

Linking Land Use and Biodiversity; an introduction and some prospects for *Drosophila* species.

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SUMMARY

A lot of biodiversity research is done on groups like birds, trees and mammals. A big disadvantage is the knowledge and experience needed for research in these groups. An appropriate indicator could simplify this kind of research. Flies belonging to the genus *Drosophila* are chosen as 'indicator' within this study. They have the advantage that they are easily collected, have a limited number of species and not much expertise is needed. Collection was standardized by using traps with banana bait. The results indicate that there are no differences in biodiversity by using a variety of diversity indices. But most of the 35 species found, have a clear preference for certain habitats. The overlap between faunas of the two most extreme land use types is not more than 10%. The *Drosophila* group seems to be useful as a fast but maybe less precise indicator. For this, it has most of the required characteristics. The only question remains if it is representative for the biodiversity in general.

INTRODUCTION

There is a large variety of living creatures like plants, birds, mammals and insects around us. The description and explanation of these biological variety is the subject in biodiversity research. The linkage between land use and biodiversity is just one of the subjects covered by biodiversity research.

In this paper, I will present a part from my project: "The relation between land use and biodiversity with the use of the *Drosophila* genus as indicator group." Fieldwork was carried out (here) in the Philippines, from June till December 1992. The focus in this paper is on the usefulness of the *Drosophila* system as indicator system for biodiversity.

Biodiversity:

Magurran (1988) defines it as: ". . . *the variety and abundances of species in different habitats.*" Biodiversity not only includes species diversity, but also genetical and ecosystem diversity. One of the reasons mankind has to protect the tropical rainforests is to prevent the loss of genetic information (=diversity). Just preserving the species will not automatically lead to the preservation of the genetic diversity. This requires more than the minimum number of individuals that will be enough for the preservation of a species.

Biodiversity is quit often translated with just the number of species. But the distribution of the individuals among the species is also of importance. If all but a few individuals belong to one species, the diversity is lower than when all the individuals are equally distributed among the species.²

Biodiversity research is very divers. It includes descriptive research like inventories, surveys and species descriptions, but also more ecological oriented research concerning

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² An example: Two plots. Both with 25 individuals of the same five species. The species richness is the same (5 species in both). In plot one, the 25 individuals are even distributed among the species and every species is represented by five individuals. The distribution is totally different in the second plot. One species is represented by 21 individuals while the other four are represented by only one individual. The evenness, the equality in the distribution of the individuals among the species is more equal in the first plot. That is why biologists consider the biodiversity of the first plot higher than the of the second plot.

mechanisms behind the evolution of species, coexistence of species and the structure of communities. Communities where different species live next to each other without excluding each other.

A community is built up from different species. Some of them are common while others are scarce. The number of observations is of influence on the number of species found. There is only a small chance that a rare species is represented in a small sample. Biologists tried to solve this problem by making indices that are insensitive for sample size. Magurran (1988) lists 13 of these indices. Some represents species richness, others evenness. Some are insensitive to sample size, other are.

I calculated all these indices for all samples. The hypothesis is that the more disturbed the habitat, the lower the biodiversity will be. The land use types under investigation vary between primary forest and grassland. All the other land use types can be ranked between them. This sequence is used to calculate the correlations with the indices. A useful index will have a high correlation with this ranking.

Land use:

I will use this term in a broad context. Primary Forest is in a strict way not a land use type. But we give it the Conservation status and that can be interpreted as a form of land use. The biological term habitat and the environmental science term land use will be used next to each other and will indicate the same.

The original habitat is the primary rain forest. All the other habitats are derived of that by human land use. The degradation process is mostly clearly recognized. The sequence in the degradation process will be used in ranking the habitats.

- (1) Closed Primary forest has a closed canopy and human influence is limited. Some gathering of Non Timber Forest Products (NTFP) by Agta's. The site was logged over a long time ago. But the canopy has closed again.
- (2) Open The big trees are logged and removed. Sometimes, seedlings of various softwood species are planted.
- (3) Patch Patches of logged over forest that remain between other habitat types like in this case *semi*-permanent agricultural fields.
- (4) Scrub Actual the same as *Open*, but all the trees of some size are removed. Remains mostly in a patchy distribution within the *grasslands*.
- (5) Pioneer Pioneer vegetation on recovering *kaïngins*. The *kaïngins* are left and all kind of pioneer softwood species are currently recolonising the lands.
- (6) Kai Logged over forest or scrub land that is converted into agricultural fields. The land is cleared by cutting all the vegetation and burning the remains. This will give a harvest for a few years. Thereafter, a new piece of land must be cleared.
- (7) Semi If clearing a new piece of land is not possible any more, **kaïngins** tend to be used for a much longer period and get a **semi**-permanent character.
- (8) Ban When the land is denuded after a few years, bananas can still grow there and are frequently planted of old **kaïngins** and **semi** permanent agricultural fields.
- (9) Ref **Grasslands** are reforested with (mostly) softwood species in order to diminish the deforestation.
- (10) Grass The final stage in the process. Sometimes used for cattle raising.

Sites 1, 2, 4, 5, 6, 9 and 10 are located east of Bintacan, a barangay of the municipality of

Ilagan, Province Isabela. Site eight is located near town proper of San Mariano, Isabela. The last two sites, 3 and 7 are in Kajappa, barangay Baliwag, municipality of Peñablanca, Cagayan.

Drosophila:

The small flies belonging to the genus *Drosophila* (Diptera, Drosophilidae) are known as vinegar or (small) fruit flies. They got their name because they are strongly attracted by (rotten) fruit. This is true for part of the species, but rotten plant material, sap fluxes, mushrooms and a variety of more bizarre substrates are also used.

43 *Drosophila* species has been recorded for the Philippines until now (Delfinado and Hardy, 1971; Okada, 1981; Baltazar, 1990; M.J. Toda, personal communication).³

The live cycle starts with an egg. The females will lay those eggs on fermenting substrates. One of the substrates mentioned before. The larva will hatch and start eating from the yeasts growing on these fermenting fruits. After a few days, the full grown larva will pupate. The period between hatching and pupation varies according the species, but is in the order of days. The adult fly will emerge after a few days more. The total development time from egg till adult ranges from 7 in the fastest species to about 15 days in the slowest species. An adult fly will live at least for few days in absence of food, but can live for a few weeks under good circumstances.

Indicator:

The aim of this study is to investigate the relation between biodiversity and land use. It is impossible to investigate all the animal and/or plant groups. It would be too expensive and laborious. The investigation of the problem will be much easier, if an appropriated indicator can be chosen. Such a tested and approved indicator is not (yet) available. So the second aim of this study is to investigate if the *Drosophila* indicator group is appropriate.

A useful indicator group has, according to Davids and Jones (in press), the following characteristics:

- **Short-lived** so that they represent the effects of the current habitat without historical effects.
- **Mobile** so that the absence of a species is caused by the unsuitability of the habitat and not a failure to colonize. If they are too mobile, all species will show up in every habitat. Regardless the suitability. The differences found would be greatly influenced by coincidence and not by the habitat.
- **Numerous** to improve the detectability of subtle differences between habitats.
- **Easily caught and abundant** to collect sufficient large data sets.

The following characteristics can be added:

- **Representative** for the aspect under monitoring. In this case biodiversity.
- **Limited number of species** so that it will not become laborious.
- Existing out of species that differ in **degree of vulnerability**, to be able to find differences along a whole gradient of disturbance.

³ After the conference, I went to Japan for a working visit to Prof. Dr. M.J. Toda. The upgraded list contains now 81 species.

Frequently used groups for biodiversity research are plants, birds and mammals. All these groups lack one or more of the characteristics mentioned above. An other sufficiently representative group of organisms must be chosen. Davis and Jones (in press) used the species of the genus *Drosophila* for their study on Borneo. The same group is used in this study.

The *Drosophila* system has most of the attributes to be a good indicator:

- **Short-lived.** Their maximum lifespan is about two months under good circumstances. Most individuals however will not even reach one month of age.
- **Mobile.** Sevenster (pers. com.) could catch them on a buoy in the panama canal at some distance from Barro Colorado Island. The results will indicate if the mobility is to high. In that case, all the samples will be the same.
- **Numerous.** Whole swarms can be found above fruits on the forest floor. A single banana can produce a few hundred individuals.
- **Easily caught and abundant.** It is easy to collect the breeding substrates in the field and to bring them into the laboratory to rear the flies out. Hanging out traps is another possibility.
- **Limited number of species.** 43 *Drosophila* species has been recorded for the Philippines until now (Baltazar (1990), Okada (1981), Delfinado and Hardy (1971), Toda (personal communication))¹.
- If the system is also:
- **Representative** for the aspect under monitoring is not known yet. Comparisons with bird and plant data could give an idea about the relations involved.
- Existing out of species that differ in **degree of vulnerability**. This is not known for the Filipino *Drosophila*'s. However, it would be a rare exception if it is not the case. As it is true for most groups of organisms in natural systems.

METHODS

I will present you the methods used in this research without going into detail in all biological aspects. The differences in land use are considerable ranking from closed canopy forest till open grassland. The environment for the flies varies also due to this differences in vegetation. Traps were used to standardise the sampling and to avoid difficulties with the comparison of habitats.

The oviposition traps were constructed out of 250 ml transparent margarine containers. A hole of 2.5 cm diameter was made into the lid and covered with 1.5 mm mesh size gauze. This is large enough for the *Drosophilas* to enter but prevented entering of large size predators, fruit eating animals and/or parasitoids. Bananas, known on the market as the "Manila", were used as bait.

The traps were exposed in the field for seven days. Two traps were hanged out in each habitat that was under investigation at that time. After that period, the adults were sampled at the collection site and put on alcohol (70%). The baits were brought to the laboratory and the flies were reared out till adults. New emerged flies were collected ones a day and preserved the same way as the adults.

The insects of the different samples were identified and sexed. The systematics of the *Drosophilas* is quit complicated, but most individuals can be assigned to the correct species.

They were assigned to the category indeterminate if positive identification was impossible.

Table 1 Indices used in this research. After Magurran (1988).

| | | |
|------|-------|--|
| (1) | ES | Rarefaction |
| (2) | DMG | Margalef's diversity index |
| (3) | DMN | Menhinick's index |
| (4) | H | Shannon diversity index for species richness |
| (5) | HE | Shannon diversity index for evenness |
| (6) | HB | Brillouin index for species richness |
| (7) | HBE | Brillouin index for evenness |
| (8) | RECD | Simpson's index |
| (9) | McU | McIntosh's index of species diversity |
| (10) | McD | McIntosh's index of dominance |
| (11) | McE | McIntosh's index of evenness |
| (12) | d | Berger-Parker diversity index |
| (13) | alpha | The alpha (α) of the log series model |

All the indices, as listed in table 1, are calculated for all the counted samples (See appendix 3 for the formulas). Correlations between the indices and the habitat ranking are done by using the Kendall Rank Correlation test.

A lot of different similarity indices are developed (Wolda, 1981). In this study I will use the percentage similarity of Renkonen (1938). This is the most straightforward index. See Appendix 3 Formula 17.

The aim of this study is to investigate the changes in the biodiversity. The primary forest is the original habitat and therefore will serve as the reference point for the comparisons between habitats.

RESULTS AND CONCLUSIONS

Two series were counted, both consisting out of adults and offspring. The time between the collections of the two series is 12 weeks. This gives the total of four groups to be analyzed:

- 1) Adults of the first series.
- 2) Offspring of the first series.
- 3) Adults of the second series.
- 4) Offspring of the second series.

All the indices are calculated for all the samples. The correlations between the different indices and the original ranking is presented in **Appendix 1**. None of the indices has, in all four series, a good correlation with the ranking.

Magurran (1988) divides the indices in two groups: Species richness indices and evenness indices. She found (strong) correlations within these groups, and no correlations between indices of these groups.

The general picture holds for my data, although the differences are not that clear. Significant ($p < 0.05$) correlations are found for all the combinations within the evenness group, and for 62% of the combinations within the species richness group. The percentage significant corre-

lations between indices of both groups is 42%.

Which indices have a good correlations with the other indices of the same group and no or a limited number of good correlations with the indices of the other group. For the species richness indices: the number of species (S). For the evenness indices: the Berger-Parker index ($1/d = N/N_{\max}$).

Adult samples have more species ($p < 0.001$ Wilcoxon matched pairs signed rank test (WMPSR)) and generally higher values for most indices ($p < 0.001$ (WMPSR) except Berger-Parker and MacIntosh species richness). Offspring samples have more individuals ($p < 0.001$ (WMPSR)) and higher values in two of the 13 indices ($p < 0.001$ (WMPSR) for Berger-Parker and MacIntosh species richness). This indicates that there is a clear influence of the bait on the faunal composition. Some species can or will not breed on banana bait, others will produce large numbers of offspring, making the offspring samples less divers.

The overlap percentages for all the samples within the four groups are given in **Appendix 2**. The overlap percentages between sites of one habitat are given in **Table 10**. The percentages vary between 15.9% and 78.0% (average 52.0%) for the adult samples and between 34.2% and 81.8% (average 63.5%) for the offspring samples. The within overlap percentages are in three of the four series larger than the between habitat overlap percentages, except the second adult series (Mann-Whitney U-test, one tail probability adult1: $p = 0.042$; adult2: $p = 0.184$; offspring1: $p = 0.034$; offspring2: $p = 0.005$).

The overlap percentages for habitats are presented in **Appendix 2**. The samples of one sites are combined and the percentages of those pooled samples are used for the calculation. The overlap between the habitats ranges from 79.8% to 7.5% for the adult samples and from 84.2% to 3.6% for the offspring samples. The habitats are arranged according the disturbance classes. The larger the difference between disturbance class, the lower the overlap percentage . The exceptions are marked with an *.

DISCUSSION

None of the diversity indices shows a clear correlation with the ranking in all the four series. This could lead to the conclusion that land use does not affect *Drosophila* diversity. But this is not true. The changes in the faunal composition are great. The overlap percentages clearly demonstrate this (Appendix 1).

The overlap percentages between samples of the same habitats are generally larger than between samples of different habitats. This is a second indication that there is an influence of land use c.q. disturbance on the *Drosophila* fauna(s). Not only are there differences, but these differences are generally larger as the degree of disturbance is larger (TABLE 11). From this, the conclusion follows that there is an influence of disturbance on the *Drosophila* fauna.

The ranking of land use types was made according the disturbances due to human activities. Almost implicit in this ranking is the idea that there was only forest before human activity changed the landscape. But there are natural habitats that look like human made habitats. For example natural grassland areas and it would be strange if there were no specialist species. Examples can be found in the birds, more specific in the Estrildid Finches (Fam.: Estrildidae) Some of them are endemic for the Philippines and restricted to grasslands (Gonzales, 1988). And culture followers (Rabor, 1977). There is no reason that this would be different for *Drosophila*'s. And they are more important as expected. From the overlap

percentages, the changes in the *Drosophila* fauna are large. However, the biodiversity indices do not show big differences. Specialist non-forest species compensate the loss of specialist forest species.

Two questions remained in the introduction: Representability and degree of vulnerability. The results indicate that the *Drosophila* system is sensitive enough to indicate changes in biodiversity. The two most extreme habitats have about 10% overlap. This means that there are at some species that are able to live in the Primary Forest as well in the grasslands. But a lot of species is restricted to the more disturbed or undisturbed habitats. If the *Drosophila* system is also representative for the biodiversity in general is still unknown. It is necessary to investigate these relations, but it was not possible within the scope and time of this research.

LITERATURE

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Tabel 4 Correlations between the biodiversity indices of the first offspring serie.

| | | | | | | | | | | | | | | | | | | | | |
|-----|-----|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|--|--|--|--|--|
| S | | | | | | | | | | | | | | | | | | | | |
| *** | N | alpha | | | | | | | | | | | | | | | | | | |
| * | | *** | H | | | | | | | | | | | | | | | | | |
| * | | *** | *** | HB | | | | | | | | | | | | | | | | |
| *** | | *** | *** | ** | DMG | | | | | | | | | | | | | | | |
| | *** | * | * | * | * | McU | | | | | | | | | | | | | | |
| | | * | *** | *** | * | * | 1/D | | | | | | | | | | | | | |
| | | * | ** | ** | * | * | * | d | | | | | | | | | | | | |
| | * | ** | *** | *** | * | ** | *** | *** | McD | | | | | | | | | | | |
| | ** | * | * | * | * | *** | * | ** | * | HE | | | | | | | | | | |
| | ** | ** | *** | *** | * | *** | *** | ** | *** | *** | EHB | | | | | | | | | |
| | * | * | * | * | * | ** | ** | ** | ** | *** | *** | McE | | | | | | | | |
| *** | | *** | ** | ** | *** | * | * | * | * | * | * | * | ES | | | | | | | |
| ** | | *** | *** | ** | *** | * | ** | * | *** | * | *** | * | *** | DMN | | | | | | |
| | | * | * | * | * | * | * | * | * | * | * | * | * | * | Rank | | | | | |

Tabel 5 Correlations between the biodiversity indices of the second offspring serie.

| | | | | | | | | | | | | | | | | | | | | |
|-----|-----|-------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|----|---|-----|------|--|--|--|--|
| S | | | | | | | | | | | | | | | | | | | | |
| * | N | alpha | | | | | | | | | | | | | | | | | | |
| ** | | * | H | | | | | | | | | | | | | | | | | |
| ** | | * | *** | HB | | | | | | | | | | | | | | | | |
| *** | | *** | * | * | DMG | | | | | | | | | | | | | | | |
| ** | *** | | * | * | * | McU | | | | | | | | | | | | | | |
| | | | ** | *** | * | * | 1/D | | | | | | | | | | | | | |
| | | | ** | ** | * | * | *** | d | | | | | | | | | | | | |
| | | | ** | *** | * | * | *** | *** | McD | | | | | | | | | | | |
| | * | | ** | * | * | * | ** | ** | * | HE | | | | | | | | | | |
| | ** | | ** | * | * | * | * | * | ** | ** | EHB | | | | | | | | | |
| | | | ** | ** | * | * | *** | *** | *** | *** | * | McE | | | | | | | | |
| ** | | *** | ** | ** | *** | * | * | * | * | * | * | * | ES | | | | | | | |
| | ** | * | * | * | * | * | * | * | * | * | * | * | * | * | DMN | | | | | |
| | | | | | | | | | | | | | | | * | Rank | | | | |

APPENDIX 2

Tabel 6 Overlap percentages of the individual samples of the first adult serie.

| | 1a | 1b | 2a | 2b | 3a | 3b | 5a | 5b | 7 | 9a | 9b | 10a | 10b |
|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1a | 100.0 | | | | | | | | | | | | |
| 1b | 55.1 | 100.0 | | | | | | | | | | | |
| 2a | 54.5 | 50.6 | 100.0 | | | | | | | | | | |
| 2b | 65.8 | 65.1 | 68.3 | 100.0 | | | | | | | | | |
| 3a | 56.2 | 67.0 | 64.4 | 70.7 | 100.0 | | | | | | | | |
| 3b | 46.1 | 62.8 | 66.9 | 69.3 | 78.0 | 100.0 | | | | | | | |
| 5a | 56.9 | 46.2 | 51.5 | 63.7 | 52.3 | 44.8 | 100.0 | | | | | | |
| 5b | 68.4 | 68.1 | 66.5 | 88.5 | 72.7 | 63.7 | 68.4 | 100.0 | | | | | |
| 7 | 40.2 | 63.2 | 55.6 | 64.4 | 69.8 | 81.7 | 48.5 | 63.5 | 100.0 | | | | |
| 9a | 43.3 | 47.1 | 55.9 | 62.9 | 47.4 | 48.5 | 64.0 | 57.4 | 50.8 | 100.0 | | | |
| 9b | 19.8 | 28.9 | 23.6 | 32.1 | 24.0 | 25.3 | 37.8 | 30.6 | 25.0 | 48.3 | 100.0 | | |
| 10a | 0.0 | 11.3 | 0.0 | 9.8 | 2.1 | 3.7 | 22.5 | 8.0 | 10.3 | 33.9 | 33.4 | 100.0 | |
| 10b | 12.1 | 12.9 | 12.1 | 21.9 | 12.3 | 7.7 | 24.9 | 20.1 | 7.1 | 44.0 | 33.1 | 31.4 | 100.0 |

Table 6 Overlap percentages of the individual samples of the first offspring serie.

| | 1a | 1b | 2a | 2b | 3a | 3b | 5a | 5b | 7 | 9a | 9b | 10a | 10b |
|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1a | 100.0 | | | | | | | | | | | | |
| 1b | 34.2 | 100.0 | | | | | | | | | | | |
| 2a | 81.7 | 41.9 | 100.0 | | | | | | | | | | |
| 2b | 71.2 | 42.6 | 75.2 | 100.0 | | | | | | | | | |
| 3a | 70.9 | 41.3 | 61.9 | 48.9 | 100.0 | | | | | | | | |
| 3b | 47.7 | 35.2 | 40.7 | 31.1 | 68.5 | 100.0 | | | | | | | |
| 5a | 66.8 | 42.9 | 73.6 | 80.4 | 47.4 | 30.3 | 100.0 | | | | | | |
| 5b | 65.5 | 44.2 | 68.7 | 89.4 | 44.9 | 28.1 | 77.1 | 100.0 | | | | | |
| 7 | 44.4 | 53.8 | 39.7 | 35.2 | 56.9 | 55.0 | 35.2 | 41.0 | 100.0 | | | | |
| 9a | 31.1 | 41.5 | 36.5 | 44.3 | 33.3 | 21.6 | 61.6 | 51.6 | 53.7 | 100.0 | | | |
| 9b | 37.2 | 37.6 | 43.1 | 50.4 | 30.8 | 18.7 | 50.6 | 57.7 | 51.2 | 70.3 | 100.0 | | |
| 10a | 0.0 | 26.5 | 5.5 | 13.3 | 6.5 | 5.7 | 27.5 | 20.5 | 39.9 | 57.1 | 47.9 | 100.0 | |
| 10b | 48.1 | 37.6 | 53.6 | 61.3 | 30.3 | 18.7 | 61.1 | 68.6 | 50.7 | 67.9 | 89.1 | 42.2 | 100.0 |

Table 7 Overlap percentages of the individual samples of the second adult serie.

| | 1a | 1b | 2a | 2b | 4a | 4b | 5a | 5b | 6a | 6b | 8 | 10a | 10b |
|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1a | 100.0 | | | | | | | | | | | | |
| 1b | 53.8 | 100.0 | | | | | | | | | | | |
| 2a | 51.6 | 47.1 | 100.0 | | | | | | | | | | |
| 2b | 48.9 | 43.2 | 76.4 | 100.0 | | | | | | | | | |
| 4a | 56.5 | 38.3 | 59.3 | 66.5 | 100.0 | | | | | | | | |
| 4b | 17.0 | 6.8 | 7.7 | 6.6 | 15.9 | 100.0 | | | | | | | |
| 5a | 43.3 | 64.2 | 45.0 | 40.1 | 32.1 | 11.0 | 100.0 | | | | | | |
| 5b | 60.4 | 45.9 | 36.7 | 35.1 | 46.1 | 36.2 | 45.6 | 100.0 | | | | | |
| 6a | 48.0 | 34.5 | 36.7 | 40.6 | 60.3 | 36.8 | 36.9 | 54.7 | 100.0 | | | | |
| 6b | 29.6 | 15.1 | 19.2 | 17.1 | 32.7 | 32.0 | 22.0 | 31.7 | 58.4 | 100.0 | | | |
| 8 | 37.3 | 27.2 | 26.5 | 25.5 | 40.7 | 55.9 | 31.1 | 47.3 | 72.7 | 56.4 | 100.0 | | |
| 10a | 16.4 | 6.0 | 7.8 | 6.7 | 20.4 | 52.4 | 13.6 | 20.8 | 34.1 | 37.2 | 30.9 | 100.0 | |
| 10b | 57.6 | 45.6 | 58.6 | 58.5 | 62.0 | 17.7 | 34.2 | 40.8 | 62.6 | 42.9 | 50.0 | 23.8 | 100.0 |

Tabel 10 Within habitat and within serie overlap percentages.

| Habitat | Adults 1 | Offspring 1 | Adults 2 | Offspring 2 |
|---------|----------|-------------|----------|-------------|
| 1 | 55.1 | 34.2 | 53.8 | 76.6 |
| 2 | 68.3 | 75.3 | 76.4 | 74.1 |
| 3 | 78.0 | 68.5 | | |
| 4 | | | 15.9 | 41.6 |
| 5 | 68.4 | 77.1 | 45.6 | 81.8 |
| 6 | | | 58.4 | 73.1 |
| 7 | | | | |
| 8 | | | | |
| 9 | 48.3 | 70.3 | | |
| 10 | 31.4 | 42.2 | 23.8 | 46.2 |
| Average | 58.3 | 61.3 | 45.6 | 65.6 |

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Tabel 9 Overlap percentages of the individual samples of the second offspring serie

| | 1a | 1b | 2a | 2b | 4a | 4b | 5a | 5b | 6a | 6b | 8 | 10a | 10b |
|-----|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| 1a | 100.0 | | | | | | | | | | | | |
| 1b | 76.6 | 100.0 | | | | | | | | | | | |
| 2a | 74.7 | 72.3 | 100.0 | | | | | | | | | | |
| 2b | 72.0 | 72.3 | 74.1 | 100.0 | | | | | | | | | |
| 4a | 67.1 | 49.6 | 57.8 | 56.4 | 100.0 | | | | | | | | |
| 4b | 36.2 | 38.1 | 41.6 | 40.8 | 41.6 | 100.0 | | | | | | | |
| 5a | 68.5 | 70.0 | 69.9 | 68.2 | 52.2 | 38.1 | 100.0 | | | | | | |
| 5b | 76.5 | 74.4 | 74.0 | 81.5 | 56.7 | 40.2 | 81.8 | 100.0 | | | | | |
| 6a | 25.8 | 8.9 | 15.1 | 15.5 | 46.3 | 50.7 | 12.0 | 18.4 | 100.0 | | | | |
| 6b | 19.9 | 3.6 | 3.6 | 2.9 | 23.1 | 38.8 | 3.6 | 8.1 | 73.1 | 100.0 | | | |
| 8 | 27.0 | 10.2 | 10.2 | 10.3 | 44.0 | 46.1 | 10.2 | 15.2 | 80.7 | 64.9 | 100.0 | | |
| 10a | 23.7 | 5.4 | 5.4 | 3.8 | 22.0 | 41.4 | 9.7 | 14.2 | 71.5 | 88.7 | 63.0 | 100.0 | |
| 10b | 21.6 | 6.4 | 3.9 | 1.7 | 35.9 | 27.3 | 10.0 | 11.3 | 58.6 | 47.8 | 74.7 | 46.2 | 100.0 |

Table 11 Overlap percentages between habitats. Sites within habitats are pooled.

| | | | | | | | |
|-------------|----------|----------|----------|----------|----------|-----------|--|
| Adult 1 | | | | | | | |
| 1 | | | | | | | |
| 70.4 | 2 | | | | | | |
| 64.6 | 73.2 | 3 | | | | | |
| 56.1 | 66.7 | 51.9 | 5 | | | | |
| 58.3* | 63.3 | 79.2* | 52.7 | 7 | | | |
| 41.5 | 46.0 | 38.2 | 54.8* | 30.1 | 9 | | |
| 12.5 | 11.2 | 7.5 | 23.8 | 12.8 | 43.2 | 10 | |
| Offspring 1 | | | | | | | |
| 1 | | | | | | | |
| 65.6 | 2 | | | | | | |
| 54.8 | 42.6 | 3 | | | | | |
| 60.9* | 84.2* | 38.0 | 5 | | | | |
| 49.1 | 36.0 | 55.9* | 38.4 | 7 | | | |
| 46.5 | 47.2* | 23.6 | 60.1* | 52.0 | 9 | | |
| 32.1 | 30.8 | 22.4 | 43.8 | 50.8 | 77.3 | 10 | |
| Adult 2 | | | | | | | |
| 1 | | | | | | | |
| 52.7 | 2 | | | | | | |
| 32.9 | 27.8 | 4 | | | | | |
| 68.4* | 42.1* | 42.2 | 5 | | | | |
| 37.6* | 32.2 | 54.4* | 44.5 | 6 | | | |
| 34.8* | 25.8 | 66.7* | 38.8 | 71.9 | 8 | | |
| 30.0 | 21.3 | 76.4* | 36.6 | 67.5 | 79.8 | 10 | |
| Offspring 2 | | | | | | | |
| 1 | | | | | | | |
| 76.1 | 2 | | | | | | |
| 47.1 | 49.7 | 4 | | | | | |
| 75.7* | 77.2* | 47.5 | 5 | | | | |
| 10.3 | 9.0 | 44.5 | 11.0 | 6 | | | |
| 14.5* | 10.8* | 45.2* | 13.5* | 72.1 | 8 | | |
| 11.5* | 3.6 | 39.7 | 12.7* | 81.7* | 78.7 | 10 | |

APPENDIX 3

Rarefraction:**1**

E(S)= expected number of species
 n= standardized sample size
 N= total number of individuals recorded
 N_i= number of individuals in the *i*th species

Margalef's diversity index:

$$D_{Mg} = \frac{S - 1}{\ln N} \quad 2$$

S= number of species
 N= total number of individuals recorded

Menhinick's index:

$$D_{Mn} = \frac{S}{\sqrt{N}} \quad 3$$

S= number of species
 N= total number of individuals recorded

Shannon diversity index for species richness:

$$H' = - \sum p_i \ln p_i \quad \text{where} \quad p_i = \frac{n_i}{N} \quad 4$$

n_i= number of individuals of the *i*th species
 N= total number of individuals recorded

Shannon diversity index for evenness:

$$E = \frac{H'}{\ln S} \quad 5$$

H'= Shannon diversity index for species richness
 S= number of species

Brillouin index for species richness:

$$HB = \frac{\ln(N!) - \sum \ln(n_i!)}{N} \quad \mathbf{6}$$

N= total number of individuals recorded
 n_i= number of individuals of the ith species

Brillouin index for evenness:

$$E = \frac{HB}{HB_{\max}} \quad \mathbf{7}$$

where HB_{max} is:

8

HB= Brillouin index for species richness
 S= number of species
 N= total number of individuals recorded
 [N/S]= integer of N/S
 and where r is:

$$r = N - S \left[\frac{N}{S} \right] \quad \mathbf{9}$$

Simpson's index:

$$\frac{1}{D} \quad \text{with} \quad D = \sum \frac{(n_i(n_i - 1))}{(N(N - 1))} \quad \mathbf{10}$$

n_i= number of individuals of the ith species
 N= total number of individuals recorded

McIntosh's index of species diversity:

$$U = \sqrt{\sum p_i^2} \quad \text{where} \quad p_i = \frac{n_i}{N} \quad \mathbf{11}$$

n_i = number of individuals of the i th species
 N = total number of individuals recorded

McIntosh's index of dominance:

$$D = \frac{N - U}{N - \sqrt{N}} \quad \mathbf{12}$$

U = McIntosh's index for species diversity
 N = total number of individuals recorded

McIntosh's index of evenness:

$$E = \frac{N - U}{N - \frac{N}{\sqrt{S}}} \quad \mathbf{13}$$

U = McIntosh's index for species diversity
 N = total number of individuals recorded

Berger-Parker diversity index:

$$\frac{I}{d} \quad \text{with} \quad d = \frac{N_{\max}}{N} \quad \mathbf{14}$$

N_{\max} = most abundant species
 N = total number of individuals recorded

The alpha (α) of the log series model:

$$\alpha = \frac{N(I - x)}{x} \quad \mathbf{15}$$

x can be calculated from the following iteration:

$$\frac{S}{N} = \left[\frac{I - x}{x} \right] [I - \ln(I - x)] \quad \mathbf{16}$$

S = number of species

N= total number of individuals recorded

Percentage overlap:

$$PS = \sum \min (p_{1i}, p_{2i}) \quad \text{with} \quad p_{ji} = \frac{n_{ji}}{N_j} \quad \mathbf{17}$$

PS=Percentage similarity

p_{ji} =proportion of sample j made up by species i

n_{ji} =number of individuals of species i

N_j =number of individuals in sample j