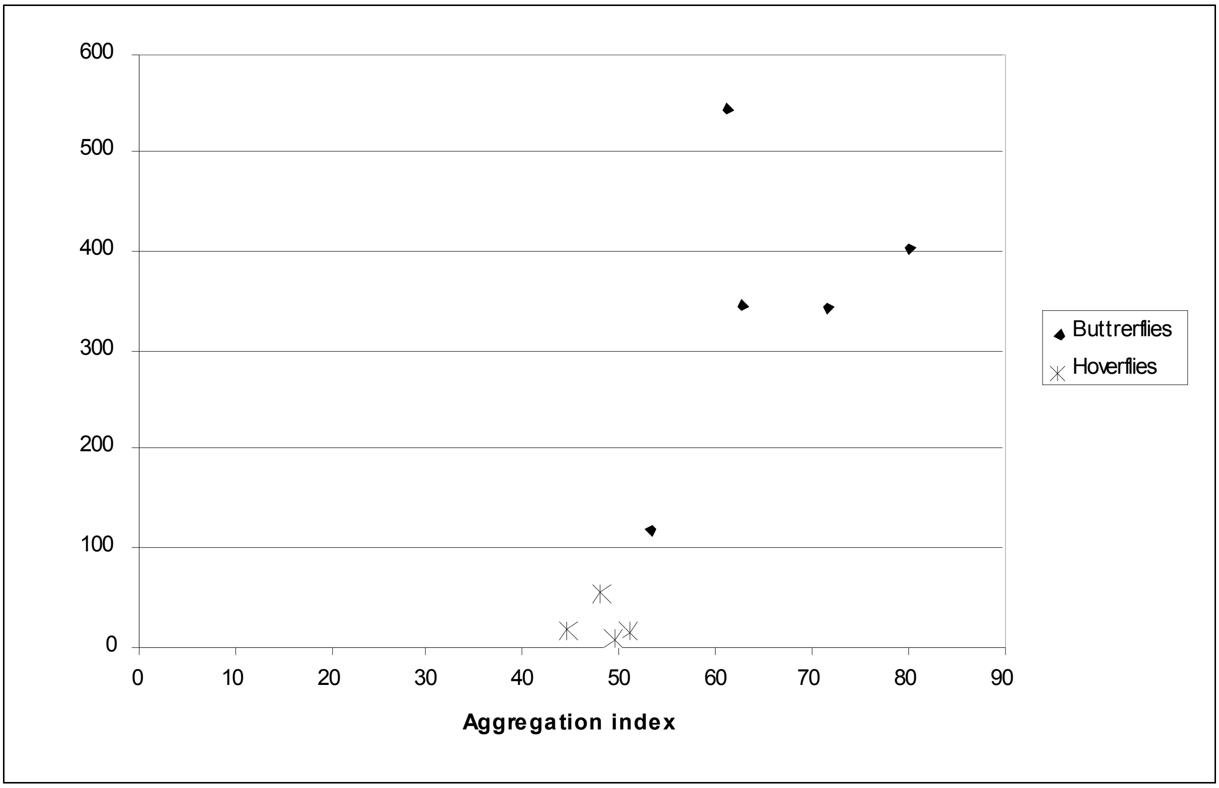

600
500
400
300
200
100
0
0
10
20
30
40
50
60
70
80
90
Aggregation index
Buttrerflies
Hoverflies

Fig. 4.

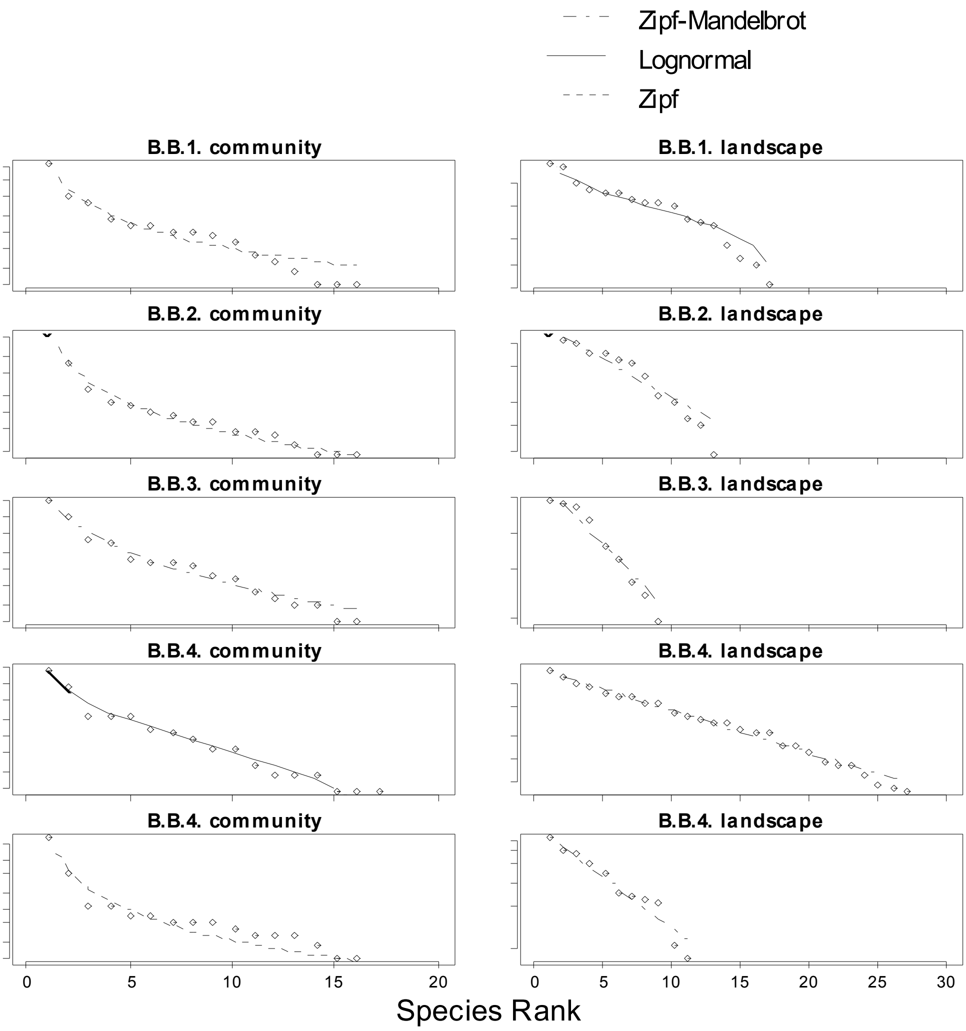
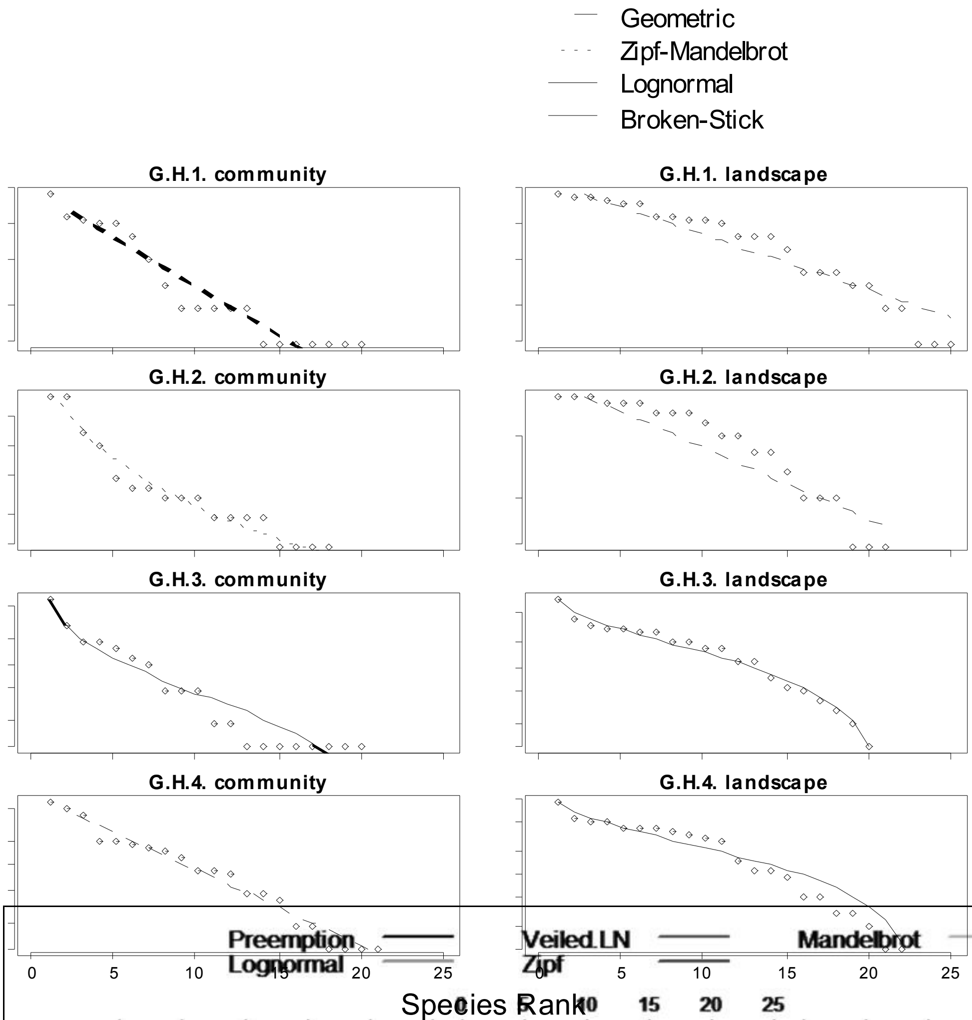

Zipf-Mandelbrot
Lognormal
Zipf
B.B.1. community
B.B.1. landscape
B.B.2. community
B.B.2. landscape
B.B.3. community
B.B.3. landscape
B.B.4. community
B.B.4. landscape
B.B.4. community
B.B.4. landscape
0 5 10 15 20
0 5 10 15 20 25 30
Species Rank

Fig. 5.


Geometric
Zipf-Mandelbrot
Lognormal
Broken-Stick
G.H.1. community
G.H.1. landscape
G.H.2. community
G.H.2. landscape
G.H.3. community
G.H.3. landscape
G.H.4. community
G.H.4. landscape
Species Rank

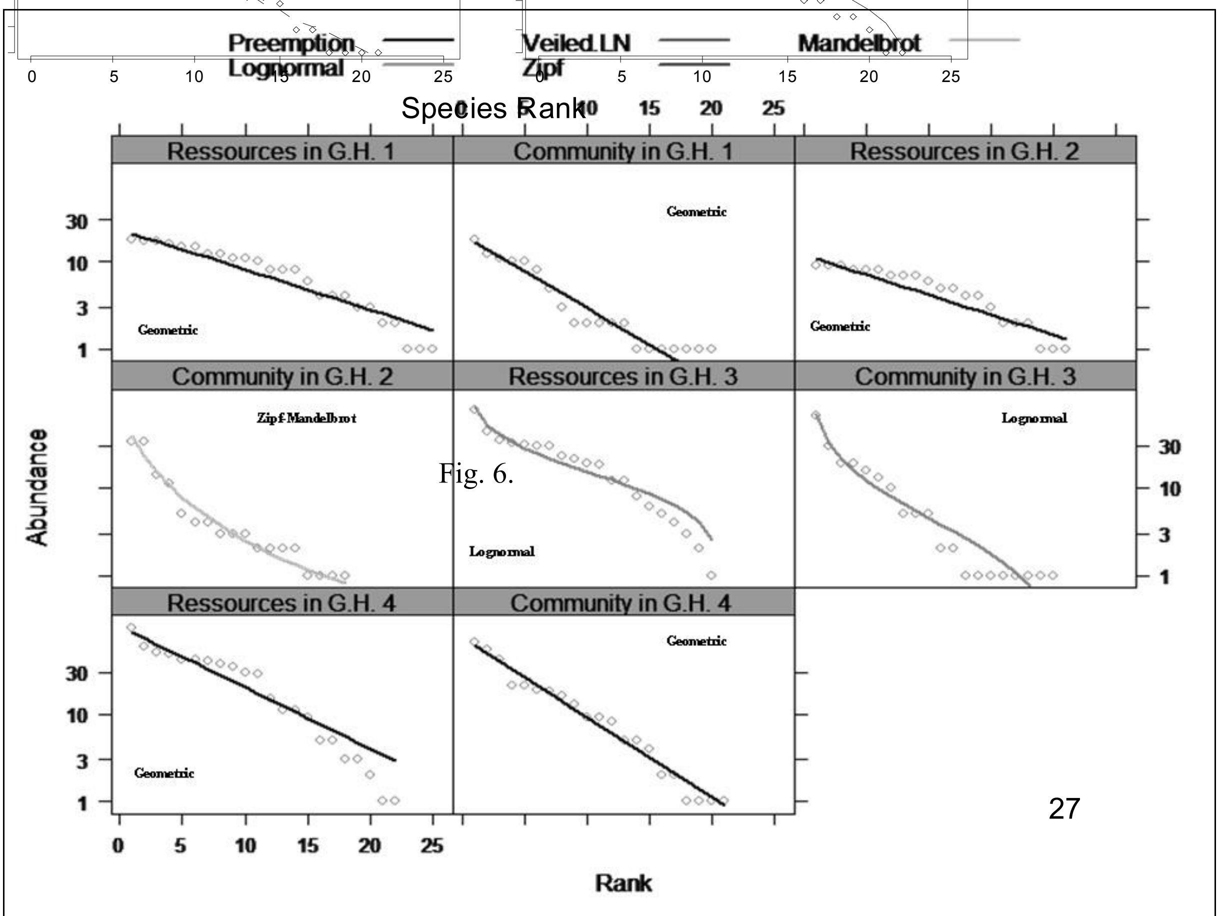

Preemption
Veiled.LN
Mandelbrot
Lognormal
Zipf
Ressources in G.H. 1
Community in G.H. 1
Ressources in G.H. 2
Community in G.H. 2
Ressources in G.H. 3
Community in G.H. 3
Ressources in G.H. 4
Community in G.H. 4
Geometric
Zipf-Mandelbrot
Lognormal
Abundance
Rank

Fig. 6.