

Noctuid moths attracted to fruit baits: testing models and methods of estimating species diversity

Dirk SÜSSENBACH & Konrad FIEDLER

Lehrstuhl Tierökologie I, Universität Bayreuth, D-95440 Bayreuth, Germany
e-mail: konrad.fiedler@uni-bayreuth.de

Summary. Using red-wine based baits we sampled 3015 noctuid moths representing 119 species over one season at two sites in northeastern Bavaria. These samples were used to address the question as to whether baiting yields adequate data for analysing the diversity of a moth community. At both sites the samples closely matched the log-series model. The diversity parameter α was estimated as 23–24 in both communities, which is in the range typical for temperate-zone noctuid communities as revealed by light-trapping. Hurlbert rarefaction analyses likewise indicated that both samples were drawn from communities of equal diversity. The numbers of noctuid species and individuals recorded varied strongly between two different bait mixtures and three exposition techniques, but the resulting diversity estimates were not significantly affected. Numbers of species and individuals recorded at baits positively correlated with ambient temperature, but were not affected by wind speed. Estimates of β -diversity showed that both communities had similar species composition, but differed in abundance relationships. Of various estimates of total species richness based on different extrapolation algorithms, the Michaelis-Menten model yielded reasonable, but conservative approximations of “true” species numbers in the communities. Collectively, these results demonstrate that recording noctuid moths at baits provides data perfectly suitable for diversity analysis, as long as effects of sampling effort and sample sizes are controlled for.

Zusammenfassung. An Rotwein-Zucker-Ködern wurden während einer ganzen Vegetationsperiode an 2 Standorten in Nordostbayern 119 Noctuidenarten in 3015 Exemplaren nachgewiesen. Jeder Standort wurde zweimal pro Woche besammelt. Anhand dieses Datenmaterials wurde die Eignung von Köderfangdaten zur Beurteilung der Diversität von Nachtfalterartengemeinschaften geprüft. An beiden Standorten entsprachen die Arten-Abundanz-Verteilungen in sehr guter Näherung dem Modell der logarithmischen Serie. Der Diversitätsparameter α der logarithmischen Serie war mit Schätzwerten von 23–24 an den beiden Standorten gleich groß und lag im Bereich publizierter, aus Lichtfangdaten abgeleiteter Werte für Noctuiden-Gemeinschaften der nördlichen gemäßigten Zonen. Ein Vergleich der Standorte mittels der Rarefaction-Methode nach Hurlbert zeigte ebenfalls, daß die 2 untersuchten Artengemeinschaften in ihrer Diversität übereinstimmten. Zwei verschiedene Ködermischungen und drei Ausbringungstechniken hatten zwar großen Einfluß auf die absolute Anzahl der

nachgewiesenen Individuen und Arten, die resultierenden Schätzungen der Diversität waren davon aber unbeeinflusst. Mit steigender Lufttemperatur nahm auch die Zahl der pro Abend anfliegenden Individuen und Arten zu, Windgeschwindigkeit oder Niederschlag hingegen hatten auf den Köderfang keinen signifikanten Einfluß. Ähnlichkeitsindizes als Maße der β -Diversität zeigten, daß sich die 2 Artengemeinschaften weniger in ihren Artenspektren als in den Abundanzverhältnissen unterschieden. Von mehreren Extrapolationsmethoden zur Schätzung der "tatsächlichen" Artenzahl ergab das Michaelis-Menten-Modell die robustesten, wenn auch konservativsten Werte. Insgesamt zeigen unsere Ergebnisse, daß Köderfangdaten für Eulenfalter in gleicher Weise wie Lichtfangdaten geeignet sind, die Diversität lokaler Artengemeinschaften zu schätzen, sofern die Einflüsse von Aufsammlungsintensität und Stichprobengröße in adäquater Weise berücksichtigt werden.

Résumé. L'utilisation d'appâts au vin rouge a permis d'échantillonner 3015 Noctuidae, représentant 119 espèces, au cours d'une saison sur deux sites du nord-est de la Bavière. Ces échantillons ont été utilisés pour savoir si l'usage d'appâts peut fournir des données satisfaisantes sur l'analyse de la diversité d'une communauté de papillons de nuit. Sur les deux sites, les échantillons se rapportent à un modèle "série-log". Les paramètres de diversité α ont été évalués à 23–24 dans les deux communautés, ce qui est un ordre de grandeur classique pour les communautés de Noctuides en zone tempérée, comme cela a déjà été montré par piégeage lumineux. L'analyse de la raréfaction par le coefficient de Hurlbert semble indiquer que les deux échantillons sont issus de communautés d'égale diversité. Le nombre d'espèces de noctuelles et d'individus recensés varie fortement entre les deux types d'appâts et les trois modalités d'application, mais la diversité résultante exprimée n'est pas significativement modifiée. Le nombre d'espèces de noctuelles et d'individus recensés par les appâts est positivement corrélé à la température ambiante, mais non affecté par la vitesse du vent. L'estimation de la diversité β montre que les deux communautés ont des compositions spécifiques similaires mais différent par les critères d'abondance. Parmi plusieurs estimations de la richesse totale basées sur plusieurs extrapolations algorithmiques, le modèle Michaelis-Menten paraît raisonnable, et compatible avec l'approximation modérée du "vrai" nombre d'espèces dans les communautés. Globalement, ces résultats démontrent que les méthodes de capture des noctuelles par appât donnent des résultats parfaitement valables pour l'analyse de la biodiversité, aussi longtemps que l'effort d'échantillonnage et que la taille des échantillons seront contrôlés.

Key words: Lepidoptera, Noctuidae, biodiversity, research methods, traps, baits, Bavaria, Germany.

Introduction

With an estimated richness of 150,000–250,000 extant species (Heppner, 1991), the Lepidoptera comprise a sizeable, yet comparatively well known fraction of biotic diversity on Earth. It is thus not surprising that many studies use butterflies or moths as model organisms for biodiversity research. A critical issue for

all such studies is the reliability and usefulness of any measures of "biodiversity" which can be derived from samples of real communities. Such samples are, by necessity, incomplete and influenced by a large (and often unknown) number of extrinsic factors. For example, unpredictable weather conditions and stochastic variation in abundance of species in communities all contribute to sampling error (Mawdesley, 1996).

For nocturnal moths, attraction to artificial light sources is the most commonly used method of sampling, although pheromone traps or other techniques have also been applied (reviewed in Muirhead-Thomson, 1991). It is well established that moth samples from light traps can be described, with reasonable accuracy, using mathematical models such as the logarithmic series (Fisher *et al.*, 1943) or the log-normal distribution (Preston, 1948). Therefore, such models have been widely and successfully applied to the analysis of moth communities from temperate (Kempton & Taylor, 1974) as well as tropical regions (Robinson & Tuck, 1996).

As early as the last century it was observed that certain moths (mainly in the family Noctuidae) can be attracted with liquids containing sugar (e.g. Steiner & Nikusch, 1994). Such artificial baits imitate natural food sources, like rotting fruits, honeydew, or sap oozing out of wounded trees. For a useful bait mixture many recipes have been described (Steiner & Nikusch, 1994), but the main ingredients are always similar. A bait is offered that provides the scent of a solution containing sugar, alcohol, and volatile compounds such as esters which naturally occur in rotting fruits. A variety of techniques has been suggested as to how to offer baits. The commonest ways of presentation are patches of liquid bait directly applied to trees or poles, or suspending materials (strings, pieces of fabric, dried fruits) which have been soaked with the liquid bait mixture (Lederer, 1959; Nippel, 1976).

Baiting has been extensively used for faunistic inventories in the past. Hartweg (cited in Cleve, 1971), for example, recorded between 1904 and 1956 nearly 80% of the noctuid species which occur in the region of Braunschweig (north-central Germany) by baiting. When baiting and light trapping are done simultaneously, moths of some noctuid genera (e.g. *Amphipyra*, *Conistra*, *Agrochola* or *Catocala*) often appear at the baits in much larger

numbers (Cleve, 1971; Mörtter, 1988), suggesting that estimates of abundance based on light-trapping results alone can be misleading. Hence Steiner & Nikusch (1994) postulated that for a “complete” faunistic or ecological inventory of the moth fauna of any given site it is necessary to combine both recording techniques. For practical purposes (e.g. nature conservation: Meineke, 1995), light-trapping seems to be the superior way of monitoring since it usually yields larger samples with smaller time effort, covers a broader range of nocturnal moth taxa, and elaborate methods of analysis have been developed (Southwood, 1978; Robinson & Tuck, 1996).

Light-trapping, however, is based on an artificial stimulus, and the behavioural mechanisms underlying the attraction of moths to UV-light sources are still not satisfactorily understood (Butler & Kondo, 1991; Muirhead-Thomson, 1991). Hence, any sampling method which makes use of a more natural behavioural context, such as the search for food resources in the case of baiting, might have the potential to reveal ecological community patterns more accurately. In fact, bait-traps are now widely used in studies on the community ecology of fruit-feeding nymphalid butterflies in tropical realms (DeVries *et al.*, 1997). We therefore set out to investigate whether recording moths at baits over one entire season in a northern temperate zone may yield adequate samples for quantitative assessments of the diversity and richness of the noctuid guild attracted to such food resources.

Most published papers, which we are aware of, present results of bait-trapping moth surveys only in a qualitative manner, e.g. as species lists (Nippel, 1976; see Kozlov *et al.*, 1996 for one of the rare exceptions). At most these lists are supplemented with subjective assessments of relative abundance (“rare”, “common”). Although most authors offer numerous, and often contrasting, subjective opinions as to how weather conditions may influence the attraction of moths to baits, or which method of presenting the bait (or preparing bait mixtures) may be most effective, practically no quantitative tests of these factors have been carried out thus far. Instead, even the proponents of baiting for faunistic studies appear to assume, at least by implication, that baiting as a sampling method is inherently subject to so much variation that its results can neither be compared between studies, nor used for more than supplementary or qualitative information (Steiner & Nikusch, 1994).

In this paper we explicitly address some questions relevant to the usefulness of bait-trapping as a method of assessing moth diversity:

1. How well do samples of noctuid moths assembled at baits correspond with the log-series model?
2. Can the log-series model, or rarefaction methods, be used to quantitatively describe and compare species diversity (α -diversity) of samples from different communities?
3. Can similarity indices (as a measure of β -diversity) successfully be applied to such samples?
4. How do various estimates of absolute species richness perform when applied to our data set?
5. Are the results obtained with different baits, or techniques, after all comparable? More precisely, this relates to the question as to whether samples obtained with different baits, or different exposition methods, yield corresponding estimates of diversity of the community from which the samples have been drawn.
6. How large is the influence of abiotic factors like temperature and wind speed on the success of bait-trapping?
7. How strongly are the estimates of diversity affected by sample size (i.e. numbers of recorded individuals) or sampling effort (i.e. recording nights per habitat)?

The results presented here strongly support the idea that, much the same as with light-trapping, data obtained by baiting can be used for estimating diversity of noctuid moths, if sufficiently large samples are obtained with a standardized sampling regime.

Materials and methods

Study sites. For our study we selected two sites near Bayreuth (Germany, north-eastern Bavaria). Both were chosen so as to represent typical habitats in a central European cultural landscape, rather than habitats where a particularly rich fauna would be expected. The first site is situated in the botanical garden (BG hereafter) of the University of Bayreuth (355 m a.s.l.) and is mainly characterized by large, almost plain meadows (ranging from moist to moderately dry), interrupted by small stands of young trees and a couple of ponds. The nearest closed forest is situated approximately 600 m to the south, while 300 m to the west an allotment area continues. At this site the bait lines and patches were installed at the south-facing edge of a small

stand of scots pine (*Pinus sylvestris*) and spruce (*Picea abies*) approximately 5 m high and 15 years old.

The second site was situated 5 km southeast of Bayreuth near Wolfsbach. The meadow at the Schlehenmühle (400 m a.s.l., SM hereafter), located on an east-facing slope to the river Roter Main, is much smaller in comparison to the botanical garden and is largely surrounded by closed woodland. The forest mainly consists of pine and spruce, but is at the edge interspersed with deciduous trees. The understorey (blueberry (*Vaccinium myrtillus*) and grasses) is sparse due to the very dense canopy. The vegetation along the river bank consists mainly of black alder (*Alnus glutinosa*) and a few oak trees (*Quercus robur*). The bait lines and patches were placed along the forest edge. Due to its facing the river, the microclimate of the Schlehenmühle site is colder and more humid than in the botanical garden.

Field Methods. We used two different bait mixtures. For the sugar mixture 500 g sucrose were dissolved in approx. 200–300 ml red wine in a glass of 600 ml volume. For the same amount of banana mixture we mixed 400–500 g of mashed bananas with 200–300 ml red wine. Bait mixtures were prepared about 4 d before first use, and were subsequently used for 3–5 d. The idea behind these two bait mixtures was that the sugar mixture may provide a carbohydrate resource suitable for a range of generalist moth species, whereas the banana mixture might preferably be used by species which regularly feed on ripe or rotting fruits.

Two different ways were used to expose the bait. Either liquid bait was painted in patches (size approx. $10 \times 15 \text{ cm}^2$) on tree trunks at a height of 50 or 200 cm ($n = 16$ each), respectively. Alternatively, we tightened a string (length approx. 6 m) at a height of 200 cm between two trees from which we suspended pieces of cotton cloth (size approx. $10 \times 15 \text{ cm}^2$, $n = 20$) soaked with the liquid bait. We expected that the latter way of bait exposition should attract a larger number of moths because the scent plume would diffuse freely in all directions. With both presentation techniques the two bait mixtures were alternated regularly so as to minimize potential positional bias in their attractiveness.

On each sampling night the baits were exposed freshly around sunset. Then, all baits were checked for the presence of moths every 30 min over a period totalling 3 h. The first check of the

baits took place in early dusk, i.e. after being exposed for approx. 30 min. The timing of the sampling throughout the season was standardized so that each evening the second check round at the baits invariably occurred at a light intensity of <10 lx (Bioblock Scientific, LX-101). At the beginning of each check, air temperature and wind speed at a height of 200 cm were measured (anemometer: Testoterm-Technovent 4000). For each sampling night, all temperature and wind speed data were averaged to provide a single rough measure of these important climatic data for subsequent analyses.

All moths encountered during each round were captured for identification (using Skou (1991) as principal reference work, supplemented by special papers where needed) and to avoid multiple counts. The complete species list and abundance data have been published elsewhere (Süssenbach & Fiedler, in press). In all analyses presented here, only species of the family Noctuidae were included.

The first sampling occurred on 01.IV.1997 and the last one on 10.X.1997. At each study site samples were taken twice a week, resulting in a database of 106 nights (53 per locality).

Data analysis. Many quantitative measures have been developed to assess “diversity” of ecological communities (Southwood, 1978; Magurran, 1988; Krebs, 1989; Mawdesley, 1996). As a measure for *a-diversity* (diversity within a habitat, or sample) we here use *Williams’ a* which is derived from the “logarithmic series”, or log-series (Fisher *et al.*, 1943). This mathematical model (see Hayek & Buzas, 1997 for a general introduction and multiple references to further applications) describes the distribution of individuals across species, and in particular accounts for the well known observation that in natural communities there are usually only very few “abundant”, but a large number of “rare” species. According to this model, species number (S) and number of individuals (N) in a sample are related to each other as:

$$S = \alpha \log_e \left(1 + \frac{N}{\alpha} \right)$$

where α can be interpreted as an index of diversity. To allow for comparisons between samples the 95% confidence limits are calculated:

$$CI_{95\%} = a \pm t_{95\%} \sqrt{\text{var } a}$$

with the estimate of variance being:

$$\text{var } a = a^3 \frac{(N + a)^2 \log_e \left(\frac{2N + a}{N + a} \right) - Na}{(SN + Sa - Na)^2}$$

where $t_{95\%} = 1.96$ is the two-tailed threshold value of statistical significance of Student's t-distribution at the selected significance level (here: $p < 0.05$) for an infinite number of degrees of freedom (Sachs, 1992). a and x were calculated using the program "logserie" of Krebs (1989), while $\text{var } a$ was calculated using the formula originally derived by Fisher *et al.* (1943). We chose this variance estimate, instead of the widely used Anscombe estimate, because for large samples (i.e., in the hundreds, as ours) its mathematical properties are superior (Hayek & Buzas, 1997).

Williams' α provides a measure of diversity that is particularly robust over a wide range of conditions as long as sample sizes are sufficiently large (say, ≥ 100 individuals: Hayek & Buzas, 1997). We test the goodness-of-fit between the log-series model and our empirical data using the Pearson correlation coefficient r between the observed and expected abundances (the latter are expressed as the Whittaker plot by the program "logserie"). In addition, we compare the observed and expected numbers of species in abundance classes (scored in octaves: Preston, 1948) using χ^2 statistics.

An alternative way to compare species diversity between samples of communities are the "rarefaction methods" (Hurlbert, 1971; Achatziger *et al.*, 1992; note that also the log-series model can be used to rarefy if one assumes it to accurately describe a community: Hayek & Buzas, 1997). Generally, it is invalid to simply compare absolute species numbers between samples unless the sample sizes are equivalent, because with increasing sample size the number of recorded species also increases due to stochastic effects, even if the samples are drawn from the identical community. The Hurlbert rarefaction allows the comparison of species numbers between samples where the total numbers of individuals are different: the larger sample(s) can be rarified to the smallest sample size, and an expected species number can

be calculated (together with a confidence interval: Simberloff, 1978) for any fixed sample size. Note that extrapolation from Hurlbert rarefaction curves is invalid (Müller-Schärer *et al.*, 1991). The necessary calculations were made with the program “*rarefact*” of Krebs (1989).

While diversity indices such as Williams’ α , or the rarified expected species richness for a given sample size, provide mathematically ‘exact’, but rather abstract figures, it might often be interesting to know about the ‘absolute’ number of species which make up a given community. Since complete inventories are practically always impossible to achieve (from statistical reasons alone), one may use *extrapolation methods*, which estimate the total number of species from empirical samples. Recent advances in mathematical methodology have provided a set of extrapolation procedures that are in part based on relatively complicated formulae and rather different assumptions (see Colwell & Coddington, 1994). These algorithms estimate species richness either from extrapolation of randomized species accumulation curves (e.g. Michaelis-Menten model, where a hyperbolic function is fitted, whose asymptote serves as richness estimator), or they derive an estimate from the ‘rare’ species in the sample, because it is most likely that all species not yet covered by sampling would belong to these lowest abundance categories (see Colwell & Coddington, 1994 for further discussion and references). An important difference between such extrapolation methods and the log-series is that mathematical models underlying extrapolation procedures are usually asymptotic (i.e. converge to a ‘true’ value of total species richness, if sampling effort increases), whereas the log-series does not have an asymptote.

We have here chosen five different estimators. First, a Michaelis-Menten model was fitted to the sampling data (after randomizing them 50 times, using the *MMMeans* procedure of Colwell, 1997). Michaelis-Menten type models describe well the accumulation of species records as sampling increases, with steadily increasing likelihood of adding new species (Lamas *et al.*, 1991). Second, four estimators which emphasize the ‘rare’ species in the samples were used. The two versions of Chao’s estimator (based on those species which occur in only one or two specimens in the entire sample: *Chao1*; based on species which occur in only one or

two sampling nights: *Chao2*) are particularly easy to calculate and have produced promising results in recent empirical tests (León-Cortés *et al.*, 1998; Peterson & Slade, 1998). Two coverage estimators (abundance-based: *ACE*, incidence-based: *ICE*) were also included because of their promising mathematical features (Lee & Chao, 1994; Colwell, 1997), although we are unaware of any experiences with real biological data sets published so far. *ACE* is based on all species represented with 10 or fewer individuals in the total sample, while *ICE* uses all species represented in 10 or fewer sampling nights.

The calculations were done with the program 'EstimateS5' (Colwell, 1997; where also the formulae for *ACE* and *ICE* and the variance estimates can be found). The definitions of *Chao1* and *Chao2* are as follows:

$$\hat{S}_{Chao1} = S_{obs} + \frac{F_1^2}{2F_2}$$

$$\hat{S}_{Chao2} = S_{obs} + \frac{Q_1^2}{2Q_2}$$

where S_{obs} is the number of species observed; F_1 the number of species represented by one specimen only (i.e. singletons); F_2 the number of species represented by two individuals only; Q_1 the number of species which occur in exactly one sample (i.e. found in just one collecting night); and Q_2 the number of species represented in just two samples. Confidence intervals were calculated using the standard deviation estimates produced by the program, multiplied with the 95% threshold value of the t-statistics (1.96).

We also wanted to know whether baiting samples of noctuids are suitable for differentiation between communities. For that purpose, we calculated similarity indices as measures of β -diversity (between-habitat diversity). In the ecological literature a plethora of similarity indices have been proposed, many of which have serious drawbacks (Wolda, 1981; Lande, 1996). Basically similarity indices can be divided in two classes: binary measures which only take into account the presence or absence of species, and others which also use abundance information.

We have selected two binary indices (the Sørensen or Czekanowski index, and the Dice or association index), and two abundance-based measures (Morisita and Renkonen index). Of the binary indices, Sørensen similarity has been widely used in community ecology. The Dice index can be advantageous if one sample is much smaller than the other, but this difference is largely due to sampling efficiency (and not an ecological property of the community: Wolda, 1981). Of the two abundance-based measures widely used, Morisita's index seems to be particularly suitable for most ecological comparisons (Wolda, 1981; Magurran, 1988).

To assess differences between samples in relation to bait mixture or method of bait presentation, we apply elementary statistical procedures (χ^2 contingency tests) in addition to the diversity measures detailed above. The influence of temperature and wind speed on sampling efficiency is tested by standard correlation techniques.

Finally, we will address the question as to how sampling effort (i.e. number of sampling nights) influences the results. We have selected two approaches. First, we apply the Shinozaki rarefaction method (Achtziger *et al.*, 1992) which yields estimates for the expected number of species to be observed as a function of the number of sampling units (here: baiting nights). Calculations were made with a program written by W. Achtziger (cf. Achtziger *et al.*, 1992). Second, we compare our results on diversity and species richness between subsets of our samples. Because we sampled both sites twice a week, a simple way of obtaining two subsamples for each site was to use either only the results of the first, or alternatively the second, sampling night per site and week.

Results

Structure, α -diversity and similarity of the two moth communities. During the entire sampling period in 1997 we recorded 106 noctuid species with 1976 individuals at site BG, and 88 species with 1039 individuals at site SM (species lists and abundance data in Süssenbach & Fiedler, in press). While the absolute abundances of moths at both localities obviously differed strongly, the rank-abundance plots showed a very similar shape. There were only a few very frequent and many rare species. At BG, 39.6% of the species were singletons or doubletons, representing

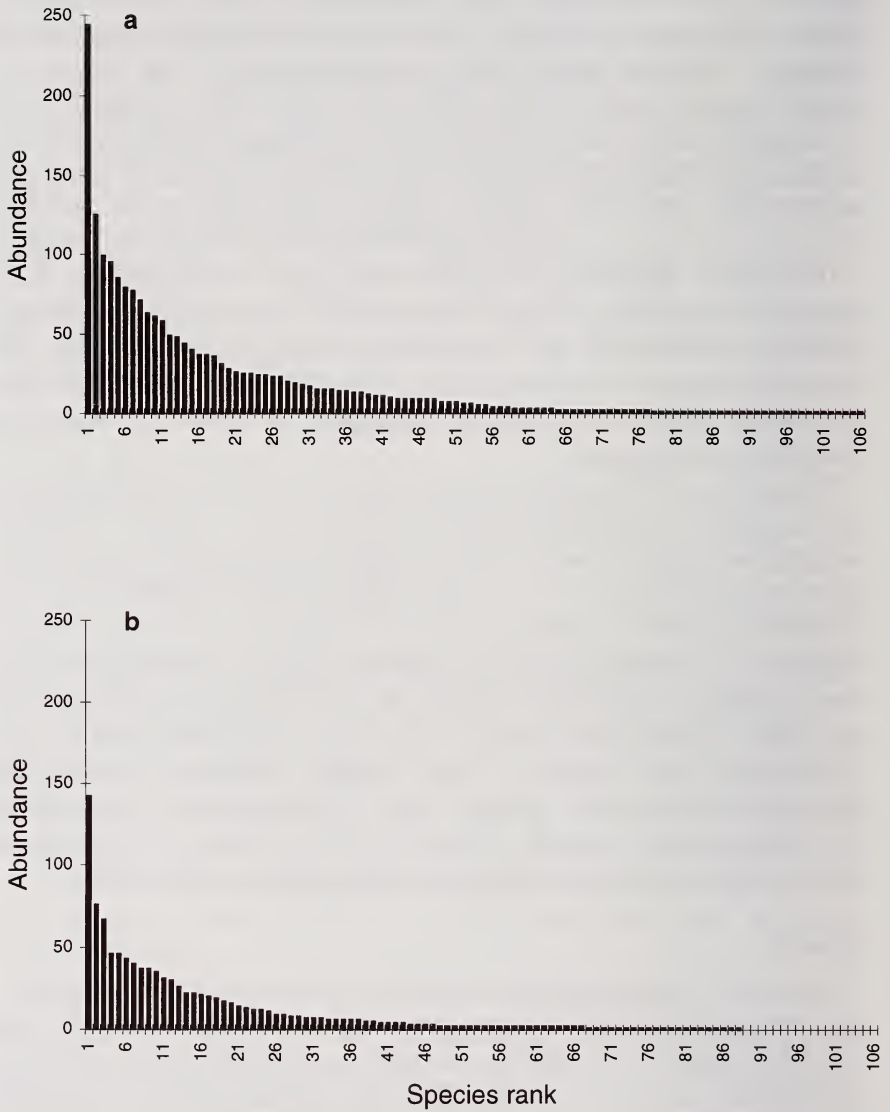
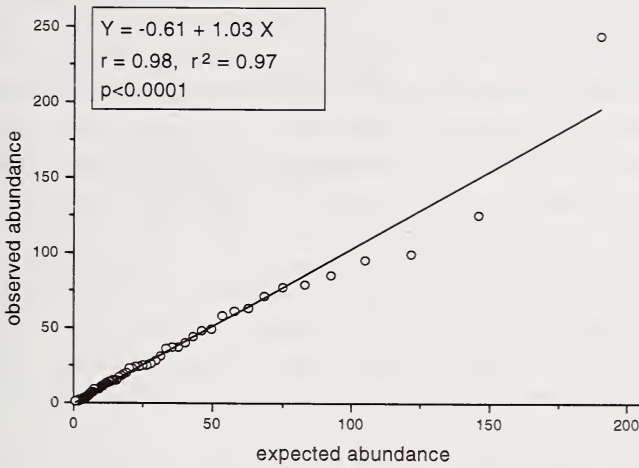


Fig. 1. Rank-abundance plots of the noctuid moth communities attracted at baits in the botanical garden BG (a) and at the Schlehenmühle SM (b).

a)



b)

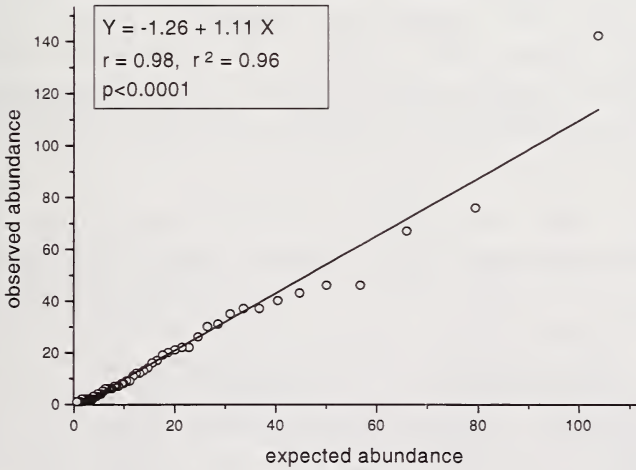


Fig. 2. Correlation between recorded abundance (Y-axis) and expected values (X-axis; from the Whittaker plot) under the log-series model, for the species community at the botanical garden BG (a) and the Schlehenmühle SM (b). At both sites observed and expected values are highly significantly correlated.

but 2.8% of all individuals. The respective proportions at SM were 46.6% of species, and 5.9% of individuals.

The empirical rank-abundance distributions closely match the log-series model (fig. 2). At both sites, observed and expected frequencies correlate highly significantly. Only for the most dominant species does the log-series model underestimate the observed abundance. Moreover, at both sites the observed numbers of species in abundance octaves closely matched predictions based on the respective parameter estimates of α and x (BG: $\chi^2_{6df} = 4.36$, $p > 0.62$; SM: $\chi^2_{6df} = 3.62$, $p > 0.72$). Therefore, the noctuid communities attracted at baits can be very well described by the log-series model, and accordingly Williams' α provides a reasonable measure of the diversity of both communities. The α -values were 23.96 ± 2.29 for site BG, and 22.95 ± 2.67 for site SM, with strong overlap of the confidence intervals.

Application of the Hurlbert rarefaction method yields analogous results (fig. 3). The curves for the two sites are almost completely congruent. Rarefaction of the larger sample (BG) to the size of the smaller sample (1039 individuals, as at the site SM) reveals that the expected number of species at both localities is identical. Collectively, the α -values and rarefaction curves for both sites strongly indicate that, in spite of the differences in the recorded numbers of species and individuals, the structure and α -diversity of both communities of noctuids attracted to baits are virtually identical.

The results of various extrapolations of the 'true' species richness from our empirical data are summarized in Table 1. Included here are four estimators which rely largely on rare species (*ACE*, *ICE*, *Chao1*, *Chao2*) and one estimator based on the Michaelis-Menten model (*MMMeans* (fig. 3); see Colwell, 1997). These estimators uniformly indicate that, as expected, the communities of noctuid moths which could have been attracted to baits were not exhaustively covered during our survey. For the BG site estimators based on rare species indicate that the fauna comprised 135–145 species, of which only 73.1–78.5% have actually been sampled. According to the Michaelis-Menten model (with a lower asymptote of 123 species), 86.2% of the expected fauna has been recorded within one single season of baiting. At

the SM site all estimators converge between 99 and 108 species, which implies that the local community has been sampled with a coverage of 81.5–88.9%.

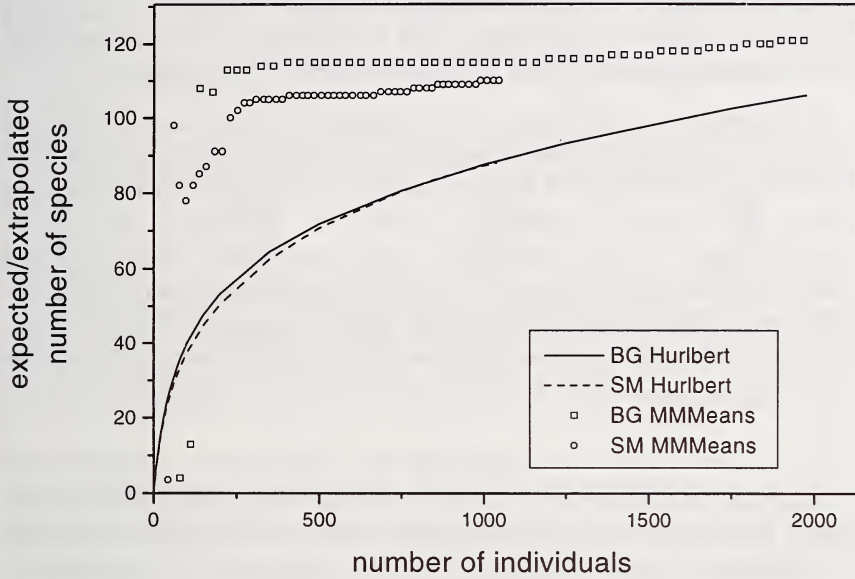


Fig. 3. Hurlbert rarefaction curves for the baited noctuid communities of the botanical garden and the Schlehenmühle, and performance of Michaelis-Menten richness estimators (MMMeans) as a function of randomized sample accumulation.

Table 1. Estimated “total” number of species ($\pm 95\%$ confidence intervals where applicable) at the two sampling sites as revealed by different extrapolation algorithms (see Colwell, 1997)

Species richness estimator	Botanical Garden (BG)		Schlehenmühle (SM)	
	“Total” species number	Percent observed of estimated total	“Total” species number	Percent observed of estimated total
ACE	144	73.6	107	82.2
ICE	135	78.5	108	81.5
Chao1	138 \pm 31	76.8	99 \pm 12	88.9
Chao2	145 \pm 35	73.1	102 \pm 14	86.3
MMMeans	123	86.2	106	83.0

The second column for each site gives the proportions of the actually recorded number of species (BG: 106; SM: 88) as percentages of the respective estimator for “total” species richness.

The communities of noctuids attracted to baits at the two sites were remarkably similar. Overlap in species composition was 0.77 (Sørensen index) to 0.85 (Dice index). When abundance data were included, the communities could be separated more clearly (Morisita index: 0.60, Renkonen index: 0.55). These data suggest that, with regard to bait-feeding noctuids, the two study sites differed in relative abundance and dominance characteristics of the component species, but less so in species composition.

Comparison of different bait mixtures and between methods of bait presentation. One central aim of our study was to test if and how the choice of bait mixtures or presentation techniques affects the noctuid samples attracted to the baits. For these analyses data of both study sites were combined since we have shown above that diversity of both communities was identical and species compositions did not differ markedly. In addition, Williams' α for the combined BG + SM sample ($\alpha = 24.73 \pm 2.11$) is not significantly different from the parameter estimate for each site.

As a first step, we compared the numbers of species and individuals attracted to the two bait mixtures (only considering moths attracted to suspended baits), the effectiveness of exposing the bait (at the same height, 200 cm) on tree trunks *vs.* suspended pieces of cloth, and the influence of presentation height at a tree trunk (50 *vs.* 200 cm). All these factors strongly (and in 5 out of 6 comparisons significantly) affected sampling efficiency (Table 2). Almost twice as many species, and almost ten times the number of individuals, were attracted to the sugar rather than the banana bait mixture. Exposing baits on freely suspended pieces of cloth attracted twice as many individuals and slightly increased the number of recorded species, as compared to painting the bait on tree trunks at the same height. Baits exposed at a height of just 50 cm were the least effective.

So, different baiting mixtures and techniques heavily influenced the absolute numbers of recorded individuals and species. If the diversity of samples is considered, however, these methodological differences largely disappear. The values of Williams' α are practically identical for all subsamples (Table 2). Likewise, Hurlbert rarefaction curves reveal a remarkably high correspondence between the two bait mixtures as well as among the various

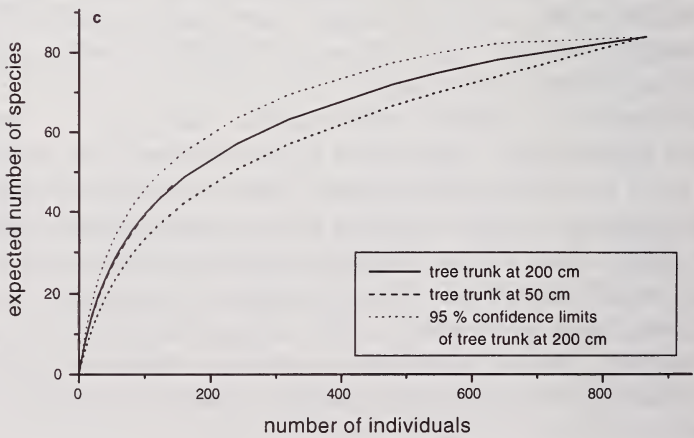
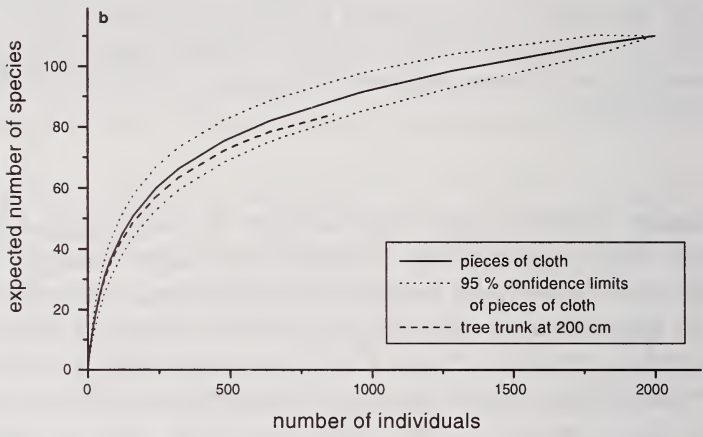
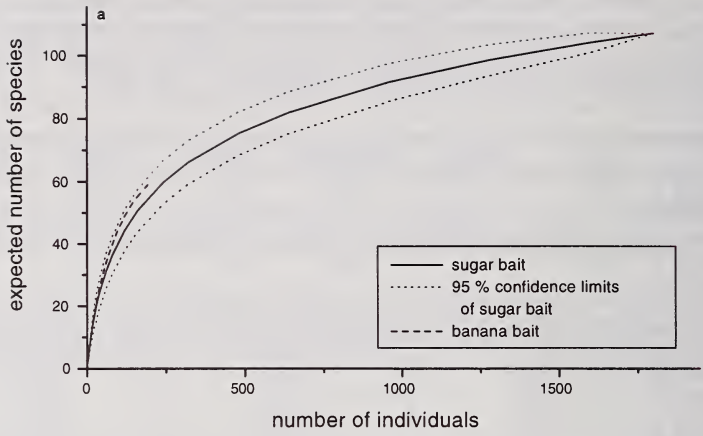
Table 2. Comparisons of recording efficiency between the two bait mixtures (sugar vs. banana; suspended baits only), and between methods of bait presentation (suspended vs. painted on tree trunks, height 200 cm (= "tree200"); painted on tree trunks, 50 (= "tree50") vs. 200 cm)

	Sugar	Banana	Suspended	Tree200	Tree200	Tree50
Number of individuals	1800	193	1993	866	866	144
Statistics	$\chi^2_{1df} = 1295.8, p < 0.0001$		$\chi^2_{1df} = 444.3, p < 0.0001$		$\chi^2_{1df} = 516.1, p < 0.0001$	
Number of species	107	59	110	84	84	47
Statistics	$\chi^2_{1df} = 13.88, p < 0.001$		$\chi^2_{1df} = 3.49, p > 0.05$		$\chi^2_{1df} = 10.45, p < 0.005$	
$\alpha \pm 95\% \text{ CI}$	24.92 ± 2.43	28.97 ± 6.47	25.04 ± 2.37	22.97 ± 2.83	22.97 ± 2.83	24.26 ± 6.28
Sørensen	0.699		0.814		0.595	
Dice	0.983		0.941		0.830	
Morisita	0.911		0.804		0.520	
Renkonen	0.887		0.698		0.673	

Statistical comparisons between numbers of species or individuals are made with χ^2 -tests (null hypothesis: equal distribution between methods). As a measure of sample diversity, values of Williams' α of the log-series (with 95% confidence interval, CI) are presented. Similarity between subsamples is expressed as Sørensen, Dice, Morisita, and Renkonen indices.

presentation methods (fig. 4). In no case do the expected species numbers differ significantly between the larger sample (when rarified) and the smaller sample. Furthermore, the subsamples were all quite similar with regard to their species composition and abundance relationships. The Dice index (which is the most appropriate binary index here since samples of different species richness are compared, but differences are due to sampling efficiency) reveals a correspondence between 83 and 98.3%. Also the abundance-based Morisita and Renkonen indices indicate similarities between 52 and 91%.

Examination at species level showed that none of the more common species (i.e. represented by more than five individuals in our total sample) was exclusively observed at the banana bait or with only one specific method of bait presentation. Only four species (*Agrochola litura*, *Euplexia lucipara*, *Phlogophora meticulosa* and *Polia nebulosa*) were exclusively caught at the sugar bait. Given the overall much lower attractiveness of the banana bait, however, this is probably a stochastic effect of sample size rather than a hint towards specific avoidance of the banana mixture.

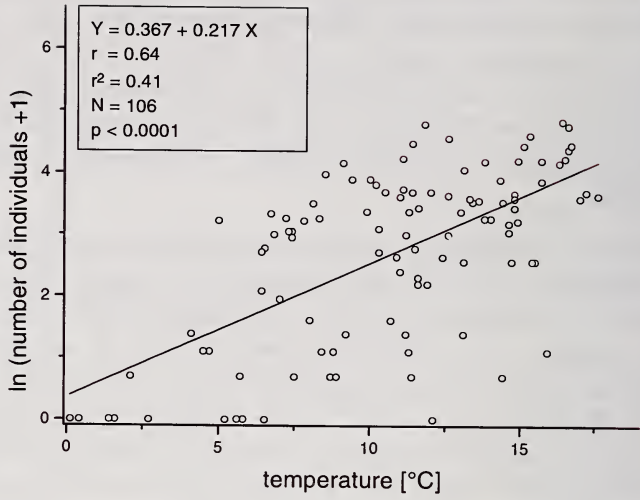


In sum, although we found considerable variation in the effectiveness of attracting moths depending on bait mixture or baiting method, there was no evidence that either bait type or method drew significantly different subsamples from the community of noctuid species which frequent such baits. The similarity between the subsamples was high, and estimates of α -diversity (based on Williams' α or Hurlbert's rarefaction method) provided entirely concordant results, irrespective of methodological details.

Influence of weather conditions on baiting success. Most moths are ectothermic animals that depend on appropriate climatic conditions (e.g. temperature) for maintaining flight activity. Even though certain noctuids which are active in winter possess elaborate methods of thermoregulation (e.g. *Lithophane*, *Eupsilia*: Heinrich & Mommsen, 1985), one should expect that overall attraction of noctuids to baits is strongly influenced by temperature. Wind speed might also interfere with the efficiency of bait-trapping. On the one hand, higher wind speed and concomitant stronger convective cooling should constrain flight activity, in particular at lower air temperatures. On the other hand, the scent plume of baits might distribute more freely, and reach further, if carried by air currents. We tested the influence of both climatic variables on the number of individuals and species attracted to the baits. For these tests we combined data from both localities and for all bait mixtures or presentation methods, and then calculated the Pearson correlation coefficient between the total nightly catch and the average temperature and wind speed score for the respective evening.

←Fig. 4. Hurlbert rarefaction curves for the comparison of samples (a) sugar vs. banana bait, (b) suspended pieces of cloth vs. bait painted on tree trunk (height 200 cm), and (c) bait on tree trunks (200 cm vs. 50 cm). In all three cases, the rarefaction curve of the smaller sample lies completely within the confidence limits of the rarefaction curve of the larger sample, i.e. the diversity of samples is not significantly different.

a)



b)

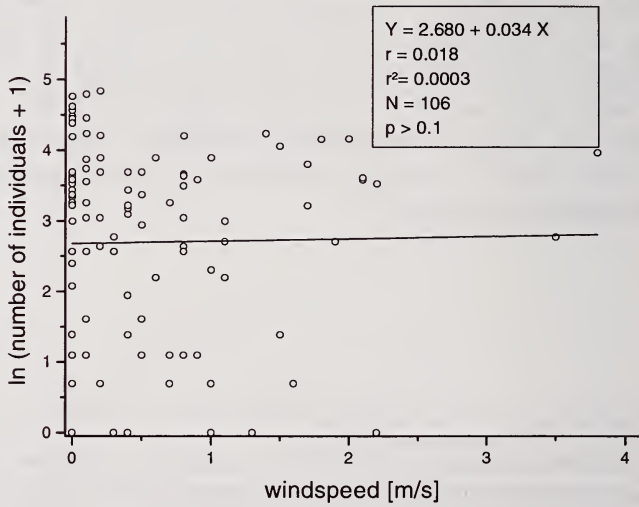


Fig. 5. Relationship between the number of individuals caught at baits (transformed as $\ln(x+1)$) and (a) temperature or (b) windspeed.

We found a significant positive correlation between the number of attracted moths and temperature (fig. 5a). A similar relationship was found between temperature and recorded number of species ($r = 0.68$, $r^2 = 0.46$, $p < 0.0001$). In contrast, wind speed had no detectable influence on the number of arriving moth individuals (fig. 5b), nor species ($r = -0.040$, $r^2 = 0.002$, $p > 0.1$), although the largest samples were taken on evenings with little wind.

Assessing the intensity of recording. As shown above, baiting noctuids at the two study sites twice a week over an entire season yielded a large, robust database, from which the diversity and species richness of the moth communities could be reliably estimated. However, this recording scheme required an immense time effort. To assess how well the communities could be described with only half the recording effort, we partitioned our samples from both sites into two subsamples. Subsample 1 consisted of only the first recording night per week at each of the localities, subsample 2 only of every second recording night per week per site. Both of these subsets of data were then compared with each other and with the complete data set. As expected, with half the sampling effort we recorded at both sites roughly half of the individuals, and approximately 70–80% of the species (Table 3). By chance, the subsample SM1 was distinctly poorer than SM2.

Table 3. Numbers of species and individuals in the subsamples and in the complete set of data for each study site

	Botanical Garden (BG)			Schlehenmühle (SM)		
	BG1	BG2	total	SM1	SM2	total
Number of species	89	86	106	65	76	88
Number of individuals	1054	916	1976	493	553	1039

Williams' α of the log-series reveals that α -diversity neither differed significantly between the subsamples at any site, nor between any subsample and the corresponding total catch (fig. 6). Similarly, the Hurlbert rarefaction method (based on recorded

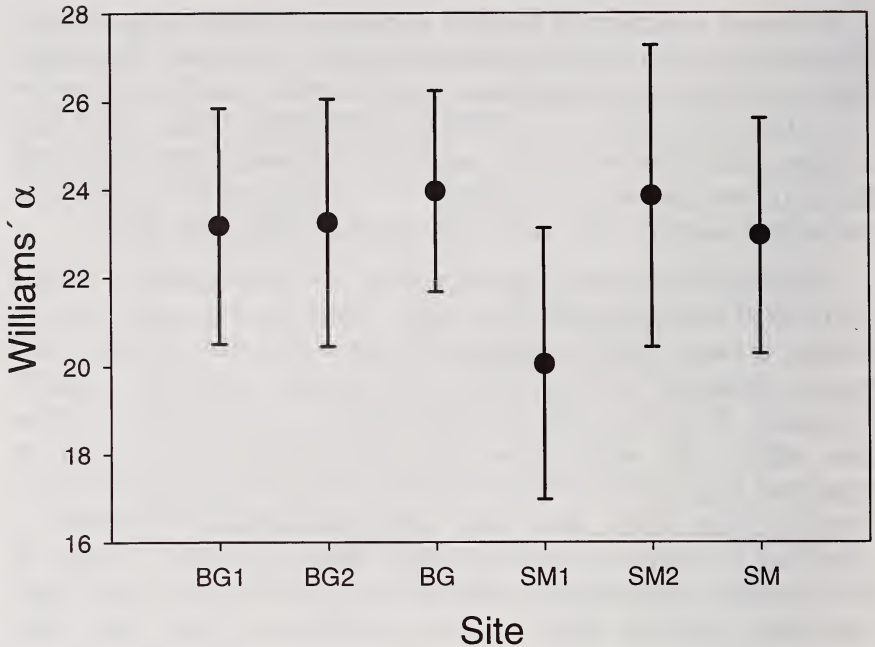
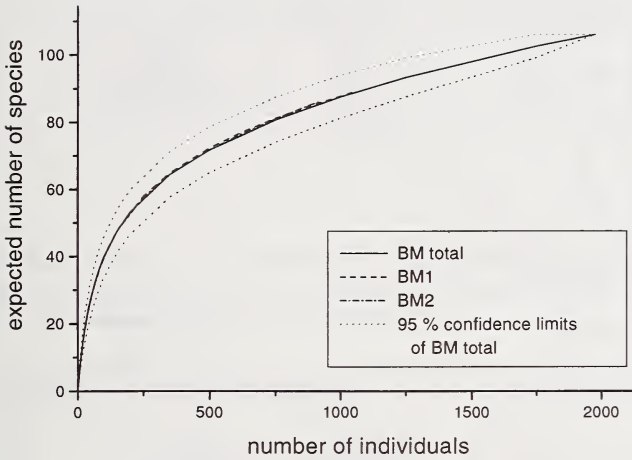


Fig. 6. Williams' α of the log series (\pm 95% confidence intervals) for the subsamples and the complete set of data for both study sites (BG, SM).

individuals: fig. 7) as well as the Shinozaki rarefaction method (based on sampling nights: fig. 8) show that at both study sites the two subsamples agree very closely with each other, as well as with the rarefaction curves for the entire data set. Hence, α -diversity and community structure of the noctuid moths attracted to baits could have been assessed with equal reliability through only one sampling event per week. Not only diversity, but also species composition was very similar between the two subsamples at each study site. The Morisita index, in particular, revealed a very close correspondence between the data subsets.

With reduced sampling effort, one invariably misses an increasing proportion of the species present in a community (Table 3, figs. 7 & 8). Therefore, it will become more and more difficult to estimate the 'true' species richness. An empirical approach to assess the potential of estimating absolute species richness from reduced samples is the application of the extrapolation estimators

a)



b)

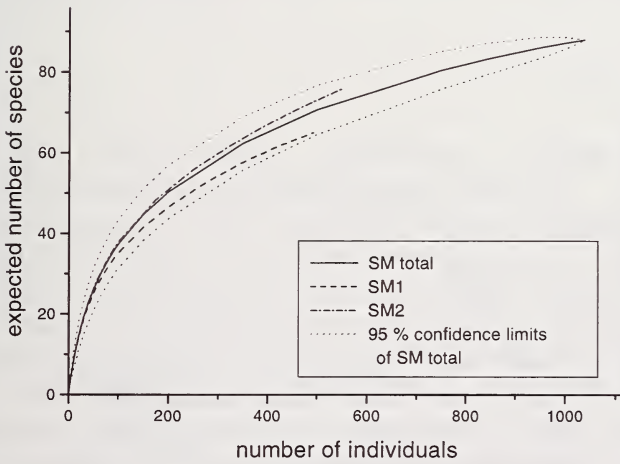
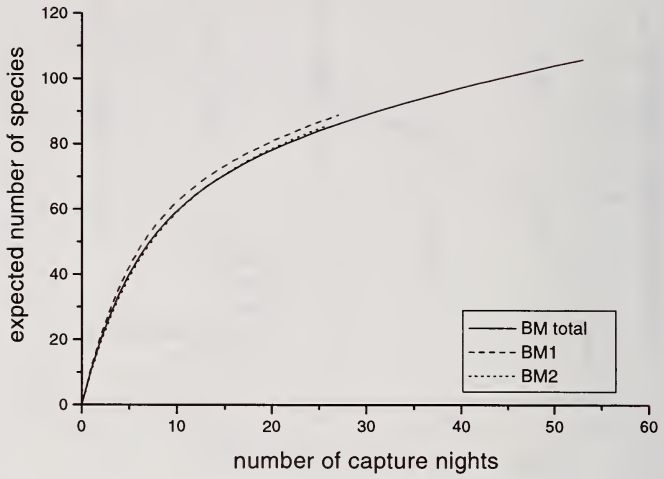


Fig. 7. Hurlbert rarefaction curves of the entire baiting samples of noctuids, and the corresponding subsamples, for both study sites (a: BG, b: SM). The rarefaction curves of the subsamples lie entirely within the 95% confidence limits of the rarefaction curve for the whole data set, indicating that diversity did not differ between subsamples, nor between any subset and the complete data set.

a)



b)

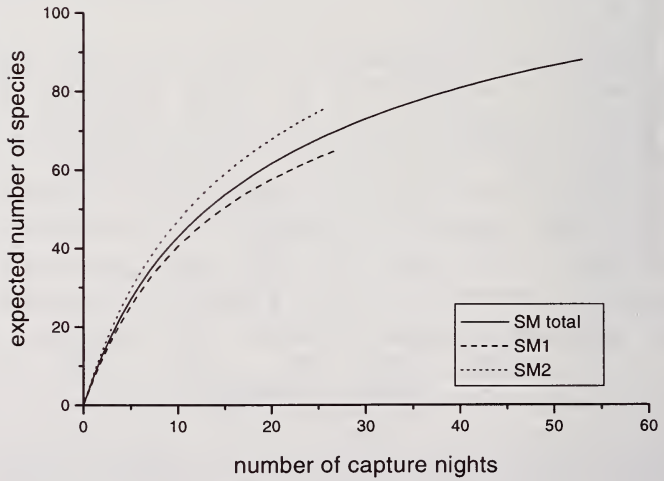


Fig. 8. Shinozaki rarefaction curves of the entire baiting samples of noctuids, and the corresponding subsamples, for both study sites.

Table 4. Indices for the comparisons between subsamples for each study site

	BG1/BG2	SM1/SM2
Sørensen	0.79	0.75
Dice	0.80	0.82
Morisita	0.96	0.94
Renkonen	0.84	0.77

Table 5. Performance of the estimators ($\pm 95\%$ confidence intervals where applicable) of "absolute" species richness (Colwell, 1997) based on the partitioned subsamples collected at both sites

Species richness estimator	Botanical Garden (BG)		Schlehenmühle (SM)	
	BG1	BG2	SM1	SM2
ACE	112 (-22.2%)	115 (-20.1%)	92 (-14.0%)	112 (+4.6%)
ICE	107 (-20.7%)	107 (-20.7%)	85 (-21.3%)	108 ($\pm 0.0\%$)
Chao1	121 \pm 31 (-12.3%)	146 \pm 66 (+5.8%)	80 \pm 16 (-19.2%)	114 \pm 37 (+15.2%)
Chao2	124 \pm 35 (-14.5%)	131 \pm 43 (-9.7%)	87 \pm 22 (-14.7%)	110 \pm 31 (+7.8%)
MMMeans	117 (-4.9%)	124 (+0.8%)	99 (-6.6%)	118 (+11.3%)

Per cent values (in parentheses) denote changes relative to the respective estimator for the entire data set (see Table 1)

(*ACE*, *ICE*, *Chao1*, *Chao2*, *MMMeans*: Colwell, 1997 and above) on the partitioned subsets of data (Table 5).

When compared to the estimator values calculated for the entire data sets (Table 1), three patterns emerge. (1) For the first four models of extrapolation (*ACE* to *Chao2*, which are based on 'rare' species in the samples) most figures as estimated from the partitioned data sets are smaller than those for the entire data set (but extrapolations for SM2 show the reverse trend). (2) Estimates based on these four algorithms tend to show quite large deviations (11 out of 16 cases differ by about 10 to 20%, SM2 again provides the only exception) from the species richness calculated for the entire data set. (3) In contrast, extrapolations according to the Michaelis-Menten model differ by less than 10% from the 'complete' estimate.

Discussion

Applicability of quantitative diversity measurers to catches at baits. Within one season of regular baiting we sampled 3015 noctuid moths representing 119 species at two study sites. This large material allowed us to test the suitability of a variety of models and methods employed in biodiversity research. For both sites the rank-abundance plots revealed the usual pattern of natural communities, which are made up by only a few very frequent species, while most species are 'rare'. Such a structure is typical for moth communities sampled by light-trapping (Kempton & Taylor, 1974; Taylor *et al.*, 1976). Our baiting data showed an excellent fit to the frequency distributions as predicted by the log-series model, which has mostly been applied thus far to light-trap data. This close correspondence is a clear indication that (a) with regular baiting a noctuid guild (namely those which feed on carbohydrate resources other than flowers) can be sampled adequately and (b) that Williams' α , as an easily computed measure of diversity, can be used to characterize such a community. Two great advantages of Williams' α are (a) that it is largely independent of sample size (so long as samples are adequately large, preferably > 100 individuals) and (b) that it condenses information of species presence and abundance into one figure (with confidence limits), thus facilitating further comparisons (see Southwood, 1978; Wolda, 1981; Hayek & Buzas, 1997).

The second type of diversity assessment, Hurlbert's rarefaction method, also performed well on our data set. Hurlbert (1971) strongly opposed the use of any 'diversity indices' and developed his alternative probabilistic parameter-free concept for assessing and comparing species richness as a function of recording intensity. With the advent of computer facilities to perform the complex calculations, these rarefaction methods are now widely used in community ecology and conservation biology (e.g. Achtziger *et al.*, 1992; Hayek & Buzas, 1997). When applied to our data set, the Hurlbert approach always led to the same conclusions about diversity as the calculation of Williams' α (see below).

Comparability of different bait mixtures and exposition techniques. Above, we have shown that quantitative analytical

Table 6. Values of Williams' α from selected studies on Noctuidae diversity (where applicable, α values were computed separately for each studied site and season)

Country	Habitat, duration of study	Source	Collection method	Diversity (Williams' α)
W Malaysia: Pahang	tropical secondary forest, 1979-1980	Barlow & Woivod, 1989	light	104.4
E Malaysia: Sarawak	various rain forest types, 1977-1978	Holloway, 1984	light	251.2
E Malaysia: Sabah	rain forests and plantations, 1987-1989	Holloway <i>et al.</i> , 1992	light	44-170
Canada: New Brunswick	coniferous forest (within canopy), 1990 (2 mon)	Thomas & Thomas, 1994	light	24.8
Canada: New Brunswick	coniferous forest (above canopy), 1990 (2 mon)	Thomas, 1996	light	29.8
USA: W Virginia	deciduous broadleaved forest, 1984-1986	Butler & Kondo, 1991	light	30.0-38.9
S Norway:	mixed forest and cultivated landscape, 1969-1971	Bakke, 1974	light	23.8-27.7
Sweden: Skane	suburb gardens, 1968-1969	Persson, 1971	light	23.3-23.5
Germany: Rhine province	various forest types, 1985-1986	Mörtter, 1988	light	11.0-25.1
Germany: S Bavaria	mixed cultural landscape, 1987-1988	Hausmann, 1990	light	19.9-30.0
Germany: NE Bavaria	mixed cultural landscape, 1997 (6.5 mon)	this study	bait	23-24
Russia: Kola Peninsula	degraded boreal forests, 1991-1993 (total 3.5 mon)	Kozlov <i>et al.</i> , 1996	bait	2.3-3.5

methods may be applied to noctuid samples from baits. However, most studies known to us about bait-trapping of moths in temperate regions are restricted to qualitative lists of species. Moreover, even proponents of baiting for faunistic studies usually emphasize that too many factors affect the success of baiting to allow for quantitative elaboration of such data (e.g. Steiner & Nikusch, 1994). We have empirically tested two sets of factors (i.e. methodological and climatic) which are commonly proposed as objections against more sophisticated analyses of baiting data.

A prime requirement to allow for comparisons between different studies (and this is the basic reason why quantitative methods have been developed at all) is that, if drawn from the same community, samples obtained with different methods must yield congruent results. Specifically, this means that neither bait mixture nor exposition method should affect the assessment of a given community. In fact, we observed that the two bait mixtures differed drastically with regard to numbers of species and individuals attracted, and bait presentation also had a profound effect on baiting efficiency. Thus, at a first glance these results seem to support the pessimistic attitude towards baiting as a quantitative method.

Calculation of Williams' α (Table 2) and application of Hurlbert's rarefaction method (fig. 4), however, demonstrated that, with regard to diversity, differences between samples were all minimal and not significant. Hence, the two bait mixtures and three presentation techniques only differed in the number of moths attracted, but all these methods drew samples of equal diversity pattern from the same natural community. Further support for this conclusion comes from the estimates of similarity between samples caught with the different methods or baits. Values of all similarity indices tested were high (mostly $\geq 70\%$). Only the sample of noctuids attracted to baits on tree trunks at a height of 50 cm differed more, but at these baits so few moths were caught that this result should not be overrated. Still, the Dice index (the most suitable for such impoverished samples) indicates a similarity of 83% to the sample caught higher up at tree trunks. Finally, we obtained no evidence that any of the commoner moth species could be exclusively observed at one bait mixture or with one exposition method. Hence, apparent

methodological differences are effects of sample size and emphasize the general notion that comparisons of mere numbers of recorded species are usually inadequate to assess diversity whenever sample sizes, or sampling effort, are variable (Mawdesley, 1996).

Why did bait mixtures or presentation techniques differ in absolute effectiveness? Since we have not addressed this question experimentally, we can only propose some explanatory arguments. It seems likely that the odour plume dissipating from baits suspended from a rope distributes more freely as compared to bait patches on tree trunks. From the same reasoning, baits at a height of 200 cm at tree trunks are probably easier to locate for a flying moth than those at 50 cm. Accordingly, the differences in effectiveness between the exposition techniques are likely due to the intensity and range of the olfactory cues which emanate from the food source.

The distinct preference for the sugar mixture over the banana bait is more difficult to explain. In particular in late summer and autumn, rotting fruits are important natural food sources of bait-visiting moths (Steiner & Nikusch, 1994; Steiner, 1997). Thus, one might have expected the banana bait, with its (for the human observer) more intensive smell of decaying and fermenting fruits, to be more attractive, but the opposite was true. For preparation of the two bait mixtures, equal fresh weights (500 g) of sucrose and bananas, respectively, had been used. Hence, the sugar content of the banana bait was certainly lower, and this might be one reason for the preference pattern observed. One should expect that noctuid moths, with their substantial energy consumption during warming up and active flight (Heinrich & Mommsen, 1985), would be predominantly attracted to the most profitable food source. The cues used for resource location, however, still need to be addressed with suitable experiments.

Our observation that, under otherwise equal conditions, a wine-sugar mixture was more effective than a wine-banana bait calls into question the significance of strongly smelling additives in baits. Nutrient concentration may be more influential than the presence of fruit esters (e.g. maleic acid diethyl ester) or the use of manifold "secret" mixtures as employed by older authors (Lederer, 1957; Steiner & Nikusch, 1994). In full agreement with

our results, Pinker (1970) and Nippel (1976) also observed highest attractiveness with simple red wine-sugar baits.

In sum, our methodological comparisons reveal that noctuid samples obtained by baiting can be used to characterize the diversity of a moth community even if different mixtures or presentation methods are employed. Methodology does affect sample sizes, but not estimates of community structure extracted from the samples. The better standardized both bait mixture and exposition are, the more reliable the results will be. Most importantly, our findings open up the venue to quantitative comparisons between studies at different locations or in different years. It is only required to obtain sufficiently large samples with a standardized recording technique, and with all species and individuals being noted. The objection (e.g. Steiner & Nikusch, 1994) that results of baiting surveys could *a priori* never be used for quantitative analyses is no longer tenable.

Climatic factors and the response to baits. As expected, the number of noctuid individuals and species attracted to baits was strongly affected by temperature: the warmer an evening the more moths appeared. Below 5°C very few moths were caught, and 9 out of 10 evenings when not a single noctuid showed up at the baits had mean temperatures below 7°C. This strong temperature-dependence corresponds well with the observations of Lederer (1959) at baits (the same applies to light-traps: Muirhead-Thomson, 1991).

Wind speed, in contrast, had no detectable influence, although the highest catches occurred at nights with but little wind. Wind may influence the effectiveness of light traps because it facilitates passive drift as well as migration flights (Hausmann, 1990; Muirhead-Thomson, 1991). Our data indicate that noctuid moths in search for food (the behavioural context in which they are attracted to baits) are less affected by wind, at least in the range of wind speeds recorded during our observation period (up to 4 m/s).

Rainfall occurred on 18 of 106 sampling evenings. We always noted at least some moths at the baits when it was raining. Numbers of attracted individuals were not noticeably lower on rainy nights. In July, the month with highest precipitation in 1997, for example, we caught between 12 and 57 individuals at

the baits on 6 evenings with rain, compared to 12–83 individuals on 12 nights without rain ($t_{16df} = 1.02$, $p > 0.3$). In early spring or autumn rainfall might even be advantageous for baiting, because then usually temperature does not drop as much as on cloudless nights. In any case, rainfall does not *per se* negatively affect bait-trapping success (see also Nippel, 1976).

Baiting versus attraction to artificial light sources. Today, most quantitative studies of moth communities use attraction to artificial light sources (termed “light-trapping” hereafter for convenience) as the basic method of sampling (e.g. Mörtter, 1988; Hausmann, 1990; Wolda *et al.*, 1994 for temperate regions; Robinson & Tuck, 1993, Chey *et al.*, 1997 for tropical communities). The applicability of quantitative diversity measures to light-trapping data has been extensively explored (Kempton & Taylor, 1974; Taylor *et al.*, 1976; Robinson & Tuck, 1996) and lends high credibility to results of such studies. However, as with any sampling method, light-trapping may be influenced by a large number of factors which all may bias or even heavily distort the results. Among the factors known to interfere with light-trapping efficiency are spectral composition of light stimulus, ambient temperature, light environment, lunar period and wind speed (review: Muirhead-Thompson, 1991). Most disturbingly, the physiological mechanisms underlying the attraction of moths to lights are not yet satisfactorily understood (Steiner & Nikusch, 1994). Even among closely related species the response to light sources may differ distinctly, and in any case the sampling procedure is based on an unnatural stimulus. Despite all these drawbacks, light-trapping data have empirically demonstrated their usefulness as a tool in community ecology and biodiversity research.

From the data presented in this study we conclude that bait-trapping data can be equally useful. Just as with light-trapping, a number of factors (such as ambient temperature, bait mixture, baiting technique) do affect the efficiency of recording, but the resulting samples can well be evaluated using much the same analytical techniques. There is no generally “superior” method of sampling nocturnal moths. Light sources have the advantage of attracting a larger taxonomic range of moths in usually larger numbers (thus increasing scope and decreasing time effort), but

often have the disadvantage of highly male-biased sex ratios in samples (Mörtter, 1988; Hausmann, 1990). Certain abundant species (such as in the genera *Amphipyra* or *Conistra*) are selectively under-represented at light as compared to records at baits. Bait-trapping, in contrast, utilizes a natural behavioural context and stimulus for attraction and yields more even sex ratios. In our sample the cumulative sex ratio was 1418 males to 1578 females (not all specimens were sexed; comparison against null hypothesis of even sex ratio: $\chi^2_{1df} = 8.55$, $p < 0.005$), thus even indicating a significant slight surplus of females. Bait-trapping therefore has the potential of revealing certain ecological aspects of a community (e.g. patterns of abundance and dominance) more accurately, but only that fraction of moths which utilize food resources similar to the exposed baits can be monitored (mainly Noctuidae, but also many Geometridae: Süssenbach & Fiedler, in press).

How does the diversity of our baiting samples rank in comparison with published data derived mostly from light-trapping? In Table 6 we have summarized examples from studies on noctuid moths where Williams' α has been presented explicitly, or could be calculated using the published data. Our diversity figures agree surprisingly well with other data obtained from light-trapping studies at medium latitudes in northern temperate zones. Only samples from industrially degraded subarctic landscapes in northernmost Russia or dense spruce plantations in western Germany have much lower, and samples from tropical moist forests much higher diversity. The close correspondence between our baiting data and the published light-trapping studies suggest that noctuid communities at latitudes between 45° and 55°N can be generally characterized by values of Williams' α ranging from 20–40, and that baiting is equally suitable to assess such values with sufficient accuracy. Unfortunately, most faunistic surveys we have come across were not conducted in a quantitative manner, or the data have not been published in a form which would allow *post hoc* calculations of diversity statistics. Hence, a critical comparative re-appraisal of diversity figures for different moth taxa and across geographical gradients still awaits to be done.

Discrimination between communities. Biodiversity research is not only concerned with adequately measuring "richness" of

communities (α -diversity), but also with discriminating between communities (β -diversity). With regard to the former, our samples indicate that noctuid α -diversity did not differ markedly between the two sites despite their different vegetation structure. The main difference was that on the BG site we captured about twice as many moth individuals as at the SM site. It is always critical to infer abundance from quantitative samples, because practically all sampling methods, at least for mobile organisms, are biased by factors such as activity or specific differences in catchability of the animals in question. Although our data indicate that at the SM site the guild of bait-visiting noctuids was less numerous, such a result needs to be validated by independent measures of abundance (e.g. based on larval densities) which we presently do not have.

However, with regard to species composition, both sites showed strong similarity. Similarity was particularly high if only presence of species was evaluated (Sørensen and Dice index: 77–85%), while the two communities could be more clearly separated using the abundance-based Morisita and Renkonen indices (55–60%). This finding agrees with Wolda's (1981) perception that Morisita's index is particularly suitable for assessing community similarity and again underlines that baiting data for noctuid moths are well suited for studies in community ecology.

Estimating diversity and species richness. Numerous methods of expressing "diversity" have been suggested, and most of these have advantages as well as disadvantages (see Southwood, 1978; Magurran, 1988; Lande, 1996 for thoughtful discussions). Two widely used ways of measuring diversity yielded congruent results in our study, namely fitting one parametric model (Williams' α) and probabilistic estimation of species richness by controlling for sample size effects (Hurlbert's rarefaction). Both these methods are highly suitable for analysing quantitative bait-trapping data, because they effectively suppress the bias resulting from variation in sample size and sampling effort, as long as all samples used for the calculations have been assembled with the same standardized methods, are randomly drawn from the community, and are sufficiently large.

A disadvantage common to both methods is that they produce rather abstract figures. For many purposes, including conservation

biology, the “real” number of species in a community would provide a more meaningful and convincing measure. However, at least with mobile organisms, it is in principle impossible to be sure that one has ever sampled a community exhaustively (i.e. that further sampling would not add any more species to the records). The collecting effort necessary to approach real saturation increases with species richness and diversity of a community.

Extrapolation from samples to communities might provide a solution to that dilemma (Colwell & Coddington, 1994). In the present study we have tested some extrapolation methods suggested by Colwell (1997). These methods have not yet been widely used, but tests using samples of Mexican hawkmoths (León-Cortés *et al.*, 1998) as well as model data sets (Peterson & Slade, 1998) both arrive at the conclusion that a Michaelis-Menten process (termed Clench’s function there) yields the most robust asymptotic estimation and that Chao’s estimates likewise give robust estimates.

From our own data set, the following patterns emerge. (1) As expected, all extrapolations arrive at higher numbers than actually recorded species. Despite very intensive sampling effort at neither site have we achieved a complete inventory of the noctuid guild attractable to baits. (2) For both habitats, the estimators converge to similar figures (123–145 spp. at the BG site, 99–108 spp. at SM), which would suggest that “true” species richness lies somewhere in these intervals. (3) The estimators perform differently on the two data sets. In the larger BG sample, the randomized species accumulation after the Michaelis-Menten model produces a low estimate, while it yields a medium estimate in the smaller SM sample. This could be an effect of sample size: all else being equal, the larger the sample is, the closer the randomized hyperbolic function should be to its asymptote. (4) The Michaelis-Menten estimator changed less when sample sizes were “experimentally” halved. The four other estimators showed no uniform response when applied to rarified samples.

How realistic are the estimated species numbers? No data are available exactly for our two study sites, but from the vicinity of Bayreuth (radius about 10 km) at least 246 Noctuidae species have been recorded thus far (Wolf, 1981; Süssenbach & Fiedler

in press). According to the multi-volume monograph of the noctuid fauna of SW Germany (Ebert, 1997; Steiner, 1997; Steiner & Ebert, 1998), about 61% of all noctuid species have been observed visiting fruit baits. Applied to the north-eastern Bavarian fauna, one might therefore expect a regional pool of 150 species (61% of 246 spp.) as potentially attracted by baits. Then, estimated totals of about 100 (SM site) or 130 (BG site) bait-visiting noctuid species are not unrealistic.

The applicability and validity of species richness estimators needs to be tested against more data sets derived from a broader (taxonomical, methodological, geographical) range of studies. The newly proposed methods from Colwell (1997; i.e. *ACE* and *ICE*), in particular, require further testing. Though promising in theory and from the results on the entire data sets, their unstable performance when applied to subsamples throws doubt on their usefulness. As it stands, the Michaelis-Menten model appears to be a robust, albeit conservative method of estimating total species richness (see also León-Cortés *et al.*, 1998; Peterson & Slade, 1998).

Baiting and recording effort. A final point worth discussion is the sampling effort needed to assemble meaningful data sets. Sampling effort is usually a cost factor (time and manpower needed to conduct the sampling, but also for mounting, sorting, and identification). Hence it seems advisable to limit the sampling effort and sample sizes so as to optimize the relationship between costs (of labour and materials) and benefits (reliability of results and conclusions). For light-trapping surveys, such strategies have already been proposed and tested (Thomas & Thomas, 1994).

We have used two approaches to assess the effect of reduced sampling effort. First, we compared the data subsets which were accumulated during either the first, or second, sampling evening of each week. Although subsamples covered only 70–80% of the species as compared to the total samples, estimates of α -diversity were not affected significantly. Subsamples were also very similar to each other in species composition and abundance. However, most estimates of true species richness tended to decrease (and confidence limits to increase) for subsamples. Thus, reducing sampling effort to one evening per site and per week did not change conclusions about α - and β -diversity, but certainly would

be less sufficient for studies aimed at compiling species inventories or estimating “true” richness.

Rarefaction methods provide a second approach to study effects of sampling effort. The Hurlbert curves show that with 500 moths sampled per site about 60–80 species will be covered, corresponding to 25 sampling evenings as revealed by Shinozaki rarefaction. The Shinozaki model assumes that with each sampling unit all species have the same likelihood of being captured. Given the strong climatic seasonality at the study sites, and the profound variation between evenings in the number of moths attracted, this assumption is oversimplistic. If sampling is limited to weather conditions where larger numbers of moths can be expected (i.e. on evenings with $>7^{\circ}\text{C}$ mean temperature, and concentrating the sampling in summer and autumn, where abundance and diversity of moths at the baits was higher than in spring: Süssenbach & Fiedler in press), then as few as 10–15 sampling nights per site and season should reveal much of the community patterns, but at a cost with regard to species coverage. As a methodological standard, a simple saturated red wine-sugar bait mixture exposed on suspended pieces of cloth at a height of 2 m above ground should be sufficient for such purposes.

Sampling methods should always be selected according to the aim of a study. As we have shown above, baiting noctuids in a standardized manner can easily reveal sufficient information to characterize the noctuid community, its diversity and principal abundance structure. Reliable results can be expected even with much reduced sampling effort. When species inventories are the objective (which from statistical reasons alone will almost never be “complete”), light-trapping (with its broader taxonomic coverage) or a combination of recording methods may be chosen as more appropriate. However, for many typical questions of community ecology and biodiversity research, including conservation biology, it is no longer justified to disregard baiting as a potentially powerful tool.

Acknowledgements

We are deeply indebted to Dr. Gaden S. Robinson (London) and one anonymous reviewer for their manifold constructive and linguistic comments which substantially improved the manuscript.

Further thanks go to Jan Beck who drew our attention to various references, to Dr. Roland Achtziger (now Freiberg) who provided access to the computer program used for calculating the Shinozaki rarefaction, and to Dr. Wolfgang Nässig (Frankfurt) who kindly read and criticized an earlier manuscript version. The district government (Regierung von Oberfranken, Bayreuth) granted permission to conduct the present study. Dr. Gregor Aas (director of the Botanical Garden, Bayreuth University) provided free access to one of our study sites.

References

- ACHTZIGER, R., NIGMANN, U. & ZWÖLFER, H., 1992. Rarefaction-Methoden und ihre Einsatzmöglichkeiten bei der zooökologischen Zustandsanalyse und Bewertung von Biotopen. — *Z. Ökol. Naturschutz* 1: 89–105.
- BAKKE, A., 1974. Abundance and diversity in the fauna of nocturnal moths at two sites in South Norway. — *Norsk ent. Tidsskr.* 21: 173–184.
- BARLOW, H. S. & WOIWOD, I. P., 1989. Moth diversity of a tropical forest in Peninsular Malaysia. — *J. Trop. Ecol.* 5: 37–50.
- BUTLER, L. & KONDO, V., 1991. Macrolepidopterous moths collected by blacklight trap at Cooper's Rock State Forest, West Virginia: a baseline study. — *Bull. agric. Forest exper. Station, West Virginia Univ.* 705: 1–25.
- CHEY, V. K., HOLLOWAY, J. D. & SPEIGHT, M. R., 1997. Diversity of moths in forest plantations and natural forests in Sabah. — *Bull. ent. Res.* 87: 371–385.
- CLEVE, K., 1971. Der Anflug der Nachtschmetterlinge an das Licht und an den Köder. — *Ent. Z.* 12: 121–136.
- COLWELL, R. K., 1997. EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. User's guide and application published at: <http://viceroy.eeb.uconn.edu/estimates>.
- COLWELL, R. C. & CODDINGTON, J. A., 1994. Estimating terrestrial biodiversity through extrapolation. — *Phil. Trans. R. Soc. Lond.* B 345: 101–118.
- DEVRIES, P. J., MURRAY, D., & LANDE, R., 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. — *Biol. J. Linn. Soc.* 62: 343–364.
- EBERT, G. (ed.), 1997. Die Schmetterlinge Baden-Württembergs. Band 3 (Nachtfalter I). — Eugen Ulmer, Stuttgart. 575 pp.
- FISHER, R. A., CORBET, A. S. & WILLIAMS, C. B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. — *J. Anim. Ecol.* 12: 42–58.
- HAUSMANN, A., 1990. Zur Dynamik von Nachtfalter-Artenspektren. Turnover und Dispersionsverhalten als Elemente von Verbreitungsstrategien. — *Spixiana*, Suppl. 16: 1–222.
- HAYEK, L.-A. C., & BUZAS, M. A., 1997. Surveying natural populations. — Columbia Univ. Press, New York. xvi + 563 p.

- HEINRICH, B., & MOMMSEN, T. P., 1985. Flight of winter moths near 0°C. — *Science* 228: 177–179.
- HEPPNER, J. B., 1991. Faunal regions and the diversity of Lepidoptera. — *Trop. Lepid.* 2, Suppl. 1: 1–85.
- HOLLOWAY, J. D., 1984. The larger moths of the Gunung Mulu National Park: a preliminary assessment of their distribution, ecology, and potential as environmental indicators. — *Sarawak Mus.J.*, N.S. 30 (51): 149–190.
- HOLLOWAY, J. D., KIRK-SPRIGGS, A. H. & CHEY, V. K., 1992. The response of some rain forest insect groups to logging and conversion to plantation. — *Phil. Trans. R. Soc. Lond. B* 335: 425–436.
- HURLBERT, S. H., 1971. The nonconcept of species diversity: a critique and alternative parameters. — *Ecology* 52: 577–586.
- KEMPTON, R. A. & TAYLOR, L. R., 1974. Log-series and log-normal parameters as diversity discriminants for the Lepidoptera. — *J. Anim. Ecol.* 43: 381–399.
- KOZLOV, M. V., JALAVA, J., LVOVSKY, A. L. & MIKKOLA, K., 1996. Population densities and diversity of Noctuidae (Lepidoptera) along an air pollution gradient on the Kola Peninsula, Russia. — *Entom. Fenn.* 7: 9–15.
- KREBS, C. J., 1989. Ecological methodology. — Harper Collins Publishers, New York. 654 p.
- LAMAS, G., ROBBINS, R. K., & HARVEY, D. J., 1991. A preliminary survey of the butterfly fauna of Pakitza, Parque Nacional del Manu, Peru, with an estimate of its species richness. — *Publ. Mus. Hist. nat. Univ. Nacion. Mayor de San Marcos, Ser. A (Zool.)* 40: 1–19.
- LANDE, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. — *Oikos* 76: 5–13.
- LEDERER, G., 1959. Nahrungssuche und Nahrungsaufnahme der in der Dämmerung und in der Nacht fliegenden Lepidopteren. — *Ent. Z., Frankf.a.M.* 69: 25–40, 42–56, 67–80, 94–100, 109–124, 126–132, 136–144.
- LEE, S.-M. & CHAO, A., 1994. Estimating population size via sample coverage for closed capture-recapture models. — *Biometrics* 50: 88–97.
- LEÓN-CORTÉS, J. L., SOBERÓN-MAINERO, J. & LLORENTE-BOUSQUETS, J., 1998. Assessing completeness of Mexican sphinx moth inventories through species accumulation curves. — *Diversity & Distributions* 4: 37–44.
- MAGURRAN, A. E., 1988. Ecological diversity and its measurement. — Croom Helm, London. 179 p.
- MAWDESLEY, N., 1996. The theory and practice of estimating regional species richness from local samples. *In*: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds.): Tropical rainforest research – current issues. — Dordrecht, Kluwer. Pp. 193–214.
- MEINEKE, T., 1995. Nachtfalter in der naturschutzrelevanten Raumplanung: Grundlagen, Methoden, Auswertung. — *Schr. Reihe Landschaftspfl. & Natursch.* 43: 79–106.
- MÖRTER, R., 1988. Vergleichende Untersuchungen zur Faunistik und Ökologie der Lepidopteren in unterschiedlich strukturierten Waldflächen im Kottenforst bei Bonn. — *Neue ent. Nachr.* 21: 1–182.
- MUIRHEAD-THOMSON, R. C., 1991. Trap responses of flying insects. — Academic Press, London. xii + 287 p.

- MÜLLER-SCHÄRER, H., LEWINSOHN, T. M. & LAWTON, J. H., 1991. Searching for weed biocontrol agents – when to move on? — *Biocontrol Sci. Technol.* 1: 271–280.
- NIPPEL, F., 1976. Erfahrungen bei dem Köderfang von Schmetterlingen. — *Mitt.int.ent.Ver.* 3: 17–35.
- PERSSON, B., 1971. Flight activity of noctuids – a study based on light trap experiments in south Sweden. — PhD thesis, Lund Univ., 59 pp. + Appendix (38 tables, 99 figures).
- PETERSON, A. T., & SLADE, N. A., 1998. Extrapolating inventory results into biodiversity estimates and the importance of stopping rules. — *Diversity & Distributions* 4: 95–105.
- PINKER, R., 1970. Ratschläge für den modernen Licht- und Köderfang. — *Ent.Z., Frankf.a.M.* 80: 241–244.
- PRESTON, F. W., 1948. The commonness, and rarity, of species. — *Ecology* 29: 254–283.
- ROBINSON, G. S. & TUCK, K. R., 1993. Diversity and faunistics of small moths (Microlepidoptera) in Bornean rainforest. — *Ecol.Entomol.* 18: 385–393.
- ROBINSON, G. S. & TUCK, K. R., 1996. Describing and comparing high invertebrate diversity in tropical forest – a case study of small moths in Borneo. In: Edwards, D. S., Booth, W. E. & Choy, S. C. (eds.): *Tropical rainforest research – current issues.* — Dordrecht, Kluwer. Pp. 29–42.
- SACHS, L., 1992. *Angewandte Statistik.* 7th ed. — Springer Verlag, Berlin. xxxii + 846 p.
- SIMBERLOFF, D., 1978. Use of rarefaction and related methods in ecology. In: Dickson, K. L. & Livingston, R. J. (eds.): *Biological data in water pollution assessment: quantitative and statistical analyses.* — Amer. Soc. Testing and Materials. Pp. 150–165.
- SKOU, P., 1991. *Nordens ugler.* — Apollo Books, Stenstrup. 565 pp.
- SOUTHWOOD, T. R. E., 1978. *Ecological methods with particular reference to the study of insect populations.* 2nd ed. — Chapman & Hall, London. xxiv + 524 pp.
- STEINER, A., 1997. Die Schmetterlinge Baden-Württembergs, Band 6: Nachtfalter IV. Noctuidae (Fortsetzung). — Eugen Ulmer, Stuttgart. 622 p.
- STEINER, A. & EBERT, G., 1997. Die Schmetterlinge Baden-Württembergs, Band 7: Nachtfalter V. Noctuidae (Schluß). — Eugen Ulmer, Stuttgart. 582 p.
- STEINER, A., & NIKUSCH, I. 1994. Beobachtungsmethoden bei Nachtfaltern. Pp. 28–50 in: Ebert, G. (ed.): *Die Schmetterlinge Baden-Württembergs. Band 3 (Nachtfalter I).* — Eugen Ulmer, Stuttgart.
- SÜSSENBACH, D. & FIEDLER, K., 1999. Faunistische Ergebnisse einer Köderfangstudie an Eulenfaltern (Noctuidae) im Obermain-Hügelland. — *Ber.naturw.Ges.Bayreuth* 24 (in press).
- TAYLOR, L. R., KEMPTON, R. A. & WOIWOD, I. P., 1976. Diversity statistics and the log-series model. — *J.Anim.Ecol.* 45: 255–272.
- THOMAS A. W., 1996. Light-trap catches of moths within and above the canopy of a northeastern forest. — *J.Lepid.Soc.* 50: 21–45.

- THOMAS A. W. & THOMAS, G. M., 1994. Sampling strategies for estimating moth species diversity using a light trap in a northeastern softwood forest. — *J.Lepid.Soc.* 48: 85–105.
- WOLDA, H., 1981. Similarity indices, sample size and diversity. — *Oecologia* 50: 296–302.
- WOLDA, H., MAREK, J., SPITZER, K. & NOVAK, I., 1994. Diversity and variability of Lepidoptera populations in urban Brno, Czech Republic. — *Eur.J.Entomol.* 91: 213–226.
- WOLF, W., 1981. Die sogenannten Großschmetterlinge des nordöstlichen Bayreuther Umlandes (Insecta, Lepidoptera). Ein Beitrag zur Kenntnis des Obermain-Hügellandes. — *Ber.naturw.Ges.Bayreuth* 17: 145–254.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: [Nota lepidopterologica](#)

Jahr/Year: 1999

Band/Volume: [22](#)

Autor(en)/Author(s): Süssenbach Dirk, Fiedler Konrad

Artikel/Article: [Noctuid moths attracted to fruit baits: testing models and methods of estimating species diversity 115-154](#)