

Community Dynamics of Insular Biotas in Space and Time

**The Dahlak archipelago, Red Sea, Eritrea and East
African Coastal forests**

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Abstract

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The various features determining species distributions remains enigmatic in ecology. This thesis deals with the spatial and temporal dynamics of land birds on the islands of the Dahlak archipelago, the Red Sea, and of mammals, birds and reptiles among the forest fragments of the archipelago-like east African coastal forest. The bird species richness on the islands of the Dahlak archipelago depended on area, isolation and extent of habitat. Similarly, species richness of the east African forest fragments was related to area, habitat diversity and isolation but the importance of each factor varied among taxa as well as among generalists and specialists. For example, area influenced species richness of most categories except specialist mammals and reptiles, habitat diversity was more important for forest specialists than generalists, and isolation was important only for birds. In both study areas, similarity in bird species composition decreased with increasing distances among isolates suggesting that dispersal from source pools and among isolates facilitate re-colonization.

The nested community structure, i.e. species composition of species-poor communities are a subset of species-rich communities, of birds in the Dahlak archipelago depended on area and the distribution of a few habitats. Similarities in community patterns and co-occurrence patterns, at both community and species levels, were mainly related to habitat preferences and corresponding distributions of habitats as well as inter-island distances. Also, the distributional patterns suggest that predator-prey interactions can be a determinant of the spatial distribution of, at least, the prey. There was no evidence of competitive exclusion.

The nested structure on the islands of the Dahlak archipelago remained fairly stable over a period of 35 years even in this arid region. The turnover dynamics were broadly predictable from the nested pattern but not always consistent with other expectations from nested community structure. Taken together my results show that mechanisms on varying spatial and temporal scales act on species distributions, and that the influence may vary among taxa mainly depending on dispersal ability. In the case of conservation, comprehensive strategies accounting for these variations are needed.

KEY WORDS : Community assembly, habitat specialization, inter-island dispersal, island biogeography, nestedness, species co-occurrence.

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**This thesis is dedicated in memory of my father
Tesfamichael Azeria**

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Appendix

Papers I-IV

The present thesis is based on the following four papers, which will be referred to by their Roman numerals.

- I. Azeria, E.T. 2004. Terrestrial bird community patterns on the coralline islands of Dahlak Archipelago, Red Sea, Eritrea. *Global Ecology and Biogeography*, 13 (2): 177-187.
- II. Azeria, E.T., Pärt, T. & Wiklund, C.G. Explaining patterns of insular land bird community structure: species-habitat and species-species associations. (*Manuscript*)
- III. Azeria, E.T., Carlson, A., Pärt, T. & Wiklund, C.G. Temporal dynamics and nestedness of an oceanic island bird fauna. (*Manuscript*)
- IV. Azeria, E.T., Sanmartín, I., Ås, S. & Carlson, A. Patterns of vertebrate distribution in the East African coastal forests: a comparative analysis of birds, mammals, and reptiles (*Manuscript*)

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INTRODUCTION

A major goal of community ecology is to find whether ecological communities [on islands and ‘habitat islands’] are structured in space and time and to reveal the underlying processes and mechanisms (MacArthur & Wilson 1967, Wiens 1989, Rosenzweig 1995, Whittaker 1998, Drake et al 2002). Ecological features on various bio-geographic scales, their relationships and the historical dimensions have been widely discussed as determinants of community dynamics, e.g. area, local competition, habitat choice and regional distribution ranges (Wiens 1989, Ricklefs & Schluter 1993, Whittaker 1998, Welter-Schultes & Williams 1999, Watson 2002). Such studies have resulted in a broad understanding of the variation in community patterns among insular biotas as well as given insights into why organisms are distributed as they are (e.g. Vitousek 2000). Moreover, knowledge of patterns and causes of community variation in insular biotas has been central in providing guidelines to the conservation of biodiversity such as reserve design (e.g. Diamond 1981a, Diamond & May 1981, Shafer 1990, Whittaker 1998).

Traditionally, the island biogeography theory (hereafter IBT) of MacArthur & Wilson (1967) has been used to describe patterns of species richness on islands and ‘habitat islands’. The theory proposes that species richness on islands is the result of a dynamic equilibrium between area-dependent extinction and isolation-dependent immigration (MacArthur & Wilson 1967, Rosenzweig 1995, Whittaker 1998). However, often nature deviates from the assumptions and generalizations of the IBT (e.g. Brown & Lomolino 2000, Whittaker 2000). For example, area and isolation may interact such that area may influence immigration rate through area-related sampling (Lomolino 1990), and isolation-related immigration may influence extinction rates due to the rescue effect (Brown & Kodric-Brown 1977). Furthermore, the isolation-immigration link is confounded by lack of a clear definition of source pools and inter-island dispersal (e.g. Connor & Simberloff 1978, Hanski 1991, Rosenzweig 1995, Whittaker 1998). In reality, area is a measure combining the direct effect of area per se and the effect of habitat diversity (MacArthur & Wilson 1967, Ås et al. 1997), which are often difficult to distinguish. Moreover, isolates differ in variables other than isolation and area, e.g. altitude, topography. Thus, to fully understand the dynamics of island faunas, analyses should extend beyond the generalizations of the IBT such as species-area and species-isolation relationships, and explicitly consider the compositional aspects (Diamond & May 1981, Wiens 1989, Wright et al. 1998, Lomolino 2000). Such a new a conceptual framework for island biogeography acknowledges differences in speciation, colonization, and extinction among taxa, differences among islands other than area and isolation as well as the turnover dynamics that may depart from equilibrium (Whittaker 1995, 1998, Brown & Lomolino 2000, Fox & Fox 2000, Heaney 2000, Lomolino 2000).

In this thesis I examine species richness patterns of birds in the Dahlak archipelago, Red Sea, Eritrea in relation to area and different measures of isolation (Paper I). Moreover, by using data collected in the 1960’s, I investigate extinction, colonisation and turnover in relation to area and isolation (Paper III). Paper IV

shows the relative influence of variation in area, isolation and altitude on species richness of three vertebrate taxa with contrasting dispersal ability, and, within these taxa, groups displaying different degrees of dependence to the forest habitat in the East African coastal forest. The IBT suggests area-related extinction and isolation-related colonization, and consequently species richness, is expected to be related to both area and isolation.

It is a logical corollary of island biogeography theory that factors that determine species number also should determine species composition (e.g. Whittaker 1998). Species composition of communities is expected to be more similar among geographically close islands and habitat islands than among more distant ones for several reasons. For example, geographically close isolates have more habitats in common, they are subject to higher rate of inter-isolate dispersal (Power 1975, Nekola & White 1999, Morand 2000) and they may share history. These patterns of composition similarity may differ among taxa depending on life history traits such as dispersal ability (e.g. birds vs. reptiles) as well as level of dependence on the resources of the isolate (specialists vs. generalists) (Gascon et al. 1999, Nekola & White 1999, Watson 2002). For example, composition similarity of bird faunas among isolates are expected to correspond to habitat similarity and geographical distance, whereas for less vagile organisms such patterns might be less obvious because similarities in community composition may mainly reflect history. Thus investigation of similarities in community composition among isolates may give further insight into the causal factors of community dynamics, e.g., dispersal. Few studies (e.g. Morand 2000, Nekola & White 1999) have investigated explicitly the 'distance decay' in community similarities and compared it among taxa.

I studied whether the compositional similarity of birds among pairs of islands in the Dahlak archipelago is related to inter-island distance and habitat similarities (Paper I & II). Moreover, the analysis was extended to the species level by examining the simultaneous occurrence of species in pair-wise comparisons of islands. In paper IV, I investigate whether the patterns of compositional similarity in relation to inter-patch distance vary among three vertebrate groups with contrasting dispersal abilities in the East African coastal forests.

A different aspect of the spatial distribution pattern is the nested subset structure, where the species composition in species poor areas is a subset of that of species rich areas. For example a species poor community only includes species 'A to F', while a species rich community include species 'A to P', where the regional incidence of each species decreases from 'A to P'. Recently, Patterson and Atmar (1986) proposed a method for quantifying nestedness in insular communities. Nestedness has been demonstrated for several island systems and taxonomic groups, e.g. birds (Fleishman et al. 2002), mammals (Patterson & Atmar 1986, Conroy et al 1999), reptiles (Hecnar et al 2002), amphibians (Yiming et al 1998, Hecnar et al 2002), butterflies (Davidar et al. 2002, Fleishman & MacNally 2002) and plants (Honnay et al. 1999, review in Wright et al., 1998). In general, differential extinction has been suggested to be the most important mechanism generating nestedness, particularly on land-bridge islands and in fragmented habitats (Patterson & Atmar 1986, Cutler 1991, Wright et al, 1998, Yiming et al. 1998). Thus, the absence of species 'G-P' in the species poor

community is assumed to be caused by small–population related extinction risk in small areas. However, other mechanisms are also plausible, such as species and taxa–dependent (Cook & Quinn 1995, Worthen et al. 1996) as well as isolation–dependent (Kadmon 1995) immigration rates, habitat nestedness, human disturbance and passive sampling (Patterson & Atmar 1986, Patterson 1987, Simberloff & Martin 1991, Atmar & Patterson 1993, Andrén 1994, Cook & Quinn 1995, Kadmon 1995, Lomolino 1996, Wright et al. 1998, Calmé & Desrochers 1999, Fernández–Juricic 2002).

Even when communities are nested, not all species and island communities follow the nested structure but some species may be absent in species rich areas (e.g. species ‘C’ in a community consisting of species ‘A to P’), whereas others may be present in species-poor islands where they are not expected (e.g. species ‘R’ in a community consisting A to F). Such species are referred to as idiosyncratic species while idiosyncratic islands refer to islands with several idiosyncratic species (Cutler 1991, Atmar & Patterson, 1993, Atmar & Patterson 1993, Patterson & Atmar 2000). Island idiosyncrasy can be caused by some unique aspects of the island, while species idiosyncrasy can be caused by the combination of habitat specialisation and unique distribution of this habitat, biased colonization, predator avoidance and competitive exclusion (Atmar & Patterson 1993, Wiklund 1998, Wright et al. 1998, Patterson & Atmar 2000). It is important to understand the causes of idiosyncratic distributions because such species may require special conservation strategies.

The nested pattern in itself does not reveal the causes of variation in community patterns. Causes of nestedness are often inferred by investigating nested patterns at the assemblage level in relation to isolation, area and habitat distribution across isolates (e.g. Patterson & Atmar 2000) or by comparing degree of nestedness among taxa, e.g., with varying dispersal (Cook & Quinn 1995). Similarly, the identification of nested and idiosyncratic species is based on an investigation of the entire assemblage (Simberloff and Martin 1991, Worthen 1996, Whittaker 1998, Wright et al 1998). For example, distributions of idiosyncratic species suggest that they are affected by biogeographic factors different from those affecting the assemblage as a whole (Atmar & Patterson 1993). However, few studies (e.g. Sfenthourakis, 2004) carry the analysis far enough to identify causal factors. In papers I and II, I investigate the nestedness of birds in the Dahlak archipelago, and the possible roles of area, isolation and habitats for the nested pattern. Paper II focuses on causes of nestedness and idiosyncrasy, namely habitat types and their distribution among islands and interspecific interactions.

As nestedness is only one type of species co-occurrence pattern, mainly suggesting positive associations, I also investigated another form of co-occurrence, namely the ‘checkerboard’ distribution, i.e. the tendency that two or more species avoid each other. The study of checkerboard distributions, the test of null models and the role of interspecific interactions, particularly competitive exclusion are issues of controversy and debate (Diamond 1975, Connor & Simberloff 1979, Gilpin & Diamond 1984, Gotelli 2000). To understand the patterns and causes of nestedness, idiosyncrasies and species associations, it is necessary to identify which pair of species shows a negative or a positive

association. For example, idiosyncratic species are expected to show a negative association to one or more of the species, and identifying exactly the corresponding species and their habitat preferences will facilitate to reveal the most likely mechanism of the negative association. Therefore, I investigated co-occurrence patterns at the community (Gotelli & Entsminger 2001) and species levels (Sfenthourakis et al. 2004) under different null models.

Several of the developments and applications of nestedness pertain primarily to conservation problems (Doak & Mills 1994, Hansson 1998, Kerr et al 2000, Davidar et al. 2002, Fleishman et al. 2002, Hecnar et al. 2002). Since nestedness is a result of hierarchical relationships among species and islands (Patterson & Atmar 2000), it might facilitate to make predictions for community composition in fragmented landscapes (Worthen 1996, but see Doak & Mills 1994). Nestedness is commonly examined a snapshot in time, but species and communities in islands are expected to show dynamic turnover. Therefore the 'Discovery of nestedness at a particular point in time does not necessarily provide clear insights as to the probability of maintaining the same set of species (or any particular species) over time' (Whittaker 1998). Hitherto, there are no studies that have examined the stability in nestedness or whether future turnover could be predicted from nestedness. In paper III, I examine whether nestedness and related characteristic of species and islands were stable over a period of some 30 years, and if one can predict turnover from nestedness established at a point in time. I used data collected during the mid-1960's to establish the nested structure and to make predictions and then tested it on current data collected during 1999–2001. The archipelago has remained roughly the same in terms of human impacts. However, the region is known for erratic rainfall and unpredictable and severe droughts that most likely affect the bird fauna on the islands.

METHODS

Study areas

The Dahlak Archipelago

The Dahlak Archipelago (Fig. 1) consists of more than 210 islands along the Eritrea coast (Department of Environment, 1999). The islands, with elevations in the order of tens of meters, range in size from very small (a few m²) to the very large island of Dahlak Kebir (about 64500 ha). The main group of islands is separated from the mainland by the Massawa Channel, about 50 km to the west, and by the Buri peninsula, about 18 km to the south. Except for the island of Dissei, which is continental, all islands are coral barrier islands deposited during the Pleistocene on a foundation of salt diapirs, i.e. domes of salt rocks from the Miocene (Lewinsohn & Fishelson, 1967; Angelluci et al., 1975). Moreover, there might have been terrestrial connections during periods of low sea levels during the last ice age. There is some variation in geomorphology among the islands despite the same origin. The islands and adjacent mainland are coastal, arid habitats with sparse vegetation.

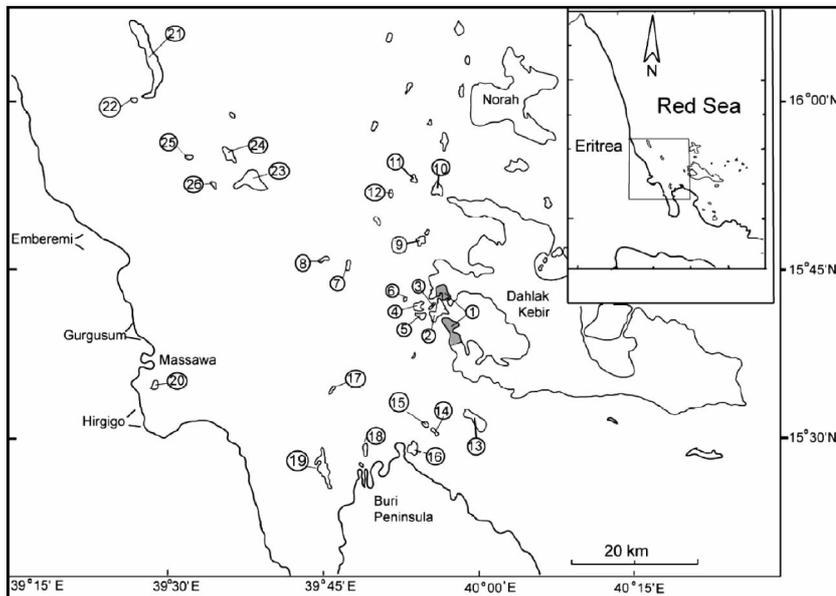


Fig. 1. Map showing the general location of the Dahlak Archipelago (top right). The islands or portions surveyed included in the study are indicated by numbers. 1: Dahlak Kebir, 2: Nocra, 3: Seil Nocra, 4: Entedebir, 5: Enteraya, 6: Kundabilu, 7: Dur-Ghella, 8: Dur Gaam, 9: Sarad, 10: Dar Ottun, 11: Duliacus, 12: Dalcus, 13: Shumma, 14: White Assacra, 15: Black Assacra, 16: Dillemi, 17: Madote, 18: Ota, 19: Dissei, 20: Shek Said, 21: Harat, 22: Shek el Abu, 23: Dehil, 24: Baradu, 25: Dehil Bahut, 26: Dahret.

The islands are well known for the large diversity of marine organisms and birds, particularly sea and shore birds, while the fauna of terrestrial vertebrates is poor (Lewinsohn & Fishelson, 1967). Although the bird fauna attracted ornithologists as early as in the 19th century (Heughlin, 1858), continuous ornithological studies did not commence until in the mid 20th century (Salvadori 1954, Smith 1955, 1957, Clapham 1964, Tornielli 1964). The islands have not been studied since then, and only a few recent avifauna recordings have been made due to a long period of war (Ministry of Fisheries, MoF, 1997). In this study, 27 islands are included. Only the largest islands of Dahlak, Nocra, Dissei, Dillemi and Dehil are inhabited. Fishermen regularly use some of the smaller islands as rest spots. In some islands, domestic animals are kept seasonally, e.g. goats were noted in Black Assacra, Entedebir and Baradu in 1999. The archipelago and the adjacent mainland are 'Important Bird Areas', i.e., part of priority areas for conservation nationally and globally (Eritrean Agency for Environment 1996, Department of Environment, DoE 1999, Coulthard 2001).

The East African Coastal forest

The East African coastal forest is one of the highest priority ecosystems for conservation in Africa and globally. In addition to the numerous endemic species,

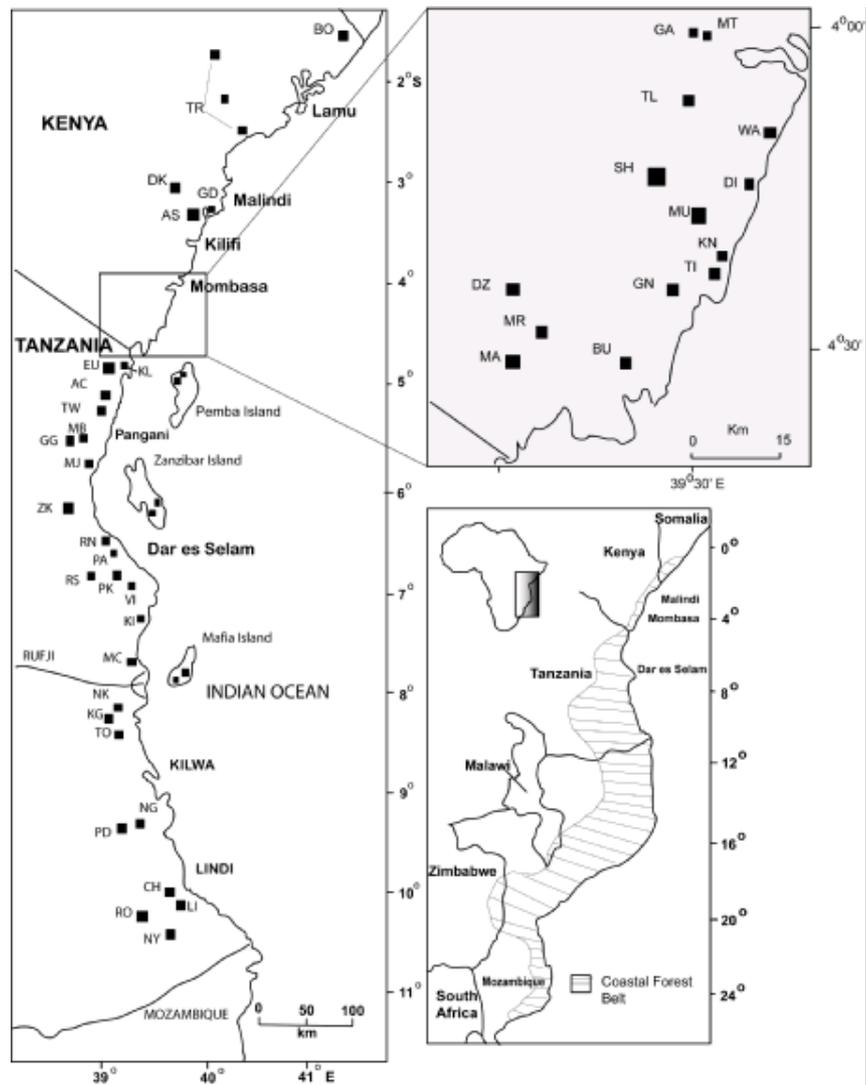


Fig. 2. Map showing the general location of the East African coastal forest (bottom right). Codes represent north to south: BO=Boni; TR=Tana river primate & delta; DK=Dakatcha; GD=Gede; AS= Arabuko Sokoke; GA= Gandini; MT=Mtswakara; TL=Teleza; WA=Waa; DI=Diani; SH=Shimba Hills; MU= Muhaka; KN=Kinondo, TI=Timbwa; GN=Gongoni; DZ=Dzombo; MR=Mrima; MA=Marenji; BU= Buda; EU= Eastern Usambara; KL= Kilulu; AC= Amboni Caves; TW= Tongwe; MB= Msubugwe; GG= Gendagenda; MJ = Mkwaja; ZK=Zaraninge-Kiono; RN =Ruvu North; PA=Pande; RS= Ruvu South; PK= Pugu & Kazimzumbwi; VI=Vikindu; KI=Kisiju; MC=Mchungu; NK=Namakutwa; KG=Kiwengoma; TO=Tong'omba; NG=Ngarama; PD=Pindiro; CH=Chitoo; RO=Rondo; LI=Litipo; NY=Nyngarama. Other localities included are Jubba river (Southern Somalia-not shown), Kimboza (Tanzania), forests in the Pemba island, the Zanzibar island, the Mafia island as well as lowland forests in Mozambique, Zimbabwe and Malawi (Redrawn from Burgess et al. 1998).

the forests harbour high concentrations of rare and threatened species and high general biodiversity. Despite their biological importance, the unique fauna and flora of the coastal forests are currently threatened by human disturbance, through increasing fragmentation and forest degradation (Burgess & Clarke 2000 and references therein).

The coastal forests of Eastern Africa form a terrestrial archipelago along the coastal plateau of East Africa from southern Somalia to northern Mozambique. The coastal forest consists of more than 260 forests varying in size and degree of isolation and covers a total area of 3172 sq. km², although most forests are less than 500 ha in size (Burgess & Clarke 2000). The forest belt extends between 10° N to 25° S and between 34°- 41° E. The limits to the coastal forest area are set by rainfall (decreasing to the North), seasonality (increasing to the South) and by altitude, from sea level to a maximum altitude of 1100 m (increasing to the West). The word “coastal forest” is used in a broad sense to define a mosaic of forest types found on the coastal plateau, often imbedded in a system of farmland, savannah-woodland, and thickets. Thus, in addition to the typical coastal forest, other vegetation types, such as montane forest, savannah-woodland, thicket, bush land, mangrove, grassland, and farmland vegetation might be included (for a definition see Hawthorne 1993, Rodgers 2000, Clarke 2000a, and references therein).

Data

Bird data -The Dahlak Archipelago

Birds were censused on each of the 27 islands (Fig. 1) once in 1999 (May–July) and a second time in 2001 (mid–February–March) except for the islands of Kundabilu, Seil Sarad and Ota, which were visited only in 1999 or in 2001, respectively. Sheik Said was visited more than 5 times. The size of the areas surveyed was equal to island size except for the survey on Dahlak Kebir (mean \pm SD = 288 \pm 466, Fig. 1., Table 1). Five mainland areas also were surveyed; northern areas (Gurgusum, Imberemi and Mersa Kubae) and southern areas (Hirgigo and at the Buri peninsula) to assess bird distribution across the coastal mainland. For this study, the coastal area is defined as the land from the shoreline to about 300 m above sea level, i.e. the most important area for bird species also found on the islands.

Maps were used to determine the position of each transect line, so that they ran straight across the longest diameter of smaller islands. On the larger islands, up to 5 transect lines of varying length were located to achieve maximum coverage. Each transect was walked, unidirectionally, at a slow and steady pace with stops made only for the identification of bird species. All resident terrestrial birds within a distance of \pm 50 m of the transect line were recorded. Moreover, areas covered by thick mangrove or bushes were carefully searched for birds. Thus, the time spent at a site depended on the encounter rate of birds as well as the habitat. The censuses were done in the morning, 06:00–10:30 h, and in the late afternoon, 16:00–18:00 h. A comparison showed that all previously recorded bird species, except for a few rare or vagrant ones (Clapham, 1964), were also recorded in this

study. In 2001, simultaneous censuses using different transects by ETA and CGW on seven islands produced the same species lists. Moreover, on the island of Sheik Said that was visited more than 5 times, the same species were observed on each visit. Therefore, I believe that there is a complete record of bird species from the smaller islands but it is possible that some species may have been missed on the larger islands, e.g. Dahlak Kebir.

Historical presence-absence data was compiled for 17 islands based on observations made during August–September 1962 (Clapham 1964), February–March 1963 (Tornielli 1964), March 1969 (Urban & Boswall 1969) and records obtained during February–May 1953 (Salvadori 1954) and from the island of Dahlak Kebir by Smith (1955). The latter two reports add rainy season data for some of the islands, which were visited only during the dry season and also complement the rain season data for the historical data set. The historical data set is thus based on variable numbers of field surveys on the islands; 8 islands were visited once, 7 islands twice, and the islands of Dissei and Dahlak Kebir 3 and 4 times, respectively. For the status of species on the mainland during the previous period, we used the published records of Smith (1957).

The taxonomy follows van Perlo (1995) and *The Birds of Africa* (Urban, 2000).

Habitat data – The Dahlak Archipelago

The vegetation varies from open grassland *Panicum turgidum*, low scrub-like halophytes *Zygophyllum* sp., *Limonium* sp., *Salicornia* sp., *Suaeda* sp. and occasional acacias *Acacia* sp., to patches of mangrove *Avicennia marina*. Also, succulent plants like euphorbia, *Euphorbia* sp., and perennial plants like tamarisk *Tamarix* sp., and other green bushes occur on the islands. General descriptions of the climate and ecology of the coastal part of Eritrea and the islands are presented by Smith (1955, 1957), Hemming (1961), Clapham (1964) and Angellucci et al (1975).

Quantitative habitat data were derived from a satellite image (Landsat 7 ETM+, acquired in 2000). A supervised classification with maximum likelihood based on training areas (Lillesand & Kiefer 1994) was used to classify the satellite image using the ER Mapper 6.3 software. This method identified pixels with similar reflectance values and thus categorised eleven different classes. Based on the training areas, the software then classified the whole image. The classification derived from the satellite images was carefully interpreted in a comparison with the habitat field notes recorded during the surveys. In another approach, unsupervised classification, the resulting class boundaries were unsatisfactorily resolved.

The classified image was imported into the software MF Works 2.03 and divided up for separate analysis of each island. Then, the total area covered by each class was calculated for each of 26 islands. The two classes representing deep and shallow water around the island were excluded. The remaining nine classes were categorized into six major habitats classes broadly reflecting the vegetation types of relevance for the distribution of birds in this area (also see Clapham 1964). Thus, all islands are categorized according to total amount of cover of each

habitat, although the habitats were not continuously distributed but rather formed mosaics.

The habitat classes were:

MM- Mangrove vegetation, mainly *Avicennia marina*, often along the shore of the islands.

GG- Green bushes, often including thickets of *Euphorbia* spp, and dense, green *Acacia* spp and other bushes growing on deeper soil along valleys.

DD- Scattered thorny *Acacia* spp, up to about 2 m high, and other dry bushes on coralline plane.

CC- Dry coral, high plateau of weathered and powdered coral with ephemeral or no vegetation.

KH- Knee high grasses and scrubs on sandy plains mainly composed of the grass *Panicum turgidum* and the halophytes *Zygophyllum* spp and *Limonium* spp.

SS- Sand and gravel plains with a cover of short grass and dwarf-scrubs (< 20 cm).

Vertebrate fauna data- East African coastal forest

Data on species distributions were obtained from three recent reviews of the East African coastal forest fauna; birds (Mlingwa et al. 2000), mammals (Burgess et al. 2000) and reptiles (Broadley & Howell 2000). In total, 193 species from 49 forests were included in this study (Fig 2). The sampling intensities of the forests varied in the original surveys, so the list of species is probably incomplete for some forests. We assume, however, that this does not affect the general interpretations (see also Burgess, et al. 1998). Bats were excluded from the mammal data set because in this case the data was clearly biased by the sampling strategy, i.e. mist netting that is strongly sensitive to sampling intensity. Including bats also would have biased the comparisons across taxa with contrasting dispersal ability, i.e. bats fly as birds do. Within each faunal group, two different categories “forest specialists” and “forest generalists” are used according to the classifications used in the original studies. For reptiles, I have data only for specialists, in which the original reptile study (Broadley & Howell, 2000) considered two categories; ‘coastal endemics’, i.e. species which are endemic to the coastal forests, and ‘forest endemics’, i.e. species that also are found in the nearby Eastern Arc Mountain forests. Data on area size (minimum forest area), median and range of altitude for each forest fragment were obtained from Burgess & Clark (2000) (Paper IV).

Analyses

Compositional similarity was investigated by cluster analysis (van Tongeren, 1995) using the Euclidean, the Sorenson's and the Simpson's indices of similarity (Paper I & IV). The Sorenson's similarity index is calculated as, $Sor = 2C/A+B$, where C is number of species common to both areas, and A and B are the total numbers of species occurring in each of the areas (Krebs, 1999). This index takes into account the differences in species numbers, and thus similarity values would depend on the difference in species richness between areas. Simpson's coefficient of similarity is insensitive to differences in species numbers and preferred in nestedness analysis (Patterson and Brown, 1991). Simpson's coefficient of similarity is calculated as, $Simp = C/N_{small}$, where C is the number of species shared by two islands and N_{small} is the number of species of the island with the smallest species number. Farthest neighbour (Paper I) and Unweighted Pair Group Method with Arithmetic Mean, UPGMA (Paper IV) dendrogram were constructed based on these similarity distances. I used Mantel test (a matrix-matrix correlation), using PC-ORD (for Windows 3.19, McCune & Mefford, 1997) to examine compositional similarity in relation to geographical distance and habitat similarity between islands (Paper I, II & IV). The Mantel test circumvents the problem of partial interdependence in tests of association among distance matrices.

To find affinities among vertebrate fauna of the east African coastal forest (Paper IV), I also used parsimony analysis of distribution, PAD (Trejo-Torres & Ackerman, 2001, also called PASA in Trejo-Torres & Ackerman 2002), which is an ecological extension of the parsimony analysis of Endemicity, PAE (Rosen 1988). PAE groups areas (analogous to taxa) based on their shared taxa (analogous to characters) according to the most parsimonious cladogram (criterion of simplicity or parsimony) (Rosen 1988, Morrone 1994). PAE cladograms are considered as hypothesis of biotic similarities between areas, and the terminal dichotomies in PAE are interpreted as areas that share the maximum biogeographic affinity. Since my analysis is based on the distribution of all species, I used the term - Parsimony Analysis of Distributions (PAD).

To investigate the nestedness of birds and habitats on the islands of the Dahlak archipelago (Paper I & II), I used the Nestedness Temperature Calculator (Atmar & Patterson 1993, 1995). The method maximally packs the species-by-island matrix; islands by decreasing species richness (top-to-bottom) and species by decreasing incidence (left-to-right) (see Fig. 3). In a perfectly nested matrix all presences would occur towards the upper left corner. In reality biotas are not perfectly nested and absences occur among presences and *vice versa*, i.e. unexpected absences and presences. This disorder is presented as 'temperature' ranging from 0° C for perfect nestedness to 100° C for a random distribution. Null models has been extensively used to test whether the community structure of islands depart from random (e.g. Strong et al 1984 and contributions there in, Sanderson et al. 1998, Gotelli 2000). I used three different null models to test if the community assembly departed from a random pattern. The first null model, T_{sim1} , is calculated as nested scores of 1000 randomly distributed data matrices using Monte Carlo simulation, and with each cell in the presence/absence matrix having equal probability of being occupied. The second one, T_{sim2} , is calculated in

a randomisation process where the probability of selecting a certain species is proportional to its actual incidence and all sites are randomly filled (Jonsson 2001, Fischer & Lindenmayer 2002). In the third one, T_{sim3} , each species is selected in proportion to the observed incidence, and the number of species of each island is equal to that observed. The latter two null-models are supposed to control for passive sampling (Jonsson 2001, Fischer & Lindenmayer 2002). For these null models, I generated random matrices by independent swapping in EcoSim 7 (Gotelli & Entsminger 2001) and, then, manually loaded the matrices into the nestedness temperature calculator. The observed temperature was tested against the mean temperature of 100 randomly generated matrices.

One way of investigating causes of nestedness is to correlate the nested ranks of islands with a chosen explanatory variable (e.g. Patterson & Atmar 2000). I examined the influences of area, isolation and habitats for nestedness (Paper I & II). The nested ranks of islands were obtained from the maximally nested matrix. Moreover, the occupancy probability of each cell (species-island combination) was calculated by Monte Carlo simulation. I applied the occupancy probabilities and the nested ranks of species and islands, based on the historical data, to investigate the stability of nestedness and to test turnover (Paper III).

I used the software EcoSim (Gotelli & Entsminger 2001) to investigate co-occurrence at the community level using the C-score module (Paper II). Species-species associations were examined using a program developed by Sfenthourakis et al. (2004). For the test of species-species associations, I used EcoSim to generate random matrices by independent swapping under different constrained null models.

To determine whether the mean size of habitats and islands occupied by a species is significantly different from random, I used the 'Runs Test' in EcoSim. The mean size of habitat or area occupied by a species was then compared to mean values calculated by randomising the occurrence of the species across the areas. More detailed descriptions of the various types of analyses are given in each paper (Paper I-IV).

RESULTS & DISCUSSION

Bird communities in the Dahlak archipelago

Species richness patterns: effects of area, isolation and habitats

Island area, isolation, type and number of habitats have been suggested as important determinants of the variation in species richness in insular communities (MacArthur & Wilson 1967, Rosenzweig 1995). In the Dahlak archipelago, species richness of terrestrial birds was positively related to island area and to the distribution of three habitat features, and negatively related to three different measures of isolation (Table 1).

Table 1. *The influences of area, isolation and habitat types on species richness and nested rank of islands among 26 islands in the Dahlak Archipelago. Isolation: DISTSHRT = the shortest distance to the mainland, DISTSTH= the shortest distance to the southern reference point on the southern part of the coast, and DISTDAH = the distance to the island of Dahlak Kebir. Habitats: MM=mangrove, GG= Green bushes, DD= thorny acacia, CC=coral plateau, KH=knee high scrubs, SS=sandy with short grass. r^2 -values are from parametric correlations and r_s -values are Spearman rank correlations*

Variables	Species richness (r^2)	Island nested rank (r_s)
Area	0.52***	-0.716 ***
DISTSHRT	0.29**	0.25
DISTSOUTH	0.31**	0.31
DISTDAH	0.17*	0.34
MM	0.001	-0.09
GG	0.32**	-0.68***
DD	0.41***	-0.573**
CC	0.05	-0.56**
KH	0	-0.04
SS	0.42***	-0.17

*** p<0.001, **p<0.01, * p<0.05

These relationships were expected due to area-related extinctions and isolation-related colonisations (MacArthur & Wilson 1967). By comparing 17 island bird communities from the 1960's with those found currently, I examined patterns of turnover, extinction and colonization (Paper III). Extinction and turnover of species was higher on small than large islands (Table 2.) Furthermore, the proportion of species colonizing an island between the two time periods was negatively related to the distance between the island and the mainland (Table 2.). Thus, area-dependent extinction, island-area related size of habitats, and isolation-dependent colonisation were important determinants of bird species richness in the Dahlak archipelago. Similar results have been obtained in some other studies (Rosenzweig 1995).

Table 2. *Extinction, colonisation and turnover of species on 17 islands of the Dahlak Archipelago in relation island area, isolation and previous nested ranks of islands. Spearman r_s - values are indicated. Sample sizes are; previous data (1960's) 27 species, and current data (1999–2001) 33 species, and pooled data 35 species*

	Area	Isolation	Previous nested rank of islands (r_s)
Proportion of extinction	-0.56***	0.38	0.36
Proportion of colonization	0.16	-0.51*	-0.08
Turnover (n=35 species)	-0.53*	0.35	0.62**

*** p<0.001, **p<0.01, * p<0.05

Compositional similarity between islands—the roles of geography and habitats

Factors determining species number should also determine species composition (e.g. Whittaker 1998). Therefore, I investigated the influences of inter-island distance and habitat for species distribution at the community and species levels in Paper II.

For the bird communities in the Dahlak archipelago, species composition was similar between islands that were close to each other (Mantel Test, Sorenson's similarity, $r_m = -0.203$, Simpson's similarity, $r_m = -0.195$, $p < 0.05$) and with similar habitat composition ($r_m = 0.33$, $p = 0.002$). This second result was related to habitat preference or avoidance by species, respectively (see below). Similarly, few species showed spatial aggregation (Table 1, in Paper II). Thus habitat similarity and inter-island dispersal were important determinants of species composition among islands. Only a few studies have investigated inter-island similarity of species composition in insular communities (Power 1975, Nekola & White 1999, Morand 2000). These studies also suggest inter-island dispersal to be an important variable in determining species richness (Morand 2000) and composition (Power 1975).

The Vertebrate fauna of the East African Coastal forest

Species richness patterns – the importance of dispersal ability and habitat specialization

The type of patterns of species richness may vary among taxa depending on life history traits, such as dispersal ability and degree of habitat specialization (e.g. Ricklefs & Lovette 1999). For example birds are expected to have higher dispersal ability than mammals and especially reptiles. I made comparisons between birds, mammals and reptiles in the insular system of East African coastal forests. Moreover, among birds and mammals, I compared species richness patterns between forest specialists and forest generalists. For reptiles, I used the categories coastal endemics and forest endemics (see Method).

Altitude is an important determinant of species richness in terrestrial communities. A coastal forest spanning over a wide altitudinal range probably have a more diverse environment than one with a narrow range (Kingdon & Howell 1993). Moreover, coastal forests with higher median altitude are expected to be better developed, i.e., moist forests with tall trees because they receive more rainfall (e.g. Hawthorne 1993, Lowe & Clarke 2000). In addition, they are probably less subjected to human disturbance (Clarke 2000b) and less prone to tidal inundations, which have flooded forests at lower altitudes in geological time (Burgess et al 1998).

Table 3. *Species richness patterns of vertebrates in East African coastal forests in relation to area, isolation and altitude (range and median). Since altitudinal range and median altitude were correlated, partial correlations, r_p , were run excluding the effect of the other altitude parameter. Significant correlations are shown in bold. r and r^2 -values are simple correlations*

Taxa	Groups	Area (r^2)	Isolation (r)	Altitude	
				Range (r_p)	Median (r_p)
Birds (n=41)	Specialists	0.33***	-0.46**	0.38*	0.17
	Generalists	0.34***	-0.38**	0.28 ¹⁾	0.04
Mammals (n=30)	Specialists	0.04	-0.26	0.39*	-0.23
	Generalists	0.31**	-0.33	0.21	-0.10
Reptiles (n=22)	Specialists	0.13	-0.20	0.12	0.09
	'Coastal endemic'	0.24*	-0.29	0.40 ¹⁾	-0.32
	'Forest endemic'	0.053	-0.21	-0.25	0.43*

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, ¹⁾ $p < 0.10$

Species richness of birds, both specialist and generalist, was higher in larger and less isolated forests (Table 3, also see Mlingwa et al. 2000). Moreover, species richness of forest specialists was higher in forests covering a larger altitudinal range (Table 3). For generalists birds, the partial correlation was only marginally significant for altitude range, where as in simple correlations both the range ($r=0.46$, $p < 0.01$) and median ($r=0.39$, $p < 0.05$) altitude seemed to be important.

The generalist mammals, but not the specialists, displayed a positive species-area relationship. Instead, the numbers of specialist mammals increased with increasing altitudinal range (Table 3). The 'coastal endemic' reptiles showed a slight increase in species richness with increasing area and altitude range. Also species richness of 'forest endemic' reptiles was positively related to the median altitude (Table 3). Neither the mammals nor the reptiles displayed a significant relationship with forest patch isolation.

My results indicate that species richness of the different faunal groups differed in their response to the independent variables, probably reflecting differences in dispersal ability and habitat specialization. The species-area relationships for birds and generalist mammals were consistent with the prediction of the IBT, probably an effect of area-dependent extinction. These results corroborate earlier findings for various East African forest ecosystems (Diamond 1981a, Stuart 1981). Only species richness of birds, i.e. species with good dispersal ability, was related to isolation, and thus birds are the most likely taxa to benefit from the 'rescue effect' (Brown & Kodric-Brown 1977). The isolation effect on species richness may not be detected when the effect is so strong that dispersal does not occur (Lomolino et al 1989). That may apply for the mammals and reptiles in this study.

As expected for habitat specialists (Ricklefs & Lovette 1999), habitat diversity as shown by altitudinal range influenced species richness of forest specialist birds and mammals as well as ‘coastal endemics’. Interestingly, species richness of ‘forest endemics’ reptiles was high in forests with a high median altitude. It is possible that they comprise relict faunas, which have escaped from coastal inundations (Burgess et al. 1998).

Together, these results suggest that differences in dispersal ability and habitat requirements may cause certain subsets of vertebrates to strongly deviate from the general IBT expectations.

Composition similarity patterns

The cladogram generated by the parsimony analysis of distribution, PAD, and cluster analyses on birds were nearly identical, and both showed that bird species compositions were more likely to be similar if the forests were located close to each other and were of similar type (Paper IV). The compositional similarity of bird communities decreased with increasing geographic distance for both specialists and generalists (Table 4). A similar pattern was observed in other forests in the region (Stuart 1981). It is likely that this spatial correspondence of bird species composition similarity is caused by ecological similarities, e.g. habitat, among geographically close forests as well as high rates of inter-patch dispersal.

The results of mammals and reptiles clearly differed from those of birds. Moreover, both the PAD and the cluster analysis suggest that the hierarchical relationship among mammal faunas do not follow a clearly defined geographical gradient, although there were such geographical correspondences in some smaller subgroups (see Fig 3 in Paper IV). Moreover, the forests showed a low similarity in mammal faunas (Paper IV).

Table 4. *Species composition similarity among East African coastal forests in relation to geographical distance between forests. Sorenson’s and Simpson’s indices were used in the analysis. Significant correlations are shown in bold. n.a. = Not applied*

		Sorenson’s	Simpson’s
Birds	Specialists	-0.23 *	-0.20 *
	Generalists	-0.15	-0.26 ***
Mammals	Specialists	-0.04	-0.083
	Generalists	-0.064	0.002
Reptiles	Specialists	0.16 *	0.19 *
	Coastal endemics	0.33 **	0.32 **
	Forest endemics	0.08	n.a.

*** p<0.001, **p<0.01, * p<0.05

Similarly, the Mantel test showed that the compositional similarity of mammals was not geographically related (Table 4). Thus, geographically close fragments did not necessarily have more similar faunas than distant ones did. Therefore geographical distance may not be such an important determinant of species composition in mammals as it is in birds, which was also suggested by the analyses of the species-isolation relationships (Table 3). The PAD of reptiles indicated no resolved tree of forest affinities. The parsimony analysis only grouped patches based on widespread shared species (e.g. Trejo-Torres & Ackerman, 2001). This pattern was confirmed by the cluster analysis (Paper IV), where the similarity in species compositions between forest patches was generally lower than that of mammals and birds. Thus, there are very few examples of forest fragments sharing endemic specialist reptiles. However, only a few areas showed pair-wise similarities that seem to be related geographically, and in fact some of the affinities were not related geographically. Consequently, composition similarities increased with increasing distance among forests (Table 4). These results may be explained rather by fragmentation history of the forests than by distance-related dispersal. Alternatively, the increase in similarity with increasing distance is a statistical artifact reflecting a close affinity among a few distant forests while there was no relationship among most of the forests, i.e. exclusion of three forests removed the significance of the relationship. Hence, dispersal ability and similarity in habitat types are important for richness and composition of birds and, consequently, for the biotic similarity among forest fragments. Overall, geographically closer fragments and islands are therefore expected to have more similar biota than more distant fragments due to a higher degree of ecological similarity and higher rates of inter-fragment dispersal (Paper I, II and IV). Since this pattern was broken by species with low dispersal ability, i.e. mammals and reptiles, similarities in species composition among fragments and islands may, to a certain degree, depend more on the dispersal ability of animals than on habitat similarity, particularly among the East African Coastal forests.

Nestedness of bird communities in Dahlak archipelago and causal factors

Whereas IBT does not make any distinctions among species but assumes that biotas are composed of species randomly drawn from a regional species pool, the nestedness analysis investigates departures from random expectations such that species compositions in species-poor islands are a subset of species-rich islands. Though differential extinction has been suggested to be the most important mechanism for nestedness (Patterson & Atmar 1986, Patterson 1990), other mechanisms such as species or taxa dependent and isolation-dependent immigration rate as well as habitat nestedness (e.g. Simberloff & Martin 1991, Cook & Quinn 1995, Kadmon 1995, Worthen et al. 1996, Calmé & Desrochers, 1999) also may account for nestedness of communities (review Wright et al 1998). Furthermore, passive sampling may also produce nestedness in insular communities (Andrén 1994), i.e. large areas sample both common and rare species

while small areas sample only common species. Yet, passive sampling has not been shown convincingly (Worthen 1996).

Like in many other island systems (e.g. Wright et al 1998) the land bird community of the Dahlak Archipelago was nested, i.e. bird faunas of species poor islands were subsets of those on species-rich islands (Fig. 3). The observed nestedness pattern was significantly different from those of all three null models tested ($p < 0.01$, Paper I) including a constrained null model accounting for passive sampling, where each of the species was selected in proportion to its observed incidence and the number of species at each island was equal to that observed. Therefore, I conclude that passive sampling was not likely to cause the observed pattern of nestedness. Rather area and species-dependent differential extinction was suggested by an association between island area and island nested rank (Table 1). Moreover, the proportion of species that became extinct between 1960's and 1999-2001 was lower in larger than in smaller islands (Table 2). Area, probably acted also on species composition through its effect on extinction and species richness. Thus, island area may be an important determinant of the nested patterns of the Dahlak Archipelago land bird community (Paper I). Similar results have been obtained in other studies of bird faunas (e.g. Wright et al 1998, but see Fleishman et al. 2002).

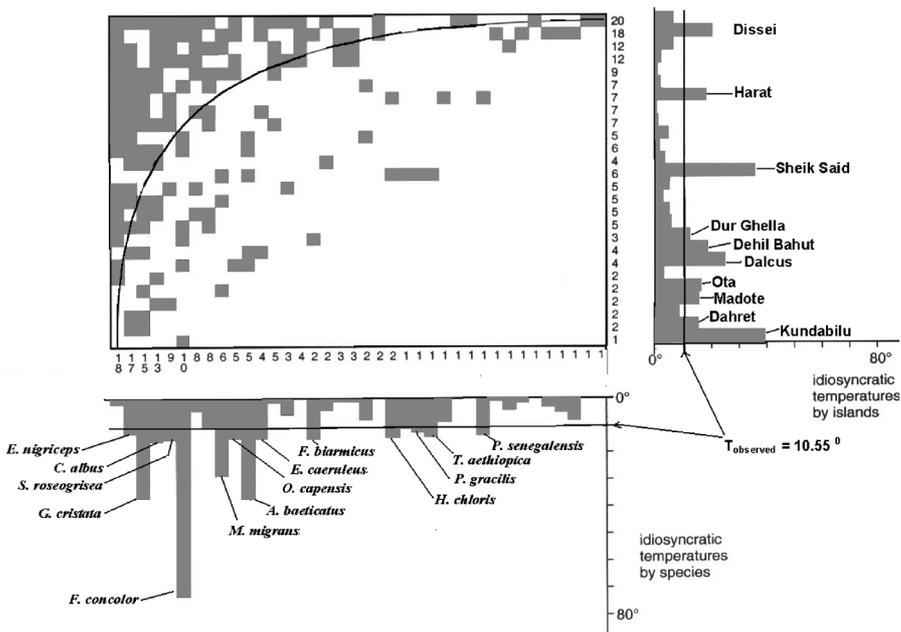


Fig. 3. Nestedness of the terrestrial bird community of the Dahlak archipelago. The diagram shows the idiosyncrasies, species (e.g. Falco concolor) and islands (e.g. Sheik Said, Dissei), and that they have higher temperatures than the matrix temperature.

Area-related nested rank of islands might reflect increasing habitat diversity and nestedness with increasing island size and that also habitats are nested (Calmé & Desrochers 1999). Habitat diversity is difficult to define objectively (Simberloff 1976 cf Ricklefs & Lovette 1999), but in the Dahlak archipelago six major habitat types, mainly based on vegetation structure, were distinguished. The six major habitat types were not nested among islands (Tobserved = 29.6°, $p = 0.29$, Paper II). However, the area covered by each of the three habitats was related to the nested rank of islands (Table 1, Paper II). All these habitat types were positively correlated with each other but a partial correlation suggested that only ‘green bushes’ (i.e. dense green bushes, acacia, euphorbia) was correlated with island nested rank (partial $r_s = -0.49$, $p = 0.016$).

Thus, compositional similarity and nestedness of island communities appear to reflect the importance of one or few habitat types influence many species in the community, while overall habitat nestedness is less important (Paper II). Perhaps habitat nestedness may not be so important as has been thought (Calmé & Desrochers 1999).

In contrast to patterns of species richness (Table 1) and colonisation (Table 2), island nested rank was not associated with isolation (Table 2). Other studies also suggest that patterns of composition and richness are not always consistent (e.g. Kadmon & Pulliam 1993). Thus, isolation-dependent, differential immigration rates or colonization are less likely to cause nestedness. It is possible that idiosyncratic distributions of some birds and variations in species distributions across the mainland may confound the isolation effect on nestedness (Paper I). Moreover, most islands were within 40 km from the mainland, which is close enough for most bird species to reach through their dispersal movement. Still frequent colonisation did not obscure the patterns of nestedness, which most likely depended on other factors such as area and habitat. Therefore, frequent colonization may not always obscure patterns of nestedness but rather enhance that pattern (Cook & Quinn 1995, but see Patterson 1990).

Together, these results suggest that the nested structure of the bird assemblages of the Dahlak archipelago was mainly caused by area-related extinction and area-related habitat distribution. Though area-related extinction has mainly been assumed to be important for land-bridge islands, resulting in nestedness (Patterson & Atmar 1986), my results show that area-dependent extinction could be the main factor influencing species composition in oceanic islands as well (see also Nekola 1999).

Why are there idiosyncratic species and islands?

Despite the fact that the Dahlak archipelago provides an insular system of nested communities, not all bird species and islands were nested. Idiosyncratic species and islands occurred among common and rare species and among species-rich and-poor islands (Fig. 3). The idiosyncratic islands differed neither in size nor in isolation from nested ones (ANOVA, $p = 0.09$ and $p = 0.44$, respectively).

Idiosyncratic islands are those inhabited by idiosyncratic species. However, the biologically important question is why do some species have an idiosyncratic distribution? Such knowledge is of paramount importance for conservation. Common explanations include species-specific requirements of non-nested habitats, negative species interactions, and biased distribution in the source pool. I investigated species–habitat associations (Table 2 in Paper II) and compared habitats on islands with unexpected absences versus those with unexpected presences (Table 3 in Paper II). The African Reed (Mangrove) Warbler *Acrocephalus baeticatus avicenniae* and the White-collared Kingfisher *Halcyon chloris* were positively associated with mangrove-habitat, which was not related to the nested rank of islands. Other idiosyncratic species showed either avoidance of one or more habitats linked to the nested rank of islands or were not related to any habitat.

Two idiosyncratic species, the Sooty falcon *Falco concolor* and the Crested lark *Galerida cristata* showed no or negative habitat associations. Interestingly these two species were consistently negatively associated (see Table 4 in Paper II). The affinity of Sooty falcons to smaller islands is consistent with its preference for hilly areas and cliffs (not covered by my six habitat classes) on small islands, where it breeds (Clapham 1964, Gaucher et al. 1995). The Crested lark often avoids hilly areas and thick acacia (Dean et al. 1992). Its preferred habitat, open habitats with short field layers, was available in large islands. However, the idiosyncratic distribution of the Crested larks is best explained by predator avoidance. There have been observations of predation attempts by sooty falcon on Crested lark (Clapham 1964), which has a conspicuous areal display.

By investigating species-species associations in the community it is possible to disentangle whether idiosyncrasies and nestedness among species were to preference of specific habitats or due to inter-specific interactions. In general, most of the nested species showed positive species-species associations (Table 4 in Paper II). These species tended to be positively associated to one or more of the three habitats found to influence nestedness at the assemblage level (Table 3 in Paper II), suggesting that positive species-species associations were driven by habitat preferences. Only a few species accounted for most of the negative species-species associations, i.e. the Crested lark, the Sooty falcon and the Mangrove warbler (Table 4 in Paper III). All these species were idiosyncratic. These negative associations also were driven by different habitat preferences between species, except that of Sooty falcon- the Crested lark (see above).

Thus my result suggests that both non-nested habitats and predator prey interactions may cause idiosyncratic distribution of species. Therefore, analysis of species–species associations may reveal which factors are more likely to cause species to be nested or idiosyncratic in the nestedness analysis. Hitherto, no study has investigated the potential causes of idiosyncrasy, although many rare idiosyncratic species may be in focus of conservation efforts such as the Sooty falcon, the Mangrove warbler, the Hoopoe lark and others.

Nestedness and temporal dynamics

Whether the nested structure of insular communities remains similar through time is of great importance for the understanding of community dynamics and can be paramount for conservation (Whittaker 1998). For example, the nestedness pattern has been suggested as a useful tool for predicting community composition in fragmented landscapes (e.g. Worthen 1996, but see Doak & Mills 1994). I investigated the temporal stability and time-related changes in extinctions and colonisations by comparing the land bird communities of the Dahlak archipelago between the 1960's and the present time.

The bird faunas of the different islands of the archipelago were nested in each of the two time periods (Table 1 in Paper III). Furthermore, most of the species and the bird communities of the islands were consistently nested and idiosyncratic, respectively, during both periods. Only three species changed status in terms of being idiosyncratic or nested (Paper III). Sample size influenced the results to a certain degree. However, the low r -values of the correlation between previous and current nested ranks of species and islands (islands: $r_s=0.69$, $p<0.01$; species: $r_s=0.60$, $p<0.01$) suggest that there was some variation in the nested structure that was related to species turnover (for details see Paper III).

The changes in the bird faunas between the two time periods broadly fit the predictions of the nested temperature calculator. In the maximally nested matrix, cell (the species–island combination of birds) occupancy probabilities between 50–100 are lying above the boundary line or extinction curve, and those between 0–50 are below the curve (see Fig. 1 in Paper II). As expected, populations occupying cells above the extinction curve were less prone to become extinct than populations among cells below the extinction curve ($\chi^2=4.255$, $p=0.04$).

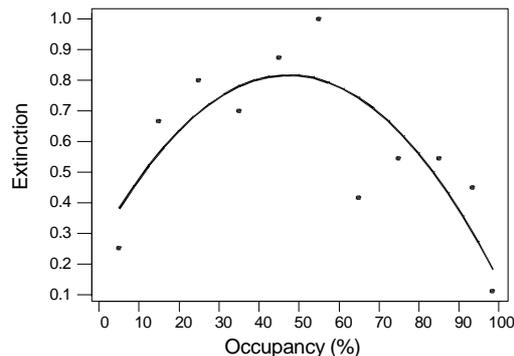


Fig. 4. The relationship between occupancy probability of cells in the nested matrix and proportion of extinction. Proportion extinction = $0.27 + 0.023$ (average occupancy) – 0.0002 (average occupancy)². $r^2=0.67$. A linear model was not significant ($r^2=0.10$).

When each of the occupancy probabilities range was taken separately (i.e. 5 for range 0-10, 15 for range 10-20, ..., 97-100), the proportion of extinction was non-linearly related to the average occupancy probability, being smaller for cells with high and low occupancy probabilities (Fig. 4). The above relationship seems to be a consequence of the association between species nested rank and the proportion of extinctions. Species' nested rank was non-linearly related both to proportion of local extinction (Fig. 5a) and occupancy turnover (Fig. 5b, $p < 0.01$), as proportion of local extinction and turnover was lower for species with low, i.e. common species, and high nested rank, i.e., rare species.

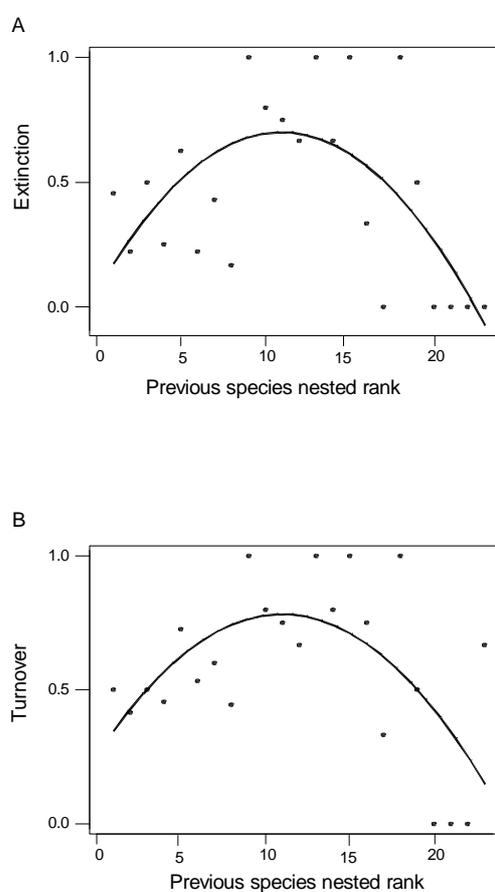


Fig. 5. The relationship between previous (1962-1969) species nested rank (SNR) and the proportion of extinction of species (A) and island occupancy turnover (B). Proportion of extinction = $0.06 + 0.12 (\text{SNR}) - 0.005 (\text{SNR})^2$. $r^2 = 0.41$; Species occupancy turnover = $0.25 + 0.10(\text{SNR}) - 0.005 (\text{SNR})^2$. $r^2 = 0.37$. Linear models were not significant ($p > 0.05$) $r^2 = 0.05$ for proportion of extinction, and $r^2 = 0.04$ for species turnover.

In the nested matrix, high occupancy probabilities often refer to combinations of common species in species-rich islands. Such species are less vulnerable to extinctions because the combination of being regionally common and occupying a species-rich, often large, island are expected to lead to stable populations (Hanski 1982, Graves & Gotelli 1983, Yiming et al. 1998). Low occupancy probabilities often refer to unexpected presences, i.e. rare species in species poor islands, here idiosyncratic species. The combinations of restricted distributional range and low proportion of extinction and low turnover of rare idiosyncratic species suggest that these species exist in small but stable numbers. A characteristic expected for habitat specialists in limited but stable environments.

The higher extinction rates and turnover for the mid rank species was linked to the changes in incidence of some species that were associated with regional changes. Such regional distribution changes could reflect natural, e.g. the Speckled pigeon, or anthropogenic causes, e.g. Egyptian Vulture (also see Smith 1957, Zinner 2001), or both.

The proportion of species that became extinct was not related to previous island nested rank. The lack of a significant relationship is probably due to the fact that the previous island nested rank was not significantly correlated with island area (Table 2), which was a determinant of extinction (lower in larger than smaller islands; Table 2). In contrast, there was a significant relationship between current nested rank of islands and island area (Paper I and II). It is not clear why the previous nested rank was not significantly related to island area but, probably, the previous nested rank did not truly reflect the hierarchical relationship among the islands. Possible reasons for this are variation in the regional dynamics, sampling artefacts and sample sizes.

As predicted, colonization was proportionally more frequent among cells above than below the boundary line or extinction curve ($\chi^2 = 10.22$, $p = 0.001$). Moreover, the proportion of colonization of islands by each of the species was negatively correlated to the previous nested rank of the species ($r_s = -0.512$, $p < 0.01$). Thus, species with low rank, common species, colonized islands they had been absent from more often than high rank species, rare species. The proportion of colonisation was not related to island nested rank but it was negatively correlated with island isolation from the mainland (Table 2). Probably, this was a consequence of the fact that island nested rank was not related to isolation (Table 1). Thus, the usefulness of the nested rank and other metrics derived from nestedness may depend on how strongly these metrics are related to the causal factors (Doak & Mills 1994).

To sum up, my study shows temporal consistency in nestedness of island bird faunas, and that the nested temperature calculator generates testable predictions for the analysis of temporal changes in faunas. Species richness on islands seemed to depend on a balance between area-dependent extinction and isolation-dependent colonization. In some cases there was either a poor fit or a non-linear relationship between current data and the predictions generated by the nestedness analysis of the previous data. These results might have been caused by (i) regional population changes, natural as well as anthropogenic, (ii) stability of some rare

species in larger islands, and (iii) stability of some idiosyncratic habitat specialists. The influence of such factors may reduce the predictive power of nestedness models and other similar models (e.g. habitat models, Johnson & Krohn 2002). Therefore, the distinction between the relative influence of local and regional dynamics is important to understand the spatio-temporal dynamics of species as well as the local coexistence of species (Pulliam 1988, Harrison 1994, Whittaker 2000, Azaria 2004).

CONCLUSION

As a dominating paradigm during the last three decades the island biogeography theory (IBT) (MacArthur & Wilson 1967) has contributed much towards the development of island ecology. However, the simplified assumptions of the IBT do not fully reflect the complexity in structure and dynamics of island communities. Recently, it has been suggested that there is a need for a new island biogeography theory that also acknowledges compositional differences, ecological differences among species and temporal dynamics (Lomolino 2000, Brown & Lomolino 2000, Whittaker 2000). Watson (2002) provided a conceptual framework that identifies eight types of ‘insular systems’ depending on differences in origin (fragments *vs* islands), age (young *vs* old) and contrast with the surrounding matrix (low *vs* high contrast) (see also Diamond, 1981b, Nekola & White 1999). He suggested that patterns of species richness could differ between insular communities depending on whether it is relict (present before fragmentation), the species are matrix-derived, or species disperse among isolates (Watson 2002). This framework does not explicitly consider the compositional aspect, however, an issue that has been addressed elsewhere (Nekola & White 1999). A general trait of the new improvements of island biogeography theory is the emphasis on differences in dispersal abilities among species and its importance for shaping insular communities (e.g. Hansson 1998, Nekola & White 1999, McDowall 2004).

In contrast to the traditional IBT view of dispersal from mainland to island, my study indicates that inter-island dispersal is important for the patterns of species richness and community structure (Paper I, II, III & IV). For example, large islands in the Dahlak archipelago may act as a source pool and thus ‘rescue’ populations particularly among islands with high extinction rates. The fact that small neighbouring islands are inhabited by similar communities (Paper I) suggests that inter-island dispersal is of general importance for structuring insular communities. Similar observations were made for the birds in the east African coastal forest (Paper IV). Hence, it is possible that initial differences in insular community patterns, caused by the origin of isolates, later will converge after time given that dispersal abilities are high (see also Watson 2002). However, such a scenario may not apply to many mammals and particularly reptiles because they lack strong enough dispersal ability (Paper IV).

Habitat diversity has been suggested to be more important for habitat specialists than generalists (Ricklefs & Lovette 1999). My results are in line with this idea,

i.e. species richness of forest specialist, but not generalist, birds and mammals increased with habitat diversity (Paper IV). Again, however, there is a strong influence of dispersal ability because the relationship between habitat diversity and species richness did not hold when the habitat specialists (1) were unable to reach sites with suitable habitats (specialist reptiles: Paper IV), (2) had clumped distributions due to inter-island dynamics (Paper III) or had evolved in isolation from other communities (endemic reptiles; Paper IV).

Although nestedness analysis has received criticism due to the treatment of null models (e.g. Fischer & Lindenmayer 2002), my studies suggest that it is a useful tool when investigating the dynamics of insular community composition. For example, the nested community structure of the Dahlak islands depended on area and distribution of only a few key habitats (Paper I & II). Thus, contrary to earlier suggestions a nested community may not require a nested structure of habitats (e.g. Calmé & Desrochers, 1999). Rather, the importance of habitat can depend on that certain habitats or vegetational structures are more important than others because they attract many species, but probably for different reason (Paper II).

The role of competition for faunal assemblages on islands is an enigma in community ecology, and, hitherto, there is no clear-cut evidence of competitive exclusion of species (Connor & Simberloff, Gilpin & Diamond, Whittaker 2000, Sfenthourakis 2004, Paper II). My results suggest, however, a case of prey-predator interaction for negative species-species associations, and, possibly, predator-prey interactions may be more important for structuring insular communities than has been shown in earlier studies (e.g. Järvinen & Haila 1984).

Whether nested communities broadly remain the same over time has been debated and, consequently, it is an important area of future research (e.g. Whittaker 1998). Here, I present the first study testing the temporal stability of nested communities. The results suggest that many species may remain nested and idiosyncratic over a period of 35 years (Paper III). Furthermore, by using the nestedness analysis I examined whether turnover dynamics could be predicted from the nested community pattern. Turnover agreed in large with the predictions, although some species deviated from the expectations based on the nested pattern (Paper III). The form of the relationship was non-linear probably due to large-scale fluctuations in population dynamics, particularly among the moderately common species (Paper III). Species with spatially restricted resources, e.g. those breeding in mangroves, may show smaller regional fluctuations in periods of general resource limitation over large areas such as during droughts, which is a recurrent event in East Africa.

Dynamics on large scales may arise due to natural, stochastic events as well as human disturbance (Whittaker 1995, Fox & Fox 2000). For instance, extinction and colonization of some birds in the Dahlak archipelago followed regional expansions and contractions. This may be related to the irregular temporal and spatial pattern of the droughts and rainfall in this region. In fact, this may be the most important reason for that many land birds in the region, nearly all in the Dahlak archipelago, are opportunistic breeders, i.e. rainfall triggers breeding (Smith 1955). Similarly, it is likely that the current patterns of the animals of the east African coastal forest have been influenced by both climate changes, i.e. a

long term increase in aridity and coastal inundations of the forests on lower altitudes (Burgess et al. 1998) and recently human disturbance (Clarke 2000b). Such events lead the insular system to be in a non-equilibrium state (e.g. Heaney 2000). This is particularly evident for taxa consisting of poor dispersers, which obviously may not be able to re-establish in forests that developed after such perturbations (e.g. reptiles Paper IV).

Hence, the identification of the types of organisms and the inter-specific interactions as well as the population dynamics, i.e. island-mainland, intra-archipelago or within islands or patches, are key elements for understanding the processes structuring communities (Haila et al. 1979, Pulliam 1988, Wiens 1989, Haila 1990, Cornel & Lawton 1992, Fox & Fox 2000, Whittaker 2000). My study emphasizes also the need of using different time-scales in studies of island biogeographical patterns and that the mechanisms influencing island biota may also change over time. Thus, it may be better to view insular systems as non-equilibrium systems (Brown 1971, Diamond 1982b, Brown & Lomolino 2000) than the traditional view of systems in equilibrium MacArthur & Wilson model (1967). The answer to the distribution of organisms may not lie in a single theory, however, but rather in diverse approaches that appreciate the diversity of ways that biotas has developed: biodiversity is but uniqueness.

Conservation implications

In view of the different spatio-temporal processes involved in the dynamics of species distributions both in the Dahlak archipelago and in the coastal forests of Eastern Africa, my thesis suggests it may be complicated to set strategies to conserve each of the various biota in insular systems. Although large, species rich areas should be a priority for conservation, conservation strategies should target also small or species poor islands with key resources for rare, idiosyncratic species. This is because endangered habitat specialists are often more sensitive to the structure and type of habitats than area per se. Therefore, the identification and protection of key habitats should be a priority in the conservation of such species. Stochastic events occurring on large scales entail that conservation of biodiversity mainly should focus on maintaining regional networks. In such situations, good dispersers such as birds may be able to colonize new suitable sites and, by doing so, the population is, not only, 'rescued' on other islands or patches but its distributional range may have shifted to another part of the network. In contrast, organisms with poor dispersal ability such as the reptiles in the east African coastal forest have to be rescued by intervention, e.g. by translocation of populations.

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