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Influences of Island Characteristics on Plant Community Structure of Farasan Archipelago, Saudi Arabia: Island Biogeography and Nested Pattern

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1. Introduction

Biogeographers have long been fascinated by the factors influencing numbers of species on islands. The increase in species number with area is one of the oldest known ecological patterns, first documented by Watson and deCandolle in the mid-nineteenth century (Rosenzweig, 1995). Island biogeographers lacked a cohesive body of theory, until island biogeography equilibrium theory (MacArthur & Wilson, 1967) attempted to explain variation in species richness between islands of different area and isolation. The theory predicts that species richness decreases with decreasing island area and increasing isolation as these two variables influence immigration and extinction (Rosenzweig, 1995). Numerous studies have examined and argued the stability of these relationships on different island groups and for different taxonomic categories.

However, the equilibrium theory should be expanded to include other aspects of insularity other than area and isolation in order to fully understand the mechanisms of island biogeography (Whittaker, 2000). In addition to area, distance, and elevation, numerous other variables have been examined as potential predictors of insular species richness, such as habitat diversity (Rafe et al., 1985; Kohn & Walsh, 1994), rainfall (Heatwole, 1991), soil type (Johnson & Simberloff, 1974), energy (Wright, 1983) and disturbance (El-Bana, 2009).

Although classical island biogeographical theory has been questioned (Gilbert, 1980; Whittaker, 2000) and a call for a new paradigm of island biogeography has been issued

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(Lomolino, 2000a), area and distance still play primary roles in alternative theories (Heaney, 2000; Lomolino, 2000b). In general island area, and to a lesser degree isolation, can hardly be disputed as important determinants of insular species richness.

Area might influence species richness directly in two ways: larger islands present larger targets for dispersing individuals and they generally support larger populations. Thus, island area may influence species richness by its effect on colonization rates or on the outcomes of several mechanisms that determine vulnerability to extinction (MacArthur & Wilson, 1967). Area might also influence species richness indirectly via its correlation with other factors that affect diversity directly. Among the most plausible of such potentially confounding variables is habitat diversity, which is often presumed to increase in direct relation to island area (Kohn & Walsh, 1994). The negative correlation between island isolation (distance from either the mainland and/or the large islands) and species richness, although not as strong, is also well documented. Since species differ in the maximum distance over which they can disperse, islands that are near the mainland will potentially receive propagules from more species than will distant islands (Rosenzweig, 1995).

During the last decade, ecologists and biogeographers have devoted increasing attention to the pattern of nested species assemblages in insular habitats. Nestedness occurs where assemblages in depauperate sites are comprised of species that constitute subsets of species that occur in successively richer sites. In nested biotas, common species tend to occur in all sites while rare species tend to occur only in the richest sites. This pattern indicates a high level of non-random organization of assemblages and has important implications for conservation (Patterson & Atmar, 1986; Patterson, 1990; Patterson & Brown 1991; Fleishman et al., 2007). Nestedness has been interpreted as a measure of biogeographic order in the distribution of species (Atmar & Patterson, 1993). This pattern indicates a high level of non-random organization of assemblages and has important implications for maintaining or maximizing species diversity in ecosystems threatened by anthropogenic effects (Maron et al., 2004; Fleishman et al., 2007).

Diverse biotic and abiotic processes are believed to generate nested distributions, including selective extinction (Atmar & Patterson 1993; Wright et al., 1998), differential colonization (Kadmon, 1995), nested habitats (Wright et al., 1998; Honnay et al., 1999), and differential environmental tolerances among species (Fleishman et al., 2007). Differences in environmental tolerances among species may interact with nested habitats to produce nestedness. According to this hypothesis, species-rich sites are those that contain the greatest habitat heterogeneity and/or have environmental conditions tolerable to the largest number of species (Cook, 1995; Honnay et al., 1999). Differential nestedness among groups of species (e.g., taxonomic groups or guilds) that vary in sensitivity to a particular environmental variable may determine how that variable contributes to the general pattern of species nestedness.

Nestedness has important implications for conservation, when species assemblages on an archipelago or habitat fragments show nestedness, it is more efficient to protect large islands or fragments than smaller islands or fragments (Patterson, 1987). Others have suggested that the management of colonization processes might also be important for the long-term maintenance of diversity (Lomolino, 1994; Cook, 1995).

On the arid archipelagoes, environmental features such as salinity, aridity, habitat diversity, elevation and human disturbance may interact with life history characteristics of plant species in determining local extinctions or colonization. The islands and archipelagos of Red Sea attracted less attention about their pattern of vegetation distribution and dynamics, compared to the Mediterranean Sea (Panitsa & Tzanoudakis, 1998, 2001; Panitsa et al., 2006; Médail & Vidal, 1998; Khedr & Lovett-Doust, 2000; Bergmeier & Dimopoulos, 2003; El-Bana, 2009).

Here we explore the patterns exhibited by plant species richness and nestedness on 20 islands of the Farasan archipelago in the Red Sea (Saudi Arabia) to identify possible effects of island size, elevation, number of habitats and distance from species pool. We also examine the best fit model for the total species richness, as well as the special patterns exhibited by certain important taxonomic and ecological subgroups of plant species.

2. Materials and methods

2.1 Study area

The Farasan archipelago consists of more than 36 vegetated islands and extends between longitudes $41^{\circ} 20'$ and $42^{\circ} 25'$ E and latitudes $16^{\circ} 20'$ and $17^{\circ} 10'$ N along the southern Red Sea (Figure 1). The islands, with elevation in the order of tens of metres, range in size from very small, a few m^2 , to the very large island of Farasan Alkabir, about $319.5 km^2$. All islands are an uplifted coral reef that formed during the Pleistocene on a foundation of salt diapirs (i.e. domes of salt rocks from the Miocene; Dabbagh et al., 1984). There is some variation in geomorphology among the islands despite their similar origin. The shore may rise gently to be followed by salt marshes and sandy plains, or be marked by small cliffs emerging from the coralline plateau and covered by coral rubble, and some islands feature a rugged structure of hillocks and outcrops. Some islands such as Zifaf and Sasu islands are hilly. Large boulders, gravels and small stones are found in the steep runnels of these islands.

The islands are an important habitats for both local and migrating birds. In addition, the islands home for the threatened and endemic Arabian gazelle and other mammals (Masseti, 2010). Most of the islands are subjected to heavy human activities such as overgrazing and wood cutting. Furthermore, the exotic and invasive tree *Prosopis juliflora* was introduced for greening landscape along roadsides in Farasan Alkabir island. It has escaped the cultivated sites and invaded the rich natural habitats such as Wadi Mattar.

Unfortunately, there are no climatic records available for Farasan Islands. The climate at Jizan city (42 km from Farasan Islands) is hot and humid with a maximum daily temperature in the range of $35-40^{\circ}C$ during July. The overriding influence on the islands is the high year-round humidity, mitigated by winds. The mean annual rainfall is about 70 mm at Jizan. As in other arid regions, the condensation of dew is very important for the growth of vegetation on these islands (Osborne, 2000).

2.2 Data collection

Vegetation surveys were commenced in 2009 and 2010 during the rainy season from January to April. Random sampling was used in selecting 20 islands to represent an array of sizes, which ranged in area from $0.081 km^2$ to $319.5 km^2$ (Figure 1). Area (km^2), distance (km) to the

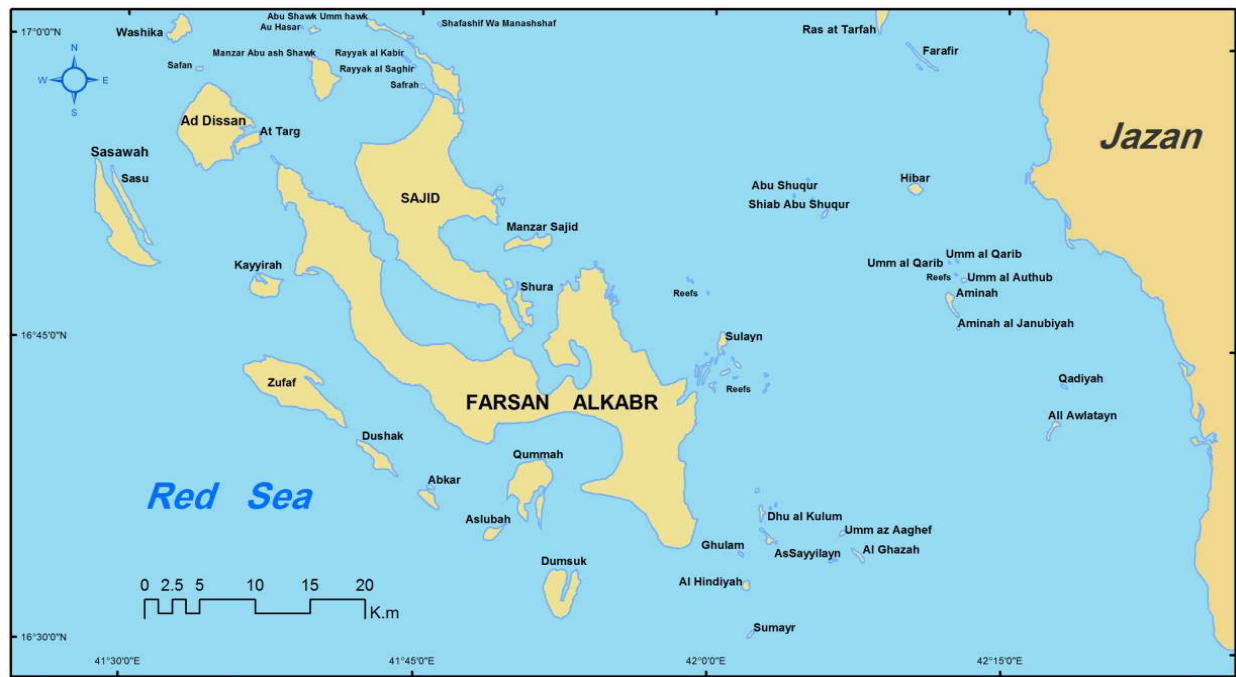


Fig. 1. Farasan archipelago showing the location of the 20 studied islands (Abkar, Abu Shawk Umm Hawk, Ad Dissan, Al Hindiyah, Aslubah, At Targ, Dumsuk, Dushak, Farasan Alkabir, Kayyirah, Manzar Abu Shawk, Manzar Sajid, North Reefs, Rayyak Al Kabir, Safrah, Sajid, Shura, South Reefs, Sulayn and Zufaf.

nearest large island, and elevation (m) of each surveyed island were calculated by the program (Arc*GIS, 2008 USA). Two hundred and ten stands were selected to represent the main habitats on each island. Seven main habitat types were recognized: wet saline marshes, dry saline marshes, sand plains, mobile sand dunes, wadi channels, and coral rocky crevices and runnels. The stand size was about 10 m × 10 m in all habitats, except for the salt marshes and the rocky crevices and runnels where vegetation appeared as strips; the shape was modified to 5 m × 20 m. In each stand, shoot presence/absence of all vascular plant species was recorded. The position of each sampled stand was georeferenced using GARMIN GPS map 276.

All plant species were identified in each island following Chaudhary (1989, 2000); Collenette (1999). Plant species were categorized in terms of their life-forms (therophytes, hemicryptophytes, geophytes, chamaephytes and phanerophytes), salt tolerance (halophytes and glycophytes) and succulence (succulents and non-succulents). Life-forms of the plants were determined according to Raunkiaer classification (Raunkiaer, 1934). This classification is of special importance for the vegetation in arid regions. These categories reflect adaptation and tolerance of vegetation to the main environmental factors such as drought and salinity. Furthermore, this classification was used as the processes and factors that underlie species richness in these groups differ, resulting in different richness patterns (Khedr & Lovett- Doust, 2000; Panitsa et al., 2006; El-Bana, 2009).

2.3 Statistical analyses

To identify factors that were important in determining the distribution of plant species and their ecological subgroups, simple linear regression was performed on the species/ecological group richness and biogeographical variables to characterize the functional relationships

between the variables, as well as to generate predictive values from empirically fitted regression models. Stepwise multiple regression analysis also was used to identify the best predictor of total species richness and the partitions of the data set of ecological subgroups, using area, elevation, shortest distance from the nearest large island and number of habitats as predictor variables. It is not always clear which measure of geographical isolation to use, i.e. distance from the mainland, the nearest large island, or just the nearest island, and usually a different measure might be necessary for different islands (Turchi et al., 1995; Sfenthourakis, 1996; Morand, 2000; Brose, 2003). In the present case, we chose distance from the nearest large island (Farasan Alkabir) because this island is the most likely candidate for serving as species pools for the other islands examined here. The regressions were run using both logarithmic and arithmetic values for all variables and the best functions according to the behaviour of residuals and the total variance explained (R^2) were chosen. All regressions and the estimations of parameters were carried out with SPSS v.16. We calculated Cole and Mao- Tau sample-based rarefaction curves (Colwell et al., 2004) using EstimateS software (Colwell, 2005, version 7.5).

2.4 Nested analyses

The data was prepared by constructing presence/absence matrices (1= present, 0 = absent) where columns and rows represented species and islands, respectively. The islands (rows) were rank ordered in relation to decreasing number of species and the species (columns) were rank ordered in relation to decreasing number of sites occupied. We then conducted nestedness analyses at two different spatial scales (entire species richness) and the ecological subgroup scales. To determine nestedness of assemblages we used the Nested Temperature Calculator computer program (Atmar & Patterson, 1995). This program calculates a temperature value (T) for the matrix ranging from 0 to 100, based on its presence/absence structure. A temperature of 0, indicates maximum order (maximum nestedness) and 100, indicates disorder (complete lack of nestedness) (Atmar & Patterson, 1993). To determine the significance of T (observed temperature) it is compared with the distribution of simulated temperatures produced by randomization of the matrix in Monte Carlo simulations (500 iterations). This method was used because of its statistical properties and because it can be directly compared among different taxonomic and ecological groups (Wright et al., 1998).

The effects of island area, number of habitats, isolation, and elevation on the degree of nestedness were evaluated by correlating the ranking order of islands in the observed matrix (arranged to maximize nestedness, Atmar & Patterson, 1995) with the order of islands after re-arranging the matrix in relation to the aforementioned factors using Spearman rank correlation. A significant relationship indicates that species are packed in a predictable order owing to the influence of a given factor (Atmar & Patterson, 1995). This procedure has proven useful for indicating possible mechanisms involved in nested structure (Atmar & Patterson, 1995; Kadmon, 1995; Honnay et al., 1999).

3. Results

3.1 Species richness

We detected a total of 191 species among 129 genera and 53 families on the surveyed islands. Most species occurred on relatively few islands (Figure 2a). About 95.5% (183 of 191) of the species occurred on ≤ 10 islands. Likewise, most islands contained relatively few

species (Figure 2b). About 80% (16 of 20) of the islands contained less than 60 species. Rarefaction curves of Cole and Mao-Tau for species richness (Figure 3) reached the asymptote before 18 islands, indicating that the sampling effort was sufficient to fully capture the richness and diversity of plant species assemblages.

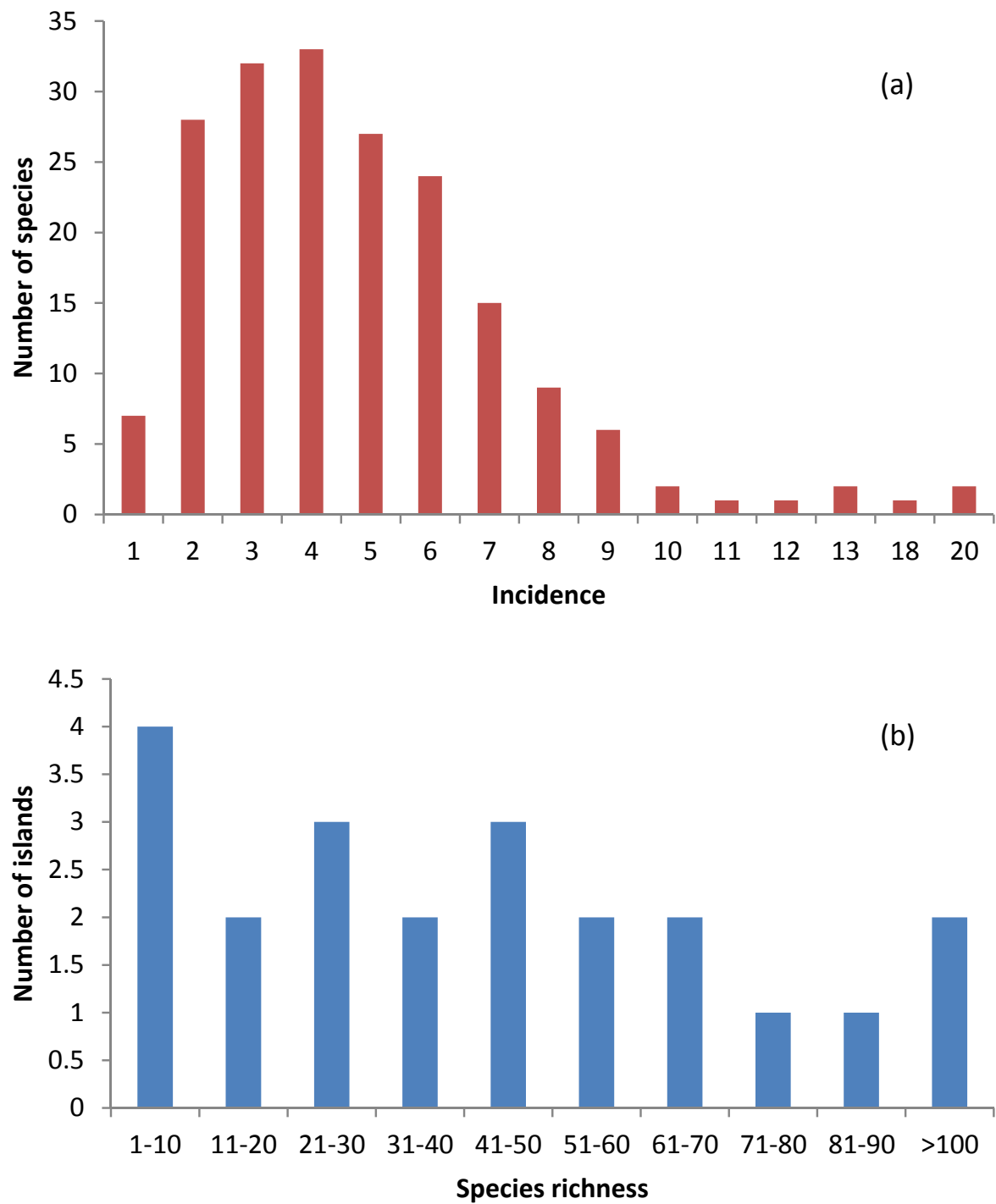


Fig. 2. Frequency distributions of incidence (i.e., the number of islands on which a species occurred) (a) and species richness (i.e. the number of species on an island) (b) for the toal flora of the Farasan archipelago.

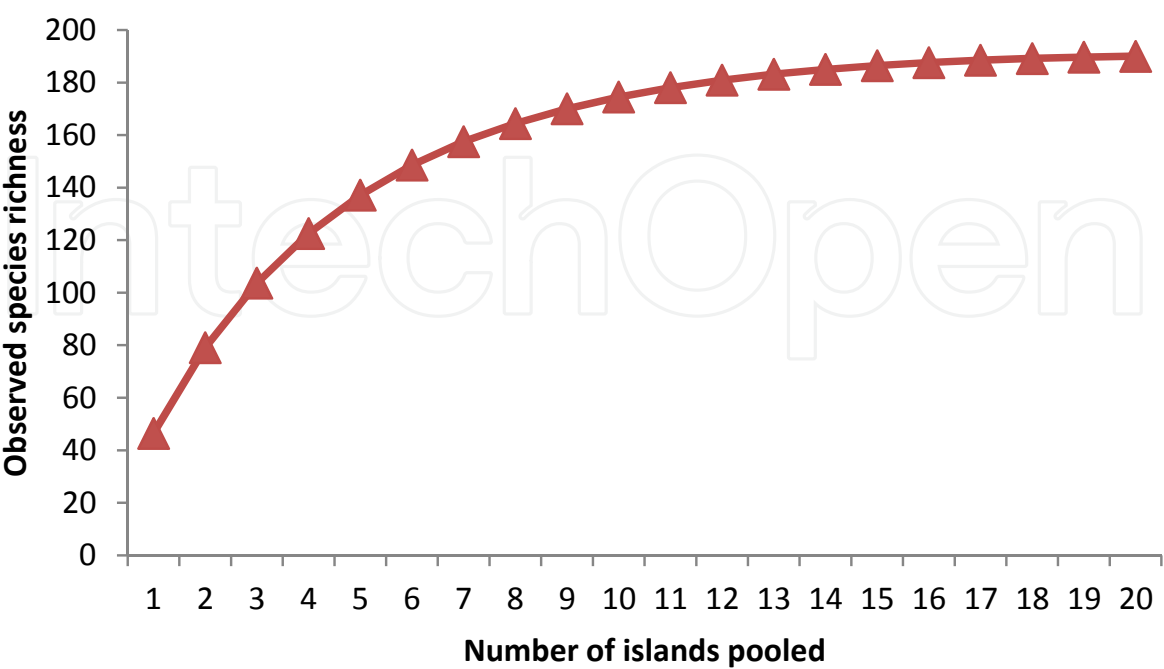


Fig. 3. Relationship between the number of islands pooled and the observed species richness of Farasan archipelago by rarefaction analysis. The asymptotic shape of the curve indicates that analysis of 18 islands provided sufficient sampling to fully capture the richness and diversity of plant species assemblages.

There was a significant positive relationship between island area and total plant species (Figure 4) with $r^2 = 0.732$ and $Z = 0.491$, $P < 0.0001$. Moreover, when the flora of each island was classified into different ecological groups and $\log S/\log A$ was constructed, it appeared that each group had significantly different regressions. There were positive relationships between island area and each of perennials ($r^2 = 0.735$ and $Z = 0.312$, $P < 0.0001$) and annuals ($r^2 = 0.691$ and $Z = 0.168$, $P < 0.0001$) (Figure 4). Similarly, island area showed positive relationships with halophytes ($r^2 = 0.426$ and $Z = 0.049$, $P < 0.041$) and glycophytes ($r^2 = 0.737$ and $Z = 0.439$, $P < 0.0001$) (Figure 5). For succulence ecological groups, island area related positively with succulents ($r^2 = 0.669$ and $Z = 0.056$, $P < 0.0001$) and non-succulents ($r^2 = 0.73$ and $Z = 0.434$, $P < 0.0001$) (Figure 5). For the different growth forms, island area showed positive relationships with shrubs ($r^2 = 0.673$ and $Z = 0.087$, $P < 0.0001$), herbs ($r^2 = 0.729$ and $Z = 0.189$, $P < 0.0001$), trees ($r^2 = 0.816$ and $Z = 0.055$, $P < 0.0001$) and grasses ($r^2 = 0.684$ and $Z = 0.069$, $P < 0.0001$) (Figure 6).

The number of habitats was related positively with the island area ($r^2 = 0.516$, $P < 0.001$) (Figure 7a). In addition, the total number of species had a positive relationship with the number of habitats ($r^2 = 0.847$, $P < 0.0001$) (Figure 7b), and elevation ($r^2 = 0.366$, $P < 0.003$, data not shown). However, the distance from the largest island (Farasan Alkabir) has no effect on the species richness ($r^2 = -0.061$, $P < 0.887$).

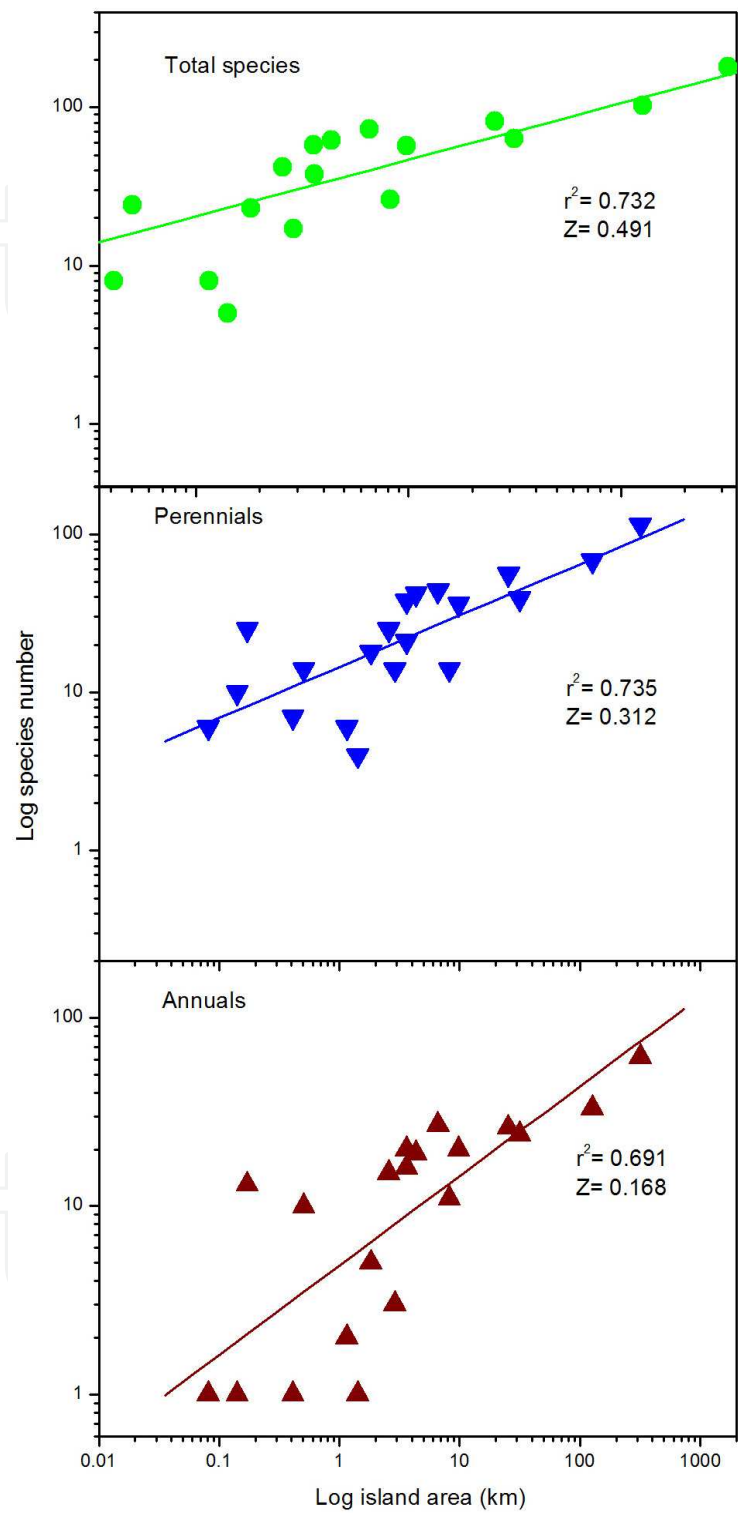


Fig. 4. Relationships of total species richness, number of perennials and annuals with island area of Farasan Archipelago

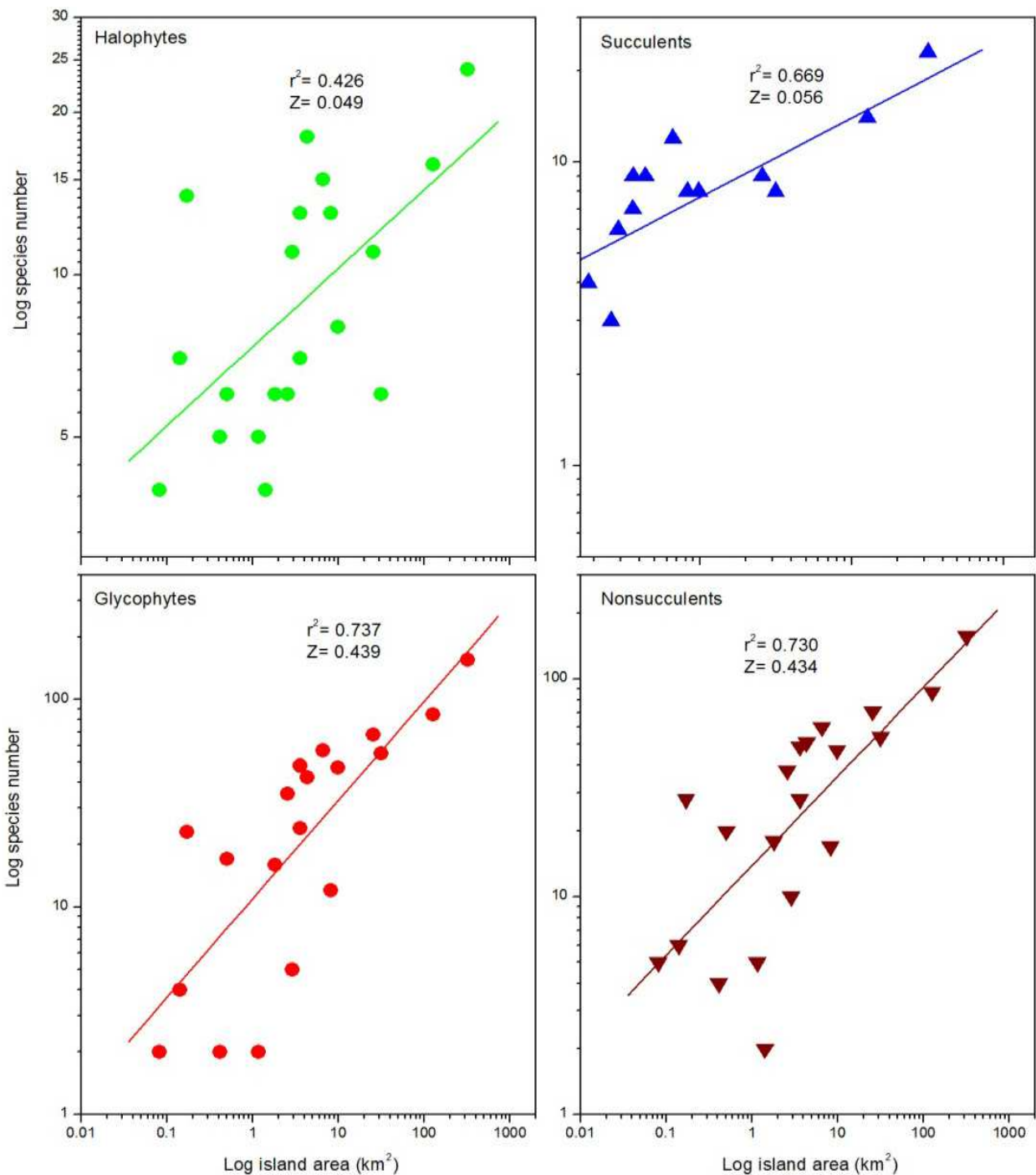


Fig. 5. Relationships of ecological groups (halophytes, glycophytes; succulents and non-succulents) with island area of Farasan Archipelago.

According to the stepwise regressions (Table 1), both island area and number of habitats affect species richness. When the same analyses were applied separately for each ecological groups, elevation was also significant parameter entering the model for perennials and annuals. Area, number of habitats and elevation explained a high percentage (88.7%) of total variance for annuals, while they explained about 72.3% of variance for the perennials. On

the other hand, the number of habitats was not entering the model for shrubs, trees, non-succuelnts and halophytes (Table 1). Area and number of habitats entered the models of grasses, herbs, succulents, and glycophytes. Area and elevation were the only variables that entered the model for both trees and non-succulents, while area alone counted for shrubs (89.2%) and halophytes (76.2%). Distance from nearest large island (Farsan Alkabr) did not affect either the total species richness or any ecological groups.

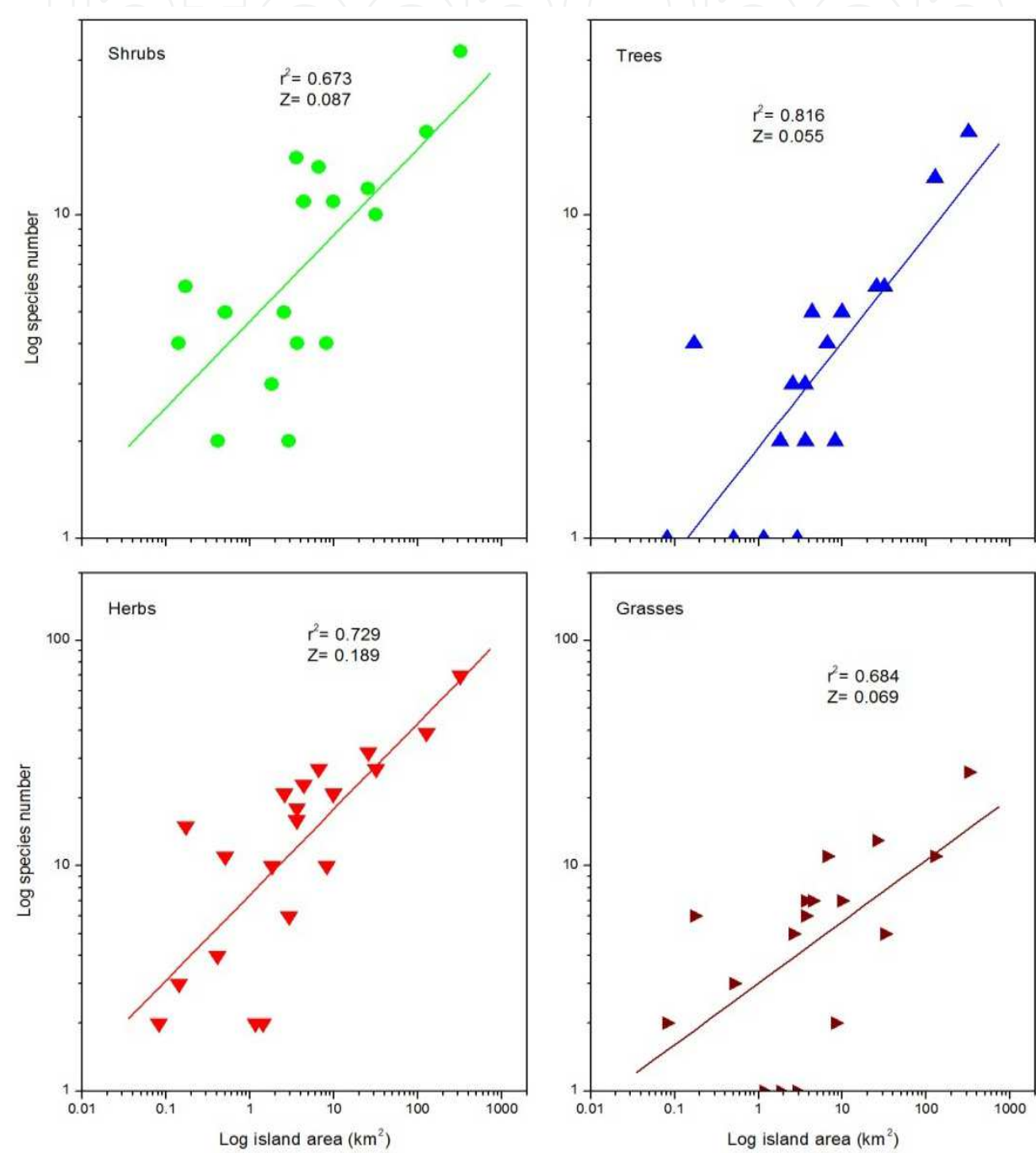


Fig. 6. Relationships of ecological groups (growth forms) with island area of Farasan Archipelago.

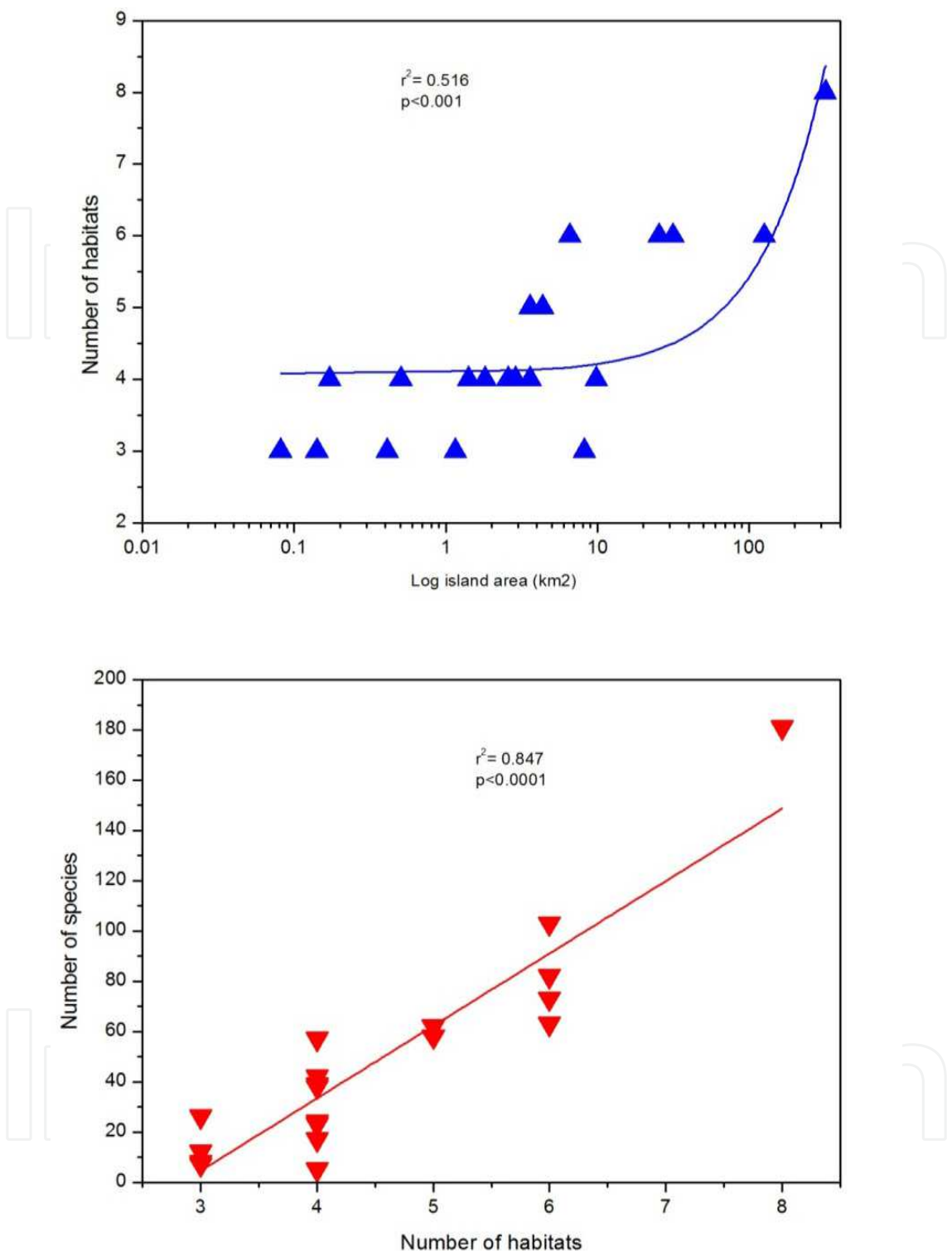


Fig. 7. Relationships of the number of habitats with island area (top) and with the total number of species (bottom) of Farasan Archipelago.

3.2 Nestedness pattern

The temperature nestedness calculator detected a high degree of nestedness for the entire flora as well as for each of the ecological subgroups (Table 2). The temperature of the maximally

packed matrix ($T_{\text{matrix}} = 12.87^{\circ}$) for the entire flora was significantly lower than the mean temperature of the random matrices generated by the Monte Carlo-derived null model ($T_{\text{random}} = 63.06^{\circ}$, $P < 0.0001$). Therefore, the plant communities were significantly nested.

Data set	Function	Adjusted R ²	P-value
All species	$S = 0.41 + 4.16 A + 6.55 H$	0.856	< 0.001
Life span			
Annuals	$S = 6.12 + 4.61A + 2.66 H + 3.52 E$	0.887	< 0.001
Perennials	$S = 7.71 + 8.39 A + 9.85 H + 1.32 E$	0.723	< 0.001
Growth form			
Grasses	$S = 3.67 + 5.05 A + 8.43 H$	0.849	< 0.003
Shrubs	$S = 4.58 + 3.19 A$	0.892	< 0.001
Herbs	$S = 2.45 + 2.31 H + 1.78 A$	0.715	< 0.001
Trees	$S = 4.28 + 2.35 A + 5.38 E$	0.921	< 0.000
Succulence			
Succulents	$S = 3.25 + 6.23 A + 2.12 H$	0.733	< 0.007
Non-succulents	$S = 6.22 + 14.12A + 1.45 E$	0.832	< 0.003
Salt tolerance			
Halophytes	$S = 3.59 + 1.16 A$	0.762	< 0.016
Glycophytes	$S = 7.64 + 4.93 A + 14.73H$	0.899	< 0.004

Table 1. Stepwise linear regressions of total species number and species number by ecological subgroup. Only variables that enter the model are shown, with the total variance explained and the statistical significance of the respective model. S abbreviates to species richness, A to island area, H to number of habitats and E to elevation.

When each ecological group was analyzed separately, the species distributions were significantly nested for all subgroups (Table 2). For the life span subgroups, the mean matrix temperatures for perennials and annuals were 13.36° and 12.69° that significantly different from the mean matrix temperatures of 62.64° and 58.92° generated randomly by Monte Carlo simulations, respectively (Table 2). The life-form distributions were significantly nested for all forms. The mean matrix temperatures were more strongly nested for therophytes, geophytes and chamaephytes with 11.14° , 13.35° and 13.63° compared to random temperatures of 58.44° , 59.87° and 58.92° , respectively ($P < 0.0001$ for all). The mean matrix temperatures of hemicryptophytes, and phanerophytes were 29.48° and 17.27° , respectively. While, their random temperatures recorded 55.48° and 45.18° , respectively. For the salt tolerance subgroups, glycophytes were more nested with a matrix temperature of 13.35° compared to the random temperature of 59.78° generated by Monte Carlo simulations. On the other hand, the matrix temperature of halophytes was 22.33° which significantly different from the random temperature of 61.43° .

The ordered accumulation of species was affected mainly by island area and number of habitats, and to a lesser degree by elevation (Spearman’s rank correlation, Table 3). Island area and number of habitats were also correlated for the different ecological groups. This indicates such that species appeared to accumulate in orderly fashion with increasing area and number of habitats. However, isolation was correlated neither to the total species richness nor to the ecological groups.

Data set	Total number of species	Matrix temperature (°C)	Random temperature (°C)	P ($T < T_{\text{Observed}}$)
All species	190	12.87	63.06	<0.0001
Life span				
Perennials	123	13.36	62.64	<0.0001
Annuals	68	12.69	58.92	<0.0001
Life-forms				
Therophytes	56	11.14	58.44	<0.0001
Geophytes	19	13.35	59.87	<0.0001
Hemicryptophytes	27	29.48	55.48	<0.0001
Chamaephytes	50	13.63	58.92	<0.0001
Phanerophytes	21	17.27	45.18	<0.0001
Growth forms				
Trees	19	19.47	45.82	<0.0001
Shrubs	35	14.62	57.03	<0.0001
Grasses	29	15.48	54.07	<0.0001
Herbs	74	12.5	60.97	<0.0001
Succulence				
Succulents	25	16.33	58.77	<0.0001
Non-Succulents	166	12.14	61.78	<0.0001
Salt tolerance				
Halophytes	26	22.68	61.43	<0.0001
Glycophytes	165	13.35	59.78	<0.0001

Table 2. Results of the nestedness analyses as calculated by the nestedness temperature calculator for total plant species and the ecological subgroups.

4. Discussion

The equilibrium theory of island biogeography (MacArthur & Wilson, 1967) identifies island size and distance from the mainland as the two most important factors affecting species richness. In the present study, there was no effect of isolation from the largest island (Farasan Alkabir) on total species richness, or on richness of the ecological subgroups. However, all categories of plants increase in richness with island size. This shows that (a) Farasan islands adhere to the species-area relationship; and (b) this relationship exists across ecological groups despite differences in the processes and factors that govern diversity for these groups. It has been suggested that the value of the exponent Z should vary between 0.2 and 0.4 (MacArthur & Wilson, 1967; Rosenzweig, 1995). In the present study, the value of the exponent Z for the total species richness is larger than 0.4. However, this is in agreement with the reported values larger than 0.4 for the exponent Z in several other studies of plants on islands (Rydin & Borgegård, 1988; Médail & Vidal, 1998; Panitsa et al., 2006; El-Bana, 2009). For example, the Z value of the log-log model for the Mediterranean arid islands is 0.56 (El-Bana, 2009). Rydin & Borgegård (1988) recorded values varying between 0.36 and 0.56. The strong correlation of species richness with island area, number of habitats and elevation suggests that these quite steep slopes would not be due to the existence of a small island effect (Gentile & Argano, 2005).

Data set	Area	Number of habitats	Isolation	Elevation
All species	0.84**	0.65**	-0.28	0.49*
Life span				
Perennials	0.73**	0.58*	-0.19	0.53*
Annuals	0.92**	0.63**	-0.08	0.60**
Life-forms				
Therophytes	0.88**	0.71**	-0.06	0.57*
Geophytes	0.79**	0.63**	-0.22	0.47*
Hemicryptophytes	0.68**	0.53*	-0.3	0.38
Chamaephytes	0.63**	0.48	-0.04	0.35
Phanerophytes	0.93**	0.70**	-0.18	0.61*
Growth forms				
Trees	0.86**	0.61*	-0.02	0.49*
Shrubs	0.64**	0.55*	-0.22	0.22
Grasses	0.68**	0.47	-0.34	0.33
Herbs	0.71**	0.57*	-0.28	0.50*
Succulence				
Succulents	0.63**	0.39	-0.04	0.28
Non-Succulents	0.82**	0.72**	-0.31	0.52*
Salt tolerance				
Halophytes	0.54*	0.32	-0.23	0.31
Glycophytes	0.87**	0.67**	-0.12	0.55*

* and ** indicate the values are significant at < 0.05 and 0.001, respectively.

Table 3. Spearman’s rank correlations between the ranking order of islands in the observed matrix and the islands were ranked by area, number of habitats, isolation and elevation for the entire plant assemblage and their ecological groups.

In the present dataset the division of island flora into different ecological groups revealed that the slopes of the species area regressions are significantly different for each subgroup. For example, the slope of the log S/log A regression of glycophytes growing on the interior rocky and sandy habitats was higher than that of halophytes growing on the shorelines of islands. Similarly, the slope regression of succulents of saline habitats is lower than those of non-succulents. A similar pattern has been recognized by other studies of island and islet floras (Rydin & Borgegård, 1988; Panitsa et al., 2006; El-Bana, 2009). Buckley (1985) divided the floras of small coastal islands on the basis of geographical origin. He found that the slope of log S/log A curves was smallest for the salt flat group growing on the coastlines of the islands (Z= 0.18) and greatest for the sand ridge group (Z= 0.6) which only occurred at the center of each island. Panitsa et al. (2006) found a difference in Z value between halophytes, therophytes, leguminosae and gramineae. El-Bana (2009) reported that the slope of log A /log S regression for the halophytes was smaller than that of psammophytes (Z = 0.48 vs. Z= 0.64).

Nestedness appears to be a common phenomenon of insular flora (Kadmon, 1995; Wright et al., 1998; Honnay et al., 1999; Koh et al., 2002). Similarly, the present study detected a high degree of nestedness for the entire flora and for each ecological group. Wright et al. (1998) suggested that four filters operate to screen species occurrence in insular habitats and produce nested biotas. Among these were area and distance effects, passive sampling and

habitat nestedness. The area filter appears to be the most important in Farasan archipelago. Species-specific resource requirements and differential minimal area requirements result in different patterns of incidence on the islands.

Area- and species-dependent extinction rates have been suggested to play important roles for species richness of oceanic islands (MacArthur & Wilson, 1967), species composition structure (Nekola & White, 1999) and nestedness in land-bridge islands and in habitat fragments (Patterson & Atmar, 1986; Cutler, 1991; Simberloff & Martin, 1991; Wright et al., 1998). Also, differential immigration may be important in producing nestedness (Simberloff & Martin, 1991; Kadmon & Pulliam, 1993). In the current study, there was a lack of several species on smaller but not on larger islands. The reason could be area-dependent extinction and/or differential immigration, and, if so, one or both of these mechanisms may be influencing nestedness in the Farasan archipelago. The largest and the smallest islands surveyed differ in area by 3 orders of magnitude. The large islands are over 319 km² and the small islands <0.5 km² in area. For the entire flora and each ecological group, the distance has no effect on either species richness or nested pattern. This may suggest that the distance is short enough for recurrent colonization (the rescue effect, Brown & Kodric-Brown, 1977), which may affect nestedness (Cook, 1995; Hecnar et al., 2002). Taking into account that most of the recorded species are wind- and bird dispersed species. This dispersal mode with the short distances from the mainland and large island can explain the absence of isolation in the nestedness pattern (Butaye et al., 2001). Therefore, rescue effects (Brown & Kodric-Brown, 1977) and/or intra-island dispersal (King, 1988) may commonly operate but would be masked considering the wide range of areas and low isolation of the islands in the current study.

Habitat nestedness could induce nested structure in species assemblages because certain habitat specialists will be restricted to less common habitats found only on large islands (Wright et al., 1998; Honnay et al., 1999). The habitats among the islands of Farasan are not distributed randomly as the vegetation is characterized by clear zonation from the shorelines to the centre of islands resulting from both chemical and hydrophysical processes (El-Demerdash, 1996). Smaller islands tend to be salty with halophytic vegetation, while larger islands often have a combination of shoreline types (salt marsh, sand formations) and their interiors are usually rocky and have shrubs and trees. Furthermore, the positive and highly significant relationship of island area with number of habitats and elevation indicates that habitats accumulate in an orderly fashion as area increases.

Although all the ecological groups were significantly nested, there were differences in the degrees of nestedness among groups- halophytes and glycophytes, succulents and non-succulents, and plants corresponding to different life-forms. Despite the fact that halophytes and glycophytes share some similarities as xero-halophytic groups, they also have important differences (Danin, 1999). For example, halophytes are relatively more aquatic and tolerant to water logging and salt spray. On the other hand, glycophytes are more terrestrial and tolerant to sand burial (El-Bana et al., 2007). Therefore, it is not surprising that glycophytes were more highly nested than halophytes. This can be explained by the increased representation of salt habitats in which halophytes tolerate, but which other plants cannot tolerate. Most of the surveyed shorelines of islands are exposed to the effects of seawater, thus sustaining more halophytes. These factors may enable halophytes to dominate the plant communities of shorelines (El-Demerdash, 1996), also taking the fact into

account that halophytes are not affected by human disturbance, such as wood cutting and grazing.

Another mechanism which has been suggested for nested pattern is passive sampling whereby, larger islands capture more dispersing individuals than do smaller islands (Lomolino, 1990; Wright et al., 1998), and common species are more likely to be encountered than rare species. In the current study, passive sampling may account for nestedness. The result of the rarefaction suggests larger islands are capturing more richness and diversity of plant species assemblages. Consistent with this is the suggestion that those species most likely to occur on islands already are widely distributed regionally (King, 1988). For example, *Cyperus conglomerates*, *Arthrocnemum macrostachyum*, *Halopeplis perfoliata*, *Limonium axillare*, *Aeluropus lagopoides*, *Zygophyllum coccineum* and *Zygophyllum simplex* have the highest incidence on the islands and they are also the species having the highest incidence on the coast of Saudi Arabia and southern Yemen (El-Demerdash et al., 1994; Hegazy et al., 1998; Kürschner et al., 1998). This suggests that a sampling filter (sensu Cutler, 1994) also may be operating in Farasan archipelago.

As suggested by Wright et al. (1998), many factors act as filters influencing the distribution of species on islands, and this differs by taxon and geographic setting (Atmar & Patterson, 1995). In this particular case, the nestedness of habitats, the tendency of common species to be widely distributed, rare species and habitats to be restricted to large islands and the differences in scale between large and small islands likely contribute jointly to nested pattern in Farasan archipelago.

5. Conclusion

In the current study, the high level of nestedness, the strong effect of area on total plant species richness and ecological groups, and the similarity of vegetation composition on the islands has several implications for conservation. First, the large and richest islands in Farasan archipelago such as Farasan Alkabir conserve higher diversity than an equivalent area of several smaller islands. This island also includes rare habitats like coral rocks and rare species. Second, the invasion of the unique habitats such as wadi channels and water catchments in this island by the exotic tree *Prosopis juliflora* should be managed to conserve the native biodiversity. Third, the current anthropogenic expansion on this island should be managed to conserve the existence of the rare habitats such as mangal vegetation where *Avicennia marina* and *Rhizophora mucronata* co-occur. Fourth, the protection of such critical mangal habitat is important on the other large island (e.g. Zufaf), due to its limited distribution in the country (Mandura, 1997; El-Juhany 2009, Zahran 2010).

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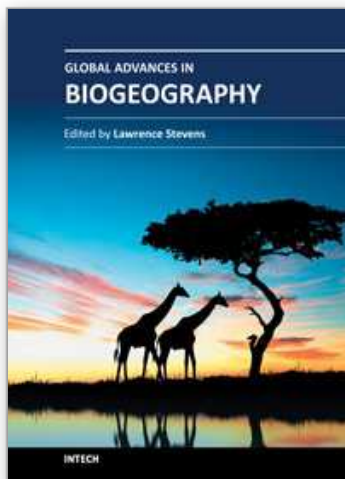
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