



# Nested assemblages of Orthoptera species in the Netherlands: the importance of habitat features and life-history traits

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## ABSTRACT

**Aim** Species communities often exhibit nestedness, the species found in species-poor sites representing subsets of richer ones. In the Netherlands, where intensification of land use has led to severe fragmentation of nature, we examined the degree of nestedness in the distribution of Orthoptera species. An assessment was made of how environmental conditions and species life-history traits are related to this pattern, and how variation in sampling intensity across sites may influence the observed degree of nestedness.

**Location** The analysis includes a total of 178 semi-natural sites in the Pleistocene sand region of the Netherlands.

**Methods** A matrix recording the presence or absence of all Orthoptera species in each site was compiled using atlas data. Additionally, separate matrices were constructed for the species of suborders Ensifera and Caelifera. The degree of nestedness was measured using the BINMATNEST calculator. BINMATNEST uses an algorithm to sort the matrices to maximal nestedness. We used Spearman's rank correlations to evaluate whether sites were sorted by area, isolation or habitat heterogeneity, and whether species were sorted by their dispersal ability, rate of development or degree of habitat specificity.

**Results** We found the Orthoptera assemblages to be significantly nested. The rank correlation between site order and sampling intensity was high. The degree of nestedness was lower, but remained significant when under- and over-sampled sites were excluded from the analysis. Site order was strongly correlated with both size of sample site and number of habitat types per site. Rank correlations showed that species were probably ordered by variation in habitat specificity, rather than by variation in dispersal capacity or rate of development of the species.

**Main conclusions** Variation in sampling intensity among sites had a strong impact on the observed degree of nestedness. Nestedness in habitats may underlie the observed nestedness within the Orthoptera assemblages. Habitat heterogeneity is closely related to site area, which suggests that several large sites should be preserved, rather than many small sites. Furthermore, the results corroborate a focus of nature conservation policy on sites where rare species occur, as long as the full spectrum of habitat conditions and underlying ecological processes is secured.

## Keywords

BINMATNEST, nature conservation, nestedness, Orthoptera, recording bias, species–area relationship, species occurrence data bases, the Netherlands.

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## INTRODUCTION

It is widely acknowledged that species richness is neither equally nor randomly distributed across the Earth's surface. Since the beginning of the 19th century, scientists have been trying to explain and generalize observed patterns in species richness. One of the general laws in ecology concerns the relationship between species and area. The theory of island biogeography (MacArthur & Wilson, 1967) attempts to explain the form of the species–area relationship: larger islands will eventually support more species than smaller ones, as the rate of extinction increases with decreasing size. This relationship has been demonstrated for many different taxa and habitat types.

Nested subset theory provides a more comprehensive view on the species–area relationship, incorporating species composition. The nested subset theory refers to the situation where species present at species-poor sites constitute a subset of the species from richer locations (Patterson & Atmar, 1986). Nested subset structure has been reported for many communities in naturally fragmented landscapes such as islands (Kadmon, 1995; Lomolino, 1996; Yiming *et al.*, 1998) and mountain peaks (Lomolino & Davis, 1997; Fleishman & Murphy, 1999; Bruun & Moen, 2003) as well as anthropogenically fragmented landscapes (Fernández-Juricic, 2002; Fischer & Lindenmayer, 2005). The literature on nestedness comprises a wide range of taxonomic groups, with an emphasis on birds and mammals. Although several studies incorporate insect data in their analysis, few studies exist where the presence and causes of nestedness within insect assemblages is examined in depth (e.g. Fleishman & Murphy, 1999; Fleishman *et al.*, 2001, 2002). However, there is a strong need to study insect taxa, as they make up the largest part of known biodiversity, fulfil important ecosystem functions and comprise many endangered species (Ponder & Lunney, 1999).

Nested subset analyses allow us to study both species richness and species composition at the same time. Therefore nested subset analysis has generated much interest among conservation biologists. Some authors claim that a positive diagnosis on nestedness can, for example, be used as a tool to determine whether it is better to establish a single large reserve or several small ones (Patterson, 1987; Cutler, 1991; Boecklen, 1997). Others find in the observation of nestedness a justification for the use of rare species as indicators for overall species diversity (Fleishman *et al.*, 2002). However, the observation of nested patterns alone does not provide any clues for nature conservation, as long as the mechanisms underlying nestedness are not fully understood (Simberloff & Martin, 1991). Many studies have tried to elucidate the mechanisms underlying nestedness. The main drivers of nestedness identified so far include selective colonization (Darlington, 1957; Cook & Quinn, 1995; Kadmon, 1995), selective extinction (Patterson & Atmar, 1986; Cutler, 1991), nestedness of habitats (Blake, 1991; Cook & Quinn, 1995; Honnay *et al.*, 1999), interspecific variation in tolerance to environmental conditions (Worthen *et al.*, 1996), and passive sampling

(Andrén, 1994; Cutler, 1994). The latter can cause nestedness as larger areas may contain more species simply by chance, because they constitute larger samples (Connor & McCoy, 1979; Haila *et al.*, 1993).

In the Netherlands, dense human population and economic growth have altered the natural landscape in fundamental ways, resulting in a reduced overall extent and increased fragmentation of natural areas. We investigated whether the spatial distribution of Orthoptera species in natural areas in the Netherlands is organized in a nested manner, and tried to elucidate the mechanisms that could underlie this type of distribution pattern. Nestedness can be regarded as the result of a species pool being filtered by local environmental conditions, in combination with the ability of the species to cope with these conditions (Wright *et al.*, 1998; Cook *et al.*, 2004). We therefore assessed how nestedness is related to the environmental variables area, spatial heterogeneity and isolation, and to the species life-history traits dispersal ability, rate of development and degree of habitat specificity.

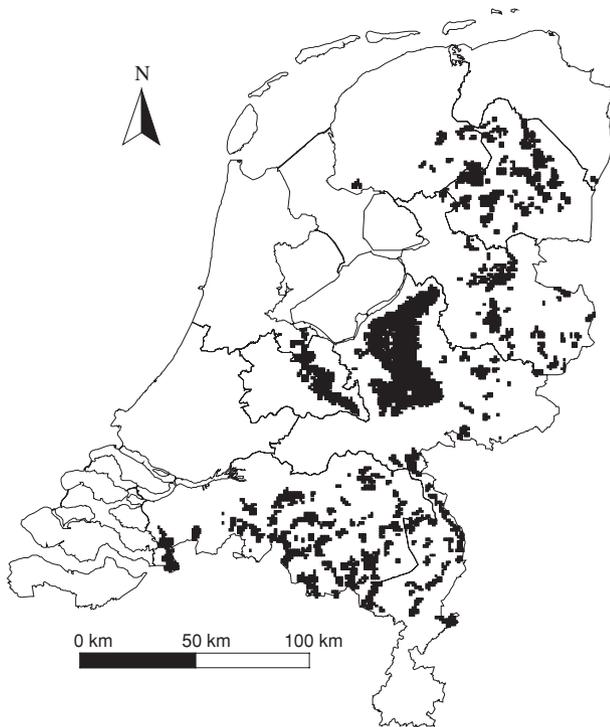
Data on the occurrence of Orthoptera species were derived from a data base of faunistic occurrences in the Netherlands. Although the Netherlands is one of the countries with the most extensive information on biodiversity, unevenness in sampling intensity does pose a problem because data were collected in an *ad hoc* way. Analogous to passive sampling, variation in sampling intensity among sites may lead to a nested structure in a given data set. At a given sampling intensity, abundant species have a higher probability of being represented in a given biota than rare species (Wright, 1991). With increasing sampling intensity, the chance of encountering rare species increases. Also, vagrant species (one-off occurrences) can cause a major overestimation of, for example, the species richness of a site if sampling effort is excessive (Grinnell, 1922; Williams *et al.*, 2002). Uneven sampling intensity across sites can thus lead to a considerable overestimation of the degree of nestedness. To account for such recording bias, we investigated how differences in sampling intensity across sites influenced the observed nested patterns.

## MATERIALS AND METHODS

### Research area

We selected 178 sites (Fig. 1) on Pleistocene sandy soil with a land cover dominated by semi-natural vegetation types. To this purpose, a grid of 1 × 1-km squares was superimposed on a detailed digital land-cover map comprising 39 land-cover classes derived from aerial and satellite imagery (Alterra, 2001). We took into account only those grid squares of which > 75% of the surface was covered by semi-natural vegetation types. Neighbouring grid squares were merged, forming the sampling units of this research.

The sampling sites ranged from 1 to 1081 km<sup>2</sup> in size (average 19.75 km<sup>2</sup>). All sites were clearly isolated from each other. The degree of isolation was measured as the distance to



**Figure 1** Geographical position of selected sites.

the nearest site. Isolation ranged from 0.1 to 14 km (average 1.7 km).

From the land-cover map, 13 habitat types (agricultural land, bare soil, coniferous forest, deciduous forest, drift sand, freshwater, heathland, marsh, natural grassland, pasture, peat bog, shrub and urbanized area) were extracted, taking into account Orthoptera requirements. Although somewhat less detailed, this classification largely corresponds to that generally applied for Orthoptera in the Netherlands (Kleukers & van Nieukerken, 2004). For each site, we counted the number of different habitat types present and calculated Simpson's index of evenness regarding these habitat types:

$$E_{1/D} = (1/D)/S$$

where  $S$  is the number of habitat types in a site, and:

$$D = \sum [n_i(n_i - 1)/N(N - 1)]$$

where  $n_i$  = the area of the  $i$ th habitat type and  $N$  = the total area. The measure ranges from 0 to 1.

### Species occurrence data set

The data on the occurrence of Orthoptera species were derived from the European Invertebrate Survey (EIS Nederland) data base. This data base comprises a diverse assortment of museum records, data from monitoring schemes, species lists of inventory trips, and incidental occurrence records collected over more than a century by many volunteers. These data were usually collected in a rather *ad hoc* fashion, resulting in taxonomically, geographically and

temporally biased records (Rich, 1998; Dennis *et al.*, 1999). Therefore the data quality varies, and the available records of species occurrences may not adequately reflect species composition of a given location. Nevertheless, this is the only type of nationwide data available.

The Orthoptera species occurrence data set contains about 85,500 records on the distribution of 45 species, collected between 1900 and 2002. For this study we used only the post-1965 data, as the older data are probably no longer representative because of the major land-use changes of the 1960s: environmental conditions in the Netherlands have gradually changed since then. However, there is always a trade-off between data quantity and accuracy with the kind of data used in this study. Species-occurrence data are available at a resolution of  $1 \times 1$  km<sup>2</sup> and are tabulated in a presence-absence matrix. For species names and the division into suborders, we followed the taxonomy of Rentz (1991). The degree of habitat specificity (Table 1) was derived from the distribution atlas (Kleukers & van Nieukerken, 2004). For all other data on the life-history traits of the individual species, we relied on the expert knowledge provided by EIS Nederland.

### Analytical methods

#### Quantification of nestedness

To quantify the level of nestedness, a large number of metrics have been proposed (e.g. Wright *et al.*, 1998; Rodríguez-Gironés & Santamaría, 2006). In this study we used the binary matrix nestedness temperature calculator (BINMATNEST; Rodríguez-Gironés & Santamaría, 2006). BINMATNEST is a recent improvement of the nested-temperature method of Atmar & Patterson (1993), using a more robust algorithm for matrix packing. In BINMATNEST, rows and columns are permuted in such a way that matrix nestedness is maximized: ordering is not done according to species richness or site area. BINMATNEST calculates a temperature (ranging from 0 to 100°C) of the deviation of a particular data set from the ideal nested structure. Deviation from perfect nestedness is assessed by comparing the observed species occurrence matrix, rearranged to gain maximum order, with a perfectly nested matrix with the same rank and fill. Highly nested assemblages, exhibiting fewer deviations from perfect nestedness, therefore score a lower temperature than less nested assemblages with many deviations. To determine the statistical significance of the observed matrix temperature, it is compared with the distribution of simulated temperatures produced by randomization (100 iterations) of the matrix. In the null model applied, the probability of each cell being occupied is the average of the probabilities of occupancy of its row and column.

#### Determinants of nestedness

The order in which sites and species are sorted by the BINMATNEST algorithm can be compared with numerous

**Table 1** Life-history traits of Orthoptera species.

Species	Rate of development	Habitat specificity	Dispersal capacity	Passive dispersal
<b>Ensifera</b>				
<i>Acheta domesticus</i>	6	1	1	Y
<i>Conocephalus discolor</i>	12	3	3	
<i>Conocephalus dorsalis</i>	12	4	3	
<i>Decticus verrucivorus</i>	24	3	2	
<i>Ephippiger ephippiger</i>	24	1	1	
<i>Gampsocleis glabra</i>	24	1	2	
<i>Gryllotalpa gryllotalpa</i>	24	1	2	Y
<i>Gryllus campestris</i>	12	2	3	
<i>Leptophyes punctatissima</i>	12	4	1	Y
<i>Meconema thalassinum</i>	12	4	3	
<i>Metrioptera brachyptera</i>	24	1	2	
<i>Metrioptera roeselii</i>	12	2	3	
<i>Nemobius sylvestris</i>	24	2	1	
<i>Phaneroptera falcata</i>	12	2	3	
<i>Pholidoptera griseoaptera</i>	24	3	1	Y
<i>Tettigonia cantans</i>	24	1	1	
<i>Tettigonia viridissima</i>	24	6	3	
<b>Caelifera</b>				
<i>Chorthippus albomarginatus</i>	12	2	2	
<i>Chorthippus biguttulus</i>	12	5	3	
<i>Chorthippus brunneus</i>	12	5	3	
<i>Chorthippus mollis</i>	12	3	2	
<i>Chorthippus montanus</i>	12	2.5	2	
<i>Chorthippus parallelus</i>	12	2	3	
<i>Chorthippus vagans</i>	12	3	2	
<i>Chrysochraon dispar</i>	12	2	2	
<i>Myrmeleotettix maculatus</i>	12	2	1	
<i>Oedipoda caerulescens</i>	12	2	2	
<i>Omocestus rufipes</i>	12	2	2	
<i>Omocestus viridulus</i>	12	2	2	
<i>Stenobothrus lineatus</i>	12	1.5	2	
<i>Stenobothrus stigmaticus</i>	12	1.5	1	
<i>Stethophyma grossum</i>	12	3	2	
<i>Tetrix bipunctata</i>	12	1	2	
<i>Tetrix ceperoi</i>	12	2	3	
<i>Tetrix subulata</i>	12	3	3	
<i>Tetrix tenuicornis</i>	12	3	2	
<i>Tetrix undulata</i>	12	3	2	

Rate of development in months, habitat specificity ranked 1 (highly specific) to 6 (generalists). Dispersal capacity: 1 = without wings, not very mobile; 2 = sometimes with functional wings, not found outside the mating biotope; 3 = (sometimes) with functional wings, regularly found outside the mating biotope. Passive dispersal by humans, animals, floating, etc: Y = yes.

possible independent correlates. Spearman's rank correlation was used to evaluate the influence of site area, habitat heterogeneity and isolation, and of species dispersal ability, rate of development and habitat specificity on the degree of nestedness of the assemblages. From the presence-absence matrix packed to maximal nestedness by BINMATNEST, we took the resulting site order and successively compared it with the area, degree of isolation and heterogeneity of the sites. The same procedure was followed for species order according to BINMATNEST, and species dispersal ability, rate of development and habitat specificity. A significant correlation between the

species and site order according to BINMATNEST, and their order in accordance with a given factor, indicates a possible influence of that factor on the formation of the nested structure (Patterson & Atmar, 2000).

#### *Coping with differences in sampling intensity*

Uneven distribution of recording data is a well known problem with the kind of species-occurrence data bases used in this study (Rich, 1998; Dennis *et al.*, 1999). To identify the effect of differences in sampling intensity among sites on the observed

patterns, we calculated the sampling intensity (number of records per km<sup>2</sup>) for each site. In three steps, we then removed the 5th, 10th and 25th upper and lower percentiles of the sites ranked according to their sampling intensity, thus filtering out both undersampled and oversampled sites.

## RESULTS

The Orthoptera assemblages were significantly nested ( $T = 7.90$ ; Table 2). The pattern was even more strongly expressed when only the species belonging to suborder Ensifera were taken into account ( $T = 3.31$ ). The degree of nestedness of species assemblages of the suborder Caelifera did not differ much from that of the Orthoptera taxon as a whole ( $T = 8.12$ ). It should be noted, however, that a straightforward comparison of nestedness temperatures is difficult because of minor differences in matrix size and fill (Greve & Chown, 2006; Rodríguez-Gironés & Santamaría, 2006). When sites with extreme sampling intensities were excluded from the analysis, the degree of nestedness decreased. Temperature rose to 13.34°C for the entire Orthoptera matrix (Table 2; Appendix S1 in Supplementary Material) when filtering out under- and

oversampled sites. This suggests that differences in sampling intensity can result in a considerable overestimation of the degree of nestedness. However, the degree of nestedness within the more evenly sampled sites remained significant ( $P < 0.001$ ).

Spearman's rank correlation indicated that the site order, as determined by BINMATNEST, was very similar to the order obtained when ordering the sites in accordance with their area, sampling intensity, or number of different habitat types present (Table 3). The correlations between site order and degree of isolation, and between site order and Simpson's index of habitat heterogeneity, are less strong. When stepwise omitting sites with low (5th, 10th, 25th percentiles) and high (95th, 90th, 75th percentiles) sampling intensity from the analysis, the influence of sampling intensity declined until it became non-significant. Site order then correlated most strongly with area (0.810,  $P < 0.01$ , Spearman's correlation) and the number of different habitat types (0.594,  $P < 0.01$ , Spearman's correlation). However, it should be noted that area and the number of habitat types present in that site are themselves correlated (0.671,  $P < 0.01$ , Spearman's correlation). Heterogeneity of habitat types ( $E$ ) was negatively

**Table 2** Summary of results obtained from calculation of nestedness temperature  $T$  (°C) of Orthoptera matrices.

	Number of species	Number of areas	Fill (%)	$T$ (°C)
All species				
All areas	37	178	24.4	7.90**
Upper and lower 5th percentile excluded	37	160	24.9	8.67**
Upper and lower 10th percentile excluded	36	144	25.3	10.34**
Upper and lower 25th percentile excluded	32	84	28.3	13.34**
Caelifera				
All areas	20	175	30.5	8.12**
Upper and lower 25th percentile excluded	18	84	34.3	11.89**
Ensifera				
All areas	17	164	19.4	3.31**
Upper and lower 25th percentile excluded	14	81	21.3	4.56**

Different sets of areas are analysed according to sampling intensity. All results presented here correspond to  $PopSize = 35$ ,  $TourSize = 7$  and  $nbGen = 5000$ . \*\* $P < 0.001$ .

**Table 3** Relationships (Spearman's  $R$  rank correlations) between ranking order of areas after packing to maximal nestedness using BINMATNEST and order of areas after rearranging the matrix regarding the explanatory variables.

	Area size (km <sup>2</sup> )	Isolation (km)	Number of habitat types	Simpson's index of evenness in habitat	Sampling intensity
All species					
All areas	0.642**	-0.194**	0.406**	-0.202**	0.503**
Equally sampled areas	0.810**	-0.347**	0.594**	-0.431**	0.07
Caelifera					
All areas	0.637**	-0.249**	0.515**	-0.193**	0.578**
Equally sampled areas	0.695**	-0.410**	0.608**	-0.438**	0.115
Ensifera					
All areas	0.495**	-0.119	0.225**	-0.173**	0.401**
Equally sampled areas	0.559**	-0.174	0.240*	-0.254*	0.106

Correlation significant at \*0.05 level; \*\*0.01 level.

**Table 4** Relationships (Spearman's *R* rank correlations) between ranking order of species after packing to maximal nestedness using BINMATNEST and order of species after rearranging the matrix according to life-history traits (Table 1).

	Rate of development	Dispersal capacity	Habitat specificity
All species			
All areas	-0.210	0.290**	0.486**
Equally sampled areas	-0.07	0.167	0.415**
Caelifera			
All areas	-	0.233	0.349
Equally sampled areas	-	0.180	0.361
Ensifera			
All areas	-0.224	0.364	0.619**
Equally sampled areas	0.040	0.207	0.495*

Correlation significant at \*0.05 level; \*\*0.01 level.

correlated with site order, and this correlation was weaker than between site order and the number of habitat types present in a site. Dividing the Orthoptera into the suborders Caelifera and Ensifera produced similar results, with the difference that site order for the Caelifera was more strongly associated to the number of habitat types per site than for the Ensifera assemblages.

Table 4 shows how species order according to life-history traits correlates with the observed rank order produced by BINMATNEST. The correlation between species order and life-history traits is weaker than the correlation between site order and environmental factors. Nevertheless, we found a significant correlation of species order and habitat specificity, and of species order and dispersal capacity. However, dispersal capacity was no longer significantly correlated with species order when under- and oversampled sites were excluded from the analysis. Habitat specificity of the individual species is the factor most probably promoting nestedness within the Orthoptera assemblages. When all species are taken into account, we found a correlation of 0.415 ( $P < 0.01$ ) between species order and habitat specificity. For the Ensifera, this correlation appeared to be somewhat higher, but of less strong significance (0.495,  $P < 0.05$ ).

## DISCUSSION

We found a high degree of nestedness within the Orthoptera assemblages. This pattern was expressed most strongly when only the species belonging to the suborder Ensifera were taken into account. The difference between the Caelifera and Ensifera assemblages can be explained from life-history traits of the species. The Ensifera species are highly diverse, varying in body size and having a broad range of diet preferences. The eggs of some Ensifera species can be dispersed passively over large distances (Table 1). The Caelifera also show a large variety in body size, but feed only on plant material and overall have a lower dispersal capacity (Table 1). Thus the Ensifera

assemblages depend on a broader range of resources and have a wider dispersal range, and would be expected to show a more nested pattern than the Caelifera assemblages.

From an environmental perspective, three factors may explain the nestedness of the Orthoptera species assemblages: area, habitat heterogeneity and isolation. All three factors showed a significant correlation with site order. Variation in the number of different habitat types in a site proved to be more important for the occurrence of nested patterns than the spatial arrangement of these habitat types in terms of heterogeneity. The heterogeneity index scored lower and, moreover, was negatively correlated with site order. This suggests that species richness would be higher in sites of a given cover type, rather than a large diversity of small fragments. Area was found to be the most important factor that could have caused the nested pattern. From a species perspective, however, the number of different habitat types appears to be more important because the relation of species order with habitat specificity is very strong. Also, it is unlikely that insects such as Orthoptera, with a relatively small range size, would need large sites ( $> 1 \text{ km}^2$ ) to sustain healthy populations. Köhler (1996), for example, assessed the population vulnerability of Orthoptera in highly fragmented Central European landscapes and found that some small populations (50–200 specimens) can persist for a long time in very small habitats (100–600  $\text{m}^2$ ). However, hardly any research has been done on the relationship between the size of a given site and the survival chances of Orthoptera populations, therefore generalizations cannot be made. There is a strong correlation between area and number of habitat types: as the area increases, more habitat types occur. Also, the number of species-occurrence records is correlated with the size of nature areas. Therefore it is difficult to distinguish which part of variation in species diversity is explained by factors correlated with size, and which part is a true effect of area. The exact role played by area in the formation of nested patterns remains unclear, as we were unable to identify life-history traits correlated with area. However, there are strong indications that the effect of area is merely caused by the increasing number of habitat types.

Fleishman and co-workers (Fleishman *et al.*, 2001, 2002; Fleishman & Murphy, 1999) studied in detail the presence and causes of nestedness within insect assemblages. In their study on the butterflies of the mountain ranges in the Great Basin of western North America, these authors found a high degree of nestedness. Selective dispersal seemed to play a minor role; several environmental variables had an effect on the occurrence of nested pattern formation, although their importance varied. Also in their study, area had an effect on nestedness but its influence varied among mountain ranges. Studies on the nestedness of non-insect taxa in fragmented landscapes (Herkert, 1994; Lomolino & Davis, 1997; Mac Nally *et al.*, 2002; Fernández-Juricic, 2004) included a broad spectrum of factors (e.g. heterogeneity, disturbance, isolation), but predominantly pointed towards area as the important factor inducing nested patterns. However, several

authors (e.g. Berglund & Jonsson, 2003; Hylander *et al.*, 2005) found that nestedness also occurs within sites of uniform size. The latter confirms our presumption that the number of different habitat types present plays a more important role than area as such.

Rank correlations showed a close relationship between the ordering of sites and the amount of sampling effort put into those sites, a phenomenon also observed by Cook *et al.* (2004). Broad-scale data bases of collecting events, as used in this study, are inaccurate because of bias in sampling effort. Such data bases often do not contain information about real absences of species (Rich, 1998); moreover, sampling intensity is usually biased towards the richest sites (Dennis & Thomas, 2000). This makes it difficult, if not impossible, to estimate true sampling intensity or to distinguish the undersampled sites from well sampled or even oversampled ones. Sampling effort may have a considerable impact on the resulting record of species richness and composition of a given site (Dennis *et al.*, 1999). To evaluate the effects of differences in sampling intensity, we investigated how nested temperatures reacted after removing from the analysis sites with both low and high sampling intensity. This revealed that differences in sampling intensity can lead to an overestimation of the degree of nestedness.

The high degree of nestedness within the Orthoptera assemblages, and the strong influence of area and habitat heterogeneity on the formation of this pattern, may have implications for nature conservation in the Netherlands. Area and, accordingly, diversity of habitats, appeared to be more important for the occurrence of nested patterns than the degree of isolation of sites. This suggests that large, diverse nature areas are expected to be effective in preserving entire assemblages of Orthoptera. However, as we do not have information on population viability or corridor effects, it is not clear whether it is more effective to enlarge or to interconnect small conservation areas. Moreover, nestedness analysis is probably not the most suitable tool for effective reserve design (Simberloff & Martin, 1991; Whittaker, 1998). Nestedness analysis certainly is an important compositional descriptor, and can give clues for nature conservation, but complementarity algorithms, for example (Williams *et al.*, 2005) provide a better tool to optimize conservation efforts.

Nestedness analyses apply to relatively homogeneous ecological regions. Therefore the outcomes of this study relate only to a specific part of the Netherlands. Our results provide support for the current nature conservation policy of the Netherlands, which is focused on the conservation of the so-called ITZ species: species for which the Netherlands carries an international responsibility (I); species with a strong decline due to habitat loss (T); and rare species (Z). This study shows that, by protecting sites where rare species with narrow habitat requirements occur, a broad array of less selective species are expected to be protected as long as the full spectrum of habitat conditions and ecological processes is secured.

## ACKNOWLEDGEMENTS

We are grateful to Miguel Rodriguez-Gironés and an anonymous referee for their valuable comments. Arnold de Boer and Robert Brinkman are thanked for critically reading the manuscript.

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## SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online:

**Appendix S1** Species-occurrence matrix.

This material is available as part of the online article from:  
<http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2699.2007.01742.x>

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Editor: Melodie McGeoch