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ORIGINAL ARTICLE

Environmental variables associated with insect richness and nestedness on small islands off the coast of northeastern Algeria

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Abstract. This study investigated the association of environmental factors with insect richness and nested patterns in the distribution of species of insects on small islands (northeastern Algeria). Insect species on eleven (11) islands were sampled using pitfall traps, sweep netting and a Japanese umbrella. To explain patterns in insect diversity on small islands, a generalized linear model (GLM) was used to determine the association of the overall richness and that of the dominant orders of insects with environmental variables (altitude, surface area, isolation, plant richness and number of habitats). To determine the nestedness pattern on these islands, the online interface NeD was used to measure total matrix nestedness. Of the variables measured, only plant richness was associated with variations in the overall species richness and that of the five dominant orders. The overall number of insects and that of the five dominant insect orders were significantly nested in all null models except the very restrictive FF model. Plant richness accounted for the nested structure of the overall number of insects and that of the five dominant orders (Coleoptera, Hymenoptera, Hemiptera, Diptera and Lepidoptera). Surface area was also important in the nested structure of overall number of insects and that of the order Lepidoptera. The nestedness of the overall number of insects and that of the five dominant orders of insects, however, did not result from passive sampling and selective colonization. The most effective way of conserving overall number of insects and that of the five dominant orders of insects on the Algerian islands studied is to protect their plant richness and to maximize the overall number of species and that of Lepidoptera on these islands, conservation should concentrate on the largest islands.

INTRODUCTION

Island biogeography theory and nested species distribution are two important concepts in biogeography and conservation (Lomolino & Smith, 2003). The theory of island biogeography considers that variation in specific richness depends on the area and isolation of islands (MacArthur & Wilson, 1967). This theory predicts that species richness decreases with decreasing island area and increasing isolation as these two variables influence immigration and the extinction equilibrium (Rosenzweig, 1995). Some authors reject island biogeography theory, as it does not consider the particularities of each species, diversity of ecosystems and their balance, as well as island-specific characteristics (Brown & Lomolino, 2000; Lomolino, 2000; Anderson & Wait, 2001; Lomolino & Weiser, 2001).

The major reason for studying island species richness and distribution was to determine the degree of nestedness in an insular environment. Nestedness occurs when assemblages at poor sites are comprised of species that constitute subsets of species that occur at rich sites (Patterson & Atmar, 1986). Nestedness is common in nature, especially, on islands (Patterson & Brown, 1991; Atmar & Patterson, 1993; Worthen, 1996; Wright et al., 1998). The results obtained only from nestedness will not provide clear explanations if environmental factors are not associated with this process (Murkami & Hirao, 2010). Thus, using environmental variables to account for the pattern of nestedness recorded for island ecosystems will enable conservationists to focus on the factors associated with diversity and protect the islands harbouring most species.

Different processes can generate patterns in nestedness: (1) passive sampling: can generate nestedness because common species are more accessible and thus easy to sample than rare species (Andrén, 1994) and (2) selective extinction of species: species inhabiting ecosystems experiencing species loss, would disappear from sites in a predictable way, which could lead to nestedness (Cutler, 1991; Lomolino, 1996), (3) differential colonization of habitats: the nested structure of isolated habitats could be due to dispersal limitations as species differ in their ability to colonize (Ryti & Gilpin, 1987; Cook, 1995; Lomolino, 1996), (4) habitat nestedness: considers the nestedness of species assemblages to be a consequence of their close association with habitats that have a nested distribution (Ward & Lakhani, 1977; Honnay et al., 1999).

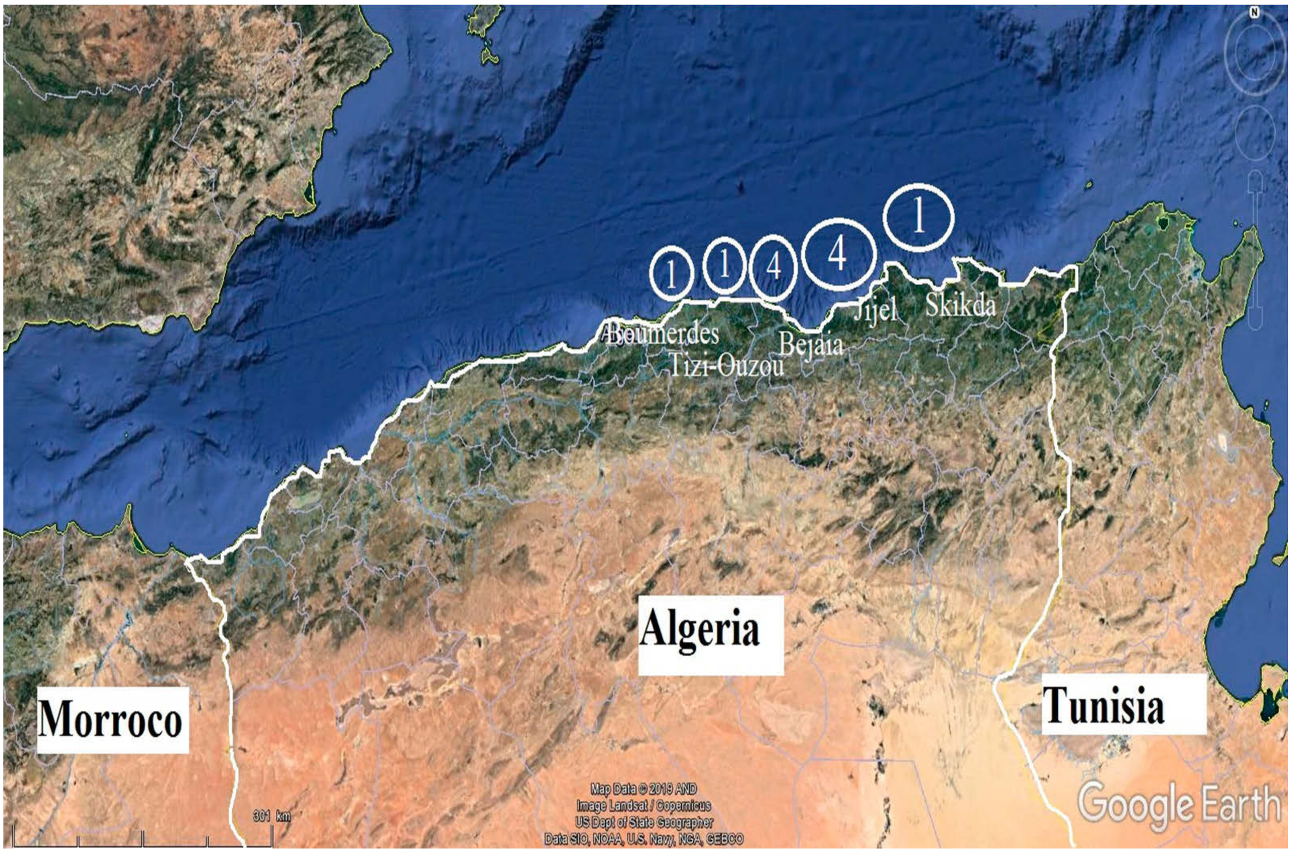

Fig. 1. Geographical location of the islands studied off the northeast coast of Algeria. Skikda region (1 island): Collo; Jijel region (4 islands): Tazrout, Petit Cavallo, Grand Cavallo, small Grand Cavallo; Bejaia region (4 islands): Sahel, Pisans, Ail, El Euch; Tizi-Ouzou region (1 islands): Tigzirt; Boumerdes region (1 island): Agueli.

Island biogeography theory and nestedness have been used to investigate the patterns in insect species richness on islands in the north of the Mediterranean Sea (Dennis et al., 2008; Fattorirni, 2010, 2011), but not in the south of the Mediterranean Sea, other than for Algerian island breeding birds (Aissat, 2020).

The fauna on islands is the least known of all Algerian ecosystems. Thus, recently there have been a few studies on the faunal diversity on some islands off the coast of Algeria (Aissat & Moulaï, 2016; Aissat, 2020; Aissat et al., 2023). Many of these islands are subjected to several disturbing factors such as the presence of large colonies of gulls and the flow of visitors throughout the year, especially in summer.

Understanding the functioning of these island ecosystems and defining the factors associated with the diversity of insects is important for determining the measures necessary for protecting their entomofauna and the conservation of their fragile habitats.

This study aimed to highlight the association of environmental variables with insect diversity on islands, and determine if the pattern in nestedness in the overall distribution of insects and that of the dominant insect orders (Coleoptera, Hymenoptera, Hemiptera, Diptera and Lepidoptera) is similar on small islands. In addition, how nestedness among these assemblages is associated with environmental variables was determined. Identifying the environmental variables associated with the variation in the overall richness of insects and that of the dominant orders, as well as those associated with the nested structure recorded for the islands studied, could be used for defining the management policy for protecting these fragile ecosystems.

MATERIALS AND METHODS

Study area

Along the Algerian coast, from Annaba (East of Algeria) to Oran (west of Algeria), there are 196 islands, islets and rocks (Vela, 2016). Of the Islands in the west of Algeria the largest are: Habibas island (60 ha) and Rechgoune (40 ha). Information on insect species diversity is recorded for only eleven (11) islands (Fig. 1, Table 1). Because of the little data for the rest of the islands, information was collected from published and unpublished field records (Aissat & Moulaï, 2016; Moulaï et al., 2016; Aissat et al., 2023) and Master students' studies (Lachouri et al., 2016; Amrane et al., 2017). The islands included in this study ranged from 7 to 50 m in altitude, and from 0.2 ha to 6 ha in size. Island area, isolation and altitude were obtained from a Google map. Area (m^2) was estimated as the planar surface of the islands. Isolation of islands (m) is measured in terms of the shortest distance between an island and the shoreline (Table 1). Information on plant richness for 11 islands was obtained from the following publications (Benhamiche-Hanifi & Moulaï, 2012; Ghermaoui et al., 2016; Lachouri et al., 2016; Amrane et al., 2017).

Insect sampling

The inventory of the insect fauna took place in spring and summer. Insects were collected for 40 days (20 days for each year

Table 1. Islands surveyed off the northeast coast of Algeria ranked in terms of isolation from 'mainland'. The coordinates, size, altitude, total number of species of insects recorded and estimates of total species richness (Chao 1), habitats surveyed and the number of samples collected on each island are also presented. Jijel region: GCI – Grand Cavallo, PCI – Petit Cavallo, TZI – Tazrout, GCi – Small Grand Cavallo. Skikda region: COI – Collo. Bejaia region: PI – Pisans, EEI – El Euch, SLI – Sahel, AI – Ail. Tizi-ouzou region: TGI – Tigzirt Boumerdes region: AGI – Agueli.

Island	Coordinates	Isolation, distance to mainland (m)	Surface area (ha)	Altitude (m)	Plant richness	Insect richness	Chao1	Habitats/ no. of samples
GCI	36°47´05.60˝N, 5°36´28.01˝E	950	6	50	82	92	103.6	4/20
PCI	36°48´05.23˝N, 5°39´06.20˝E	750	4	10	101	140	150	3/15
COI	36°51´57.60˝N, 6°03´58.63˝E	1000	2.8	25	18	34	40	3/15
PI	36°49´31.01˝N, 4°59´50.88˝E	1250	1.2	30	52	72	96	3/6
EEI	36°53´34.08˝N, 4°47´20.30˝E	120	0.8	20	60	58	83	3/6
AI	36°48´55.61˝N, 4°58´41.85˝E	100	0.4	15	21	34	36	2/6
TGI	36°53´53.80˝N, 4°07´15.45˝E	150	0.35	20	36	29	38	2/6
AGI	36°47´42.01˝N, 3°21´10.25˝E	1000	0.25	20	6	18	20	2/6
SLI	36°47´38.69˝N, 5°01´23.33˝E	7	0.2	15	23	42	55	2/6
TZI	36°51´58.45˝N, 6°03´58.68˝E	20	0.2	15	15	15	18	2/6
GCi	36°46´42.74˝N, 5°36´03.90˝E	50	0.15	30	23	25	27	2/6

sampled) on 11 islands during April and July of the year 2016–2017. Sites sample per island was related to their surface area and habitat heterogeneity. Islands with large surfaces (Grand Cavallo island: 6 ha, Petit Cavallo island: 4 ha; Collo island: 2.8 ha) were surveyed for 5 days and those with small surfaces (not exceeding 1.2 ha) were surveyed for 3 days (Table 1). It was not possible to sample the islands in the different regions at the same time due to logistical reasons and the distances between the islands. Surveys were conducted during daytime between 8:00 and 16:00 h. In total, 98 sites were sampled, which included all the habitats in the areas studied (high mattoral, herbaceous strata, rocky zones and sand dunes) (Table 1). Most of the sites were sampled using three sampling methods. For ground dwelling insects pitfall traps were used, which consisted of plastic cups, 10 cm in diameter and 15 cm deep, which were filled to one third of their capacity with a mixture of seawater (80%) and ethanol (10%) and laundry powder (10%). Forty (40) pitfall traps were used on the largest island and 20 on the smallest island, with a minimum distance of 5 m between traps. The contents of pots were recorded according to the time of sampling. The insects in the herbaceous layer were collected by sweep netting for 10 min. For each island there was a minimum of twenty 10-min samples and sampling continued until no new species were recorded. Insects on shrubs and trees were collected by using a Japanese umbrella, which consisted of a square piece of canvas of light colour (120 × 120 cm) stretched on a folding wooden frame. The umbrella was held with one hand under the foliage of shrubs and branches of trees which were rigorously shaken by the other hand. Each sample consisted of 20 min of collecting between 08:00 and 16:00. Active collection took place within a 200 m radius of the pitfall traps. Insects caught sweep netting were preserved in 70% ethanol. For each type of sampling, collections were considered complete when no new species were recorded for some time. Collected insects were identified using the reference collection of the laboratory of Applied Zoology and Ecophysiology of the University of Bejaia (Algeria), and available literature: Portevin (1924); Perrier (1935, 1961, 1963, 1964); Bernard (1968); Plateaux-Quénu (1972); Delvare & Aberlenc (1989); Auber (1999).

Data analysis

Sampling effort

Cook (1995) suggests that before carrying out a nestedness analysis, it is first necessary to verify that the list of species is as complete as possible. To estimate the true species richness for each island a non-parametric chao1 estimator was used. Past software was used to generate the estimate of the true species richness.

Collinearity and relationships of the environmental variables

To verify collinearity between independent variables a multiple regression analysis was used. Myers (1990) suggests removing the variables with the highest variance inflation factor (VIF) values and redoing the analyses until all remaining variables obtain a VIF value below the designed threshold (i.e. < 10). The level of collinearity between the environmental variables was quantified with the variance inflation factor calculated using Exelstat software. For this analysis all the variables were log-transformed.

The effects of island area, island isolation, altitude, plant richness and number of habitats on overall number of insects and that of species in the dominant orders were analysed using a generalized linear model (GLM). All analyses were done using Excelstat software.

Nestedness analysis

Nestedness analysis was carried out on the overall number of insects and that of each of the five dominant insect orders, Coleoptera, Hymenoptera, Diptera, Lepidoptera and Hemiptera. The hypothesis tested was that overall number of insects and that of the dominant orders are nested within each other based on the overlap and decreasing fill (NODF) values, which range from 0 to 100, with large numbers indicating increased nestedness (Almeida-Neto et al., 2008; Ulrich et al., 2009).

Nestedness data for overall number of insects and that of the dominant orders was organized in binary presence/absence matrix, where each row was a species ($n_{\text{Overall species}} = 216$; $n_{\text{Coleoptera}} = 68$; $n_{\text{Hymenoptera}} = 48$; $n_{\text{Hemiptera}} = 48$; $n_{\text{Diptera}} = 36$; $n_{\text{Lepidopptera}} = 16$) and each column an island (n = 11). The online interface "NeD" was used to calculate the nestedness value (https://ecosoft.alwaysdata.net/) developed by Strona et al. (2014). Five null models were run to test the significance level of nestedness: EE: equiprobable rows and column totals null model; CE: proportional rows and column totals null model; EF: equiprobable rows totals and equiprobable column totals null model; FE: Fixed row totals and equiprobable column totals null model; FF: Fixed column and row totals. The FF null model is highly restrictive and EE the least restrictive (Ulrich & Gotelli, 2012; Strona & Fattorini, 2014; Matthews et al., 2015). All of these null models have strengths and weaknesses (Ulrich & Gotelli, 2012; Strona & Fattorini, 2014).

The random placement model was used to test the passive sampling hypothesis. According to this model, the number of species S(α) in a given relative area α, $\alpha = AK/\sum_{k-1}^{k} AK$, and the overall

Table 2. Multiple regression analysis of the collinearity between the independent variables. VIF – variance inflation factor.

Statistics	Surface area	Isolation	Plant richness	Number of habitats	Altitude
Tolerance	0.264	0.327	0.442	0.382	0.693
VIF	3.786	3.058	2.264	5.233	1.443

abundance n_1, n_2,...ns of the S species in collection C (Coleman, 1981; Coleman et al., 1982): $S(\alpha) = S - \sum_{i=1}^{s}(1-\alpha)^{ni}$. The variance σ^2 of $S(\alpha)$ is $\sigma^2(S) = \Sigma_{i=1}^{s}(1-\alpha)^{ni} - \sum_{i=1}^{s}(1-\alpha)^{2ni}$. The random distribution hypothesis should be rejected if more than one-third of the points lie outside one standard deviation of the expected curve (Coleman, 1981; Coleman et al., 1982).

To test the presence of nestedness in the overall number of insects and that of the five dominant orders, the order in which the islands were sorted using NeD software were correlated with that based on environmental variables. Partial Spearman's rank correlation was used to determine the associations between island area, island isolation, plant richness and number of habitats, in order to test: (1) the selective extinction of species hypothesis, (2) differential colonization of habitat hypothesis and (3) habitat nestedness hypothesis. All analyses were done using IBM SPSS software (IBM Corp., Armonk, NY, USA).

RESULTS

Species richness and survey completeness

In total, 216 species were collected on the 11 Algerian islands, belonging to five orders: Coleoptera (68 species), Hemiptera (48 species), Hymenoptera (48 species), Diptera (36 species) and Lepidoptera (16 species) (Table S1).

The number of species collected on each island varied between 15 and 140 species. Survey completeness for the 11 islands ranged between 69.87% and 92.59%. According to the estimated species richness, for 7 of the 11 islets more than 80% of the species were collected and for the rest the mean values were higher than 74.38% (Table 1). This indicates that in general the islands studied were well sampled.

Relationships of environmental variables and nestedness analysis

The VIF values obtained in the first analyses were acceptable (VIF < 10) (Table 2). Thus surface area, island isolation, plant richness, altitude and the number of habitats were used in the subsequent analysis.

GLM test indicated plant richness was the only variable significantly associated with variation in overall number of insects and that of the dominant orders (Coleoptera, Hymenoptera, Hemiptera, Diptera and Lepidoptera) (Table 3).

The overall number of insects and that of the five dominant insect orders were significantly nested according to all null models except the very restrictive FF model (Table 4).

The nested structure of the overall number of insects and that of the five (5) dominant orders was not attributable to passive sampling (Fig. 2). For the overall number of insects and that of the five dominant orders, more than one third of the observed data points lay outside ±1 SD of the expected species-area curves computed using the random placement models (Fig. 2).

There was a strong correlation between island rank in terms of nestedness of overall numbers of insects and that of Lepidoptera with that in terms of surface area and plant richness. The island nested ranks for four (4) orders of insects (Coloeptera, Hymenoptera, Hemiptera and Diptera) were also strongly correlated with island rank in terms of plant richness (Table 5).

Table 3. Summaries of generalized linear models (GLMs) of the relationships between the overall number of insects and that of the dominant orders, and the environmental variables of the Algerian islands studied (Est. – estimate, SE – standard error, *P* – p-value, Sig. – statistical significance, ** – *P* < 0.01, * – *P* < 0.05, ns – *P* > 0.05).

Environmental variables					
Overall no. of insects	Est.	SE	z-value	*P*	Sig.
Intercept	29.974	22.812	1.314	0.246	ns
Surface area	4.186	3.774	1.109	0.318	ns
Isolation	0.016	0.009	1.768	0.137	ns
Plant richness	1.113	0.202	5.499	0.003	**
Altitude	–0.677	0.439	–1.541	0.184	ns
Number of habitats	–8.615	13.564	–0.635	0.553	ns
Coleoptera	Est.	SE	z-value	*P*	Sig.
Intercept	27.552	8.470	3.253	0.023	*
Surface area	3.064	1.401	2.186	0.080	ns
Isolation	0.007	0.003	2.017	0.100	ns
Plant richness	0.456	0.075	6.065	0.002	**
Altitude	0.130	0.163	0.799	0.460	ns
Number of habitats	–16.282	5.036	-3.233	0.230	ns
Hymenoptera	Est.	SE	z-value	*P*	Sig.
Intercept	20.780	7.527	2.761	0.040	*
Surface area	1.879	1.245	1.509	0.192	ns
Isolation	–0.002	0.003	–0.620	0.562	ns
Plant richness	0.246	0.067	3.683	0.014	*
Altitude	0.121	0.145	0.831	0.444	ns
Number of habitats	–9.001	4.476	–2.011	0.100	ns
Hemiptera	Est.	SE	z-value	*P*	Sig.
Intercept	–6.314	7.209	–0.876	0.431	ns
Surface area	–2.107	1.127	–1.870	0.135	ns
Isolation	0.003	0.003	1.013	0.368	ns
Plant richness	0.284	0.063	4,480	0,011	*
Altitude	–0.092	0.164	–0.563	0.604	ns
Number of habitats	3.252	4.455	0.730	0.506	ns
Lepidoptera	Est.	SE	z-value	*P*	Sig.
Intercept	2.812	5.331	0.528	0.620	ns
Surface area	1.244	0.882	1.410	0.218	ns
Isolation	0.001	0.002	0.481	0.651	ns
Plant richness	0.089	0.047	1.891	0.012	*
Altitude	–0.086	0.103	–0.838	0.440	ns
Number of habitats	–1.008	3.169	–0.318	0.763	ns
Diptera	Est.	SE	z-value	*P*	Sig.
Intercept	4.678	7.027	0.666	0.535	ns
Surface area	–0.451	1.163	–0.388	0.714	ns
Isolation	0.005	0.003	1.661	0.158	ns
Plant richness	0.267	0.062	4.279	0.008	**
Altitude	–0.116	0.135	–0.860	0.429	ns
Number of habitats	–2.219	4.178	–0.531	0.618	ns

DISCUSSION

This study revealed the environmental variables associated with the variation in the overall number of insects and that of the five dominant orders recorded on Algerian islands and the occurrence and causes of nestedness.

Relationships between species richness and environmental variables

The overall number of insects and species richness of the five dominant orders was strongly correlated with plant

Table 4. Comparative analyses of nestedness for overall number of insects and that of five dominant orders, on the 11 Algerian islands studied. Nestedness metrics and related parameters are provided for overall number of insects and that of the five dominant orders. *P*-values were based on 1,000 Monte Carlo simulations: EE – equiprobable rows and column totals null model; CE – proportional rows and column totals null model; EF – equiprobable rows totals and equiprobable column totals null model; FE – fixed row totals and equiprobable column totals null model; FF – fixed column and row totals null model SD, standard deviation; * significant nestedness ($P < 0.05$), ** ($P < 0.001$), *** ($P < 0.0001$).

Matrix	$NODF_{obs}$	$NODF_{EE}$	$NODF_{CE}$	NOD_{EF}	$NODF_{FE}$	$NODF_{FF}$
Overall no. of insects	39.69	25.41***(0.66)	32.14** (1.43)	26.81***(0.21)	37.96 * (1.05)	42.69 (0.34)
Coleoptera	39.68	25.14***(1.38)	30.85* (2.56)	25.99***(0.71)	36.11* (2.21)	42.75 (0.64)
Hemiptera	31.91	24.05***(2.08)	29.45* (3.44)	22.26***(1.06)	28.54* (2.69)	35.26 (0.54)
Hymenoptera	38.66	27.36***(1.42)	32.12* (2.87)	30.90***(0.88)	34.10* (1.99)	40.45 (0.71)
Diptera	49.34	28.22***(2.54)	36.59***(4.23)	32.13***(1.66)	42.43**(4.20)	51.44 (0.79)
Lepidoptera	61.36	31.20***(3.82)	40.27***(6.77)	34.21***(3.16)	50.71* (5.33)	64.19 (1.65)

richness, which highlights the importance of this variable in predicting the variation in species richness on the islands studied. Previous studies on different groups of insects on many islands report different results. Ren et al. (2009)report that only surface area is associated with the variation in the richness of arthropods, Lee et al. (2008) that the number of species of insects is associated with, surface area and distance to the mainland, Dennis et al. (2008) that the number of species of butterflies is mainly associated with the area of the island and isolation, Will et al. (1995) that there is a positive association between the number of species of beetles and island area, Spengler et al. (2011) that species richness of both bees and wasps is associated with island isolation, but not island size and Morrison (2005) highlights an association between Diptera richness and vegetation structure. Borges & Brown (1999), however, report that plant richness is a poor predictor of Hemiptera species richness (suckers and chewers) in the Azores.

The majority of the species collected on the islands in this study are phytophagous, which accounts for the general association of insect richness with plant richness. For example, the shrubby plant cover on some islands accounts for the presence there of several leaf eating species of beetle, such as, *Magdalis* sp., *Lixus* sp., *Agapanthia cardui*, *Calamobius filum* and *Anthaxia* sp. Many species of Hymenoptera (*Apis mellifera*, *Halictus intumescens*, *Ceratina cyanea*; Diptera (C*hloromyia formosa*, *Villa modesta*) and Lipidoptera (*Pieris rapae*, *Polyommatus icarus*, *Lycaena phlaeas*, *Vanessa atalanta*, *Utetheisa pulchella* and *Lampides boeticus*), were observed visiting flowers of several plants (*Sonchus tenerimus*, *Dittrichia viscosa*, *Hyoserus radiata*, *Lotus criticus*). Most of species of Hemiptera, such as, *Calocoris* sp.1, *Plagiotylus* sp., *Issus coleoptratus, Lygus* sp.1 were collected only on *Asteriscus maritimus*, *Chenopodium album* and *Pistacia lentiscus.*

There was no general relationship between altitude and overall insect species richness. The low altitude of most islands (< 30 m), however, resulted in them being flooded periodically, which has resulted in the formation of temporary ponds on these islands. This may favour the transfer of marine resources that could influence the structure of their insect communities. Several studies report that small islands generally benefit from the transfer of resources from aquatic environments (Anderson & Wait, 2001; Jonsson et al., 2009). Barrett et al. (2003) even suggest that the transfer of so called aquatic subsidies can affect the species richness of an island.

In Algeria, the Yellow-legged gull (*Larus michahellis*) is a disturbing factor, especially in coastal ecosystems, because they can be very abundant and their decaying waste has a strong effect in terms of soil acidification, which in turn favours the establishment of invasive species of plants (Vidal, 1998). On the islands studied, the effect of gull colonies on insect species richness is reflected clearly in the presence of a few families like the Calliphoridae, Muscidae and Sarcophagidae, which are capable of exploiting the decaying corpses of gulls.

Patterns in nestedness

The nested structure recorded was not related to passive sampling. Although as a general rule the data collected should be examined for passive sampling before testing hypotheses, in the case of island insects this is rarely done probably because of the lack of or the difficulty of obtaining data on the abundance of species (Xu et al., 2017). In the present study, passive sampling plays no role in the nested structure of the overall number of insects and that of the five dominant orders.

Simberloff (1976) states that the nested structure of assemblages of insects on islands, particularly depends on the capacity of dispersion of different taxa. In the case the

Table 5. Results of partial Spearman rank correlations of the rank order of island nestedness with that of the islands environmental variables. Environmental variables include surface area, island isolation, plant richness and number of habitats. * $P < 0.5$, ** $P < 0.01$.

Environmental variables	Overall no. of insects	Hemiptera	Coleoptera	Hymenoptera	Lepidoptera	Diptera
Surface area	0.51*	0.30	0.28	0.33	0.54*	0.24
Isolation	–0.08	–0.01	–0.07	–0.04	–0.13	–0.04
Plant richness	0.90**	0.93**	0.80*	0.74*	0.81*	0.74*
Number of habitats	–0.04	–0.08	–0.14	–0.22	–0.04	0.16

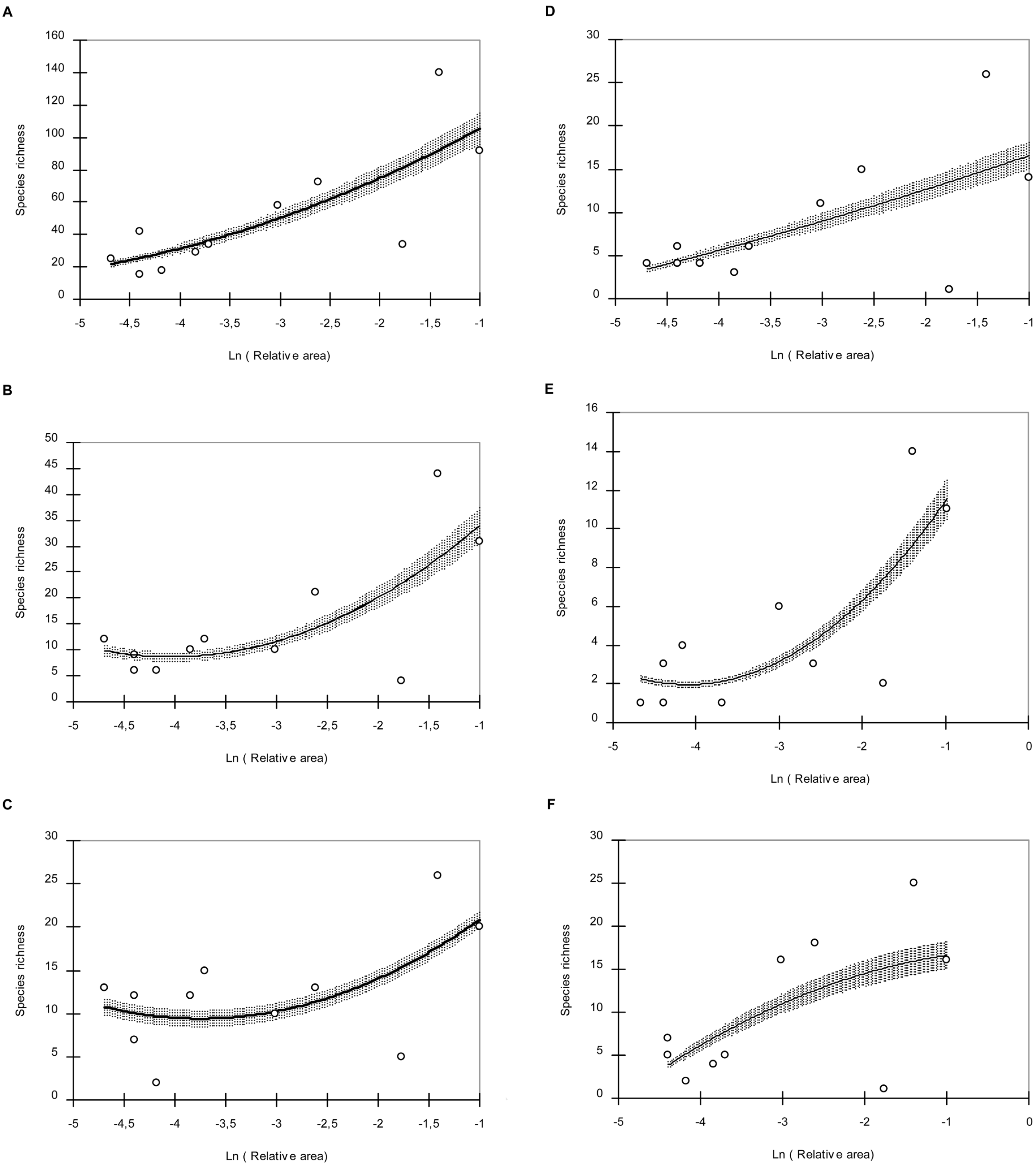

Fig. 2. Comparison of observed data with expected values generated by the random placement models for (A) overall number of insects, (B) Coleoptera, (C) Hymenoptera, (D) Diptera, (E) Lepidoptera and (F) Hemiptera on the Algerian islands studied. Expected values (solid line) and associated standard deviations (±1 SD; dashed lines) are shown. Open circles are the observed species richness.

islands studied, the nestedness did not appear to result from selective colonization, as it was not correlated with isolation. Many species of insects can actively disperse (Murakami & Hirao, 2010), often over great distances (Carlquist, 1965; Holzapfel & Harrell, 1968; Lee et al., 2008), which may weaken correlations between isolation and species nestedness. In this study, particular insect orders appear to be good island colonizers and are present even on islands far from the mainland on which they are abundant. Consequently, the absence of particular patterns of colonization may be attributable to their ability to disperse. It is necessary to consider the role of human activity in the general structure of some taxa on the islands studied. Although the islands studied are not inhabited, they are connected to the mainland as fisherman use their boats to ferry visitors to the islands. Thus species of continental origin with limited powers of dispersal, like ants, could to be unintentionally introduced on to small islands (Blard et al., 2003).

That the analysis of nestedness was done for the overall number of insects and that of the five dominant orders, provides an opportunity of determining how they are structured among islands and with which environmental variables they are associated. The overall number of insects and that of the five dominant orders were all significantly nested, but differently associated with the environmental variables. Plant richness was the single best variable influencing the nestedness of the overall number of insects and that of five dominant orders, because almost all of these insects assemblages are phytophagous, e.g. Chrysomelidae, Coccinellidae, Mordellidae, Apidae, Colletidae, Miridae, Pentatomidae, etc. Thus, the plant richness on the islands might determine the distribution of the overall numbers of Coleoptera, Hymenoptera, Hemiptera, Lepidoptera and Diptera. The association of plant richness with the nestedness pattern may account for the effect of environmental variables on the nested structure of insect distribution. Island surface area, however, was associated with the nested structure of overall numbers of insects and Lepidoptera. These results indicate island surface area is important in determining the overall distribution of insects and species of Lepidoptera. The importance of island surface area on the pattern of nestedness in overall number of insects and species of Lepidoptera indicate the role of selective extinction of species in structuring the overall number insects and species of Lepidoptera on the islands studied. Similarly, Murakami & Hirao (2010) indicate the relative importance of spatial factors (island isolation) and environmental factors (vegetation height and island area) in determining the nested distributions of insect species on small islands in the Bahamas.

In addition, the nested distribution may be due to other factors. Coleoptera are the first to colonize environments (Jeffries, 1994), thus older environments are more likely to harbour more rare species (Fattorini, 2011). Unfortunately, there is no information on the age of the islands to confirm this. Furthermore, in terms of colonization and dispersal ability, aquatic Coleoptera quickly colonize new environments (Eyre et al., 1992). For Diptera, decomposing carcasses in gull colonies on all islands probably contribute to the diversity and distribution of insects. In this context, at least at the scale of an island, Morrison (2005) emphasizes the importance of the decomposition of marine algae in the Bahamas islands for the distribution Diptera.

CONCLUSION

This study revealed the association between plant richness and the variation in insect species richness and that of five dominant insect orders (Coleoptera, Hymenoptera, Hemiptera, Lepidoptera and Diptera). The mechanisms determining nestedness differed for the overall number of insects and that of five dominant orders of insects. These results have implications for the conservation of insect diversity on the Algerian islands studied. First, for the overall number of insects and that of the five dominant orders of insects, plant richness is the best predictor. Accordingly, the plant richness on these islands should at least be protected from the effect of colonies of Yellow-legged gulls and human activity. Second, as surface area is significantly associated with nestedness the larger islands are the most important in terms of conservation.

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Supplementary Table S1 follows on next page.

Table S1. Presence and absence of insects of the dominant orders on all of the islands studied: ICO: Collo (Lachouri et al., 2016); ITZ: Tazrout (Amrane et al., 2017); IPC: Petit Cavallo (Aissat & Moulaï, 2016); IGC: Grand Cavallo (Aissat & Moulaï, 2016); iGC: Small Grand Cavallo (Aissat & Moulaï, 2016); IP: Pisan (Aissat et al., 2023); IEE: El Euch (Aissat et al., 2023); IA: Ail (Aissat et al., 2023); ISL: Sahel (Aissat et al., 2023); ITG: Tigzirt (Moulaï et al., 2016); IAG: Agueli (Moulaï et al., 2016).

	ICO	ITZ	IPC	IGC	iGC	IP	IEE	IA	ISL	ITG	IAG
Coleoptera											
Oxythyrea funesta	0	0	1	1	1	0	0	0	1	0	0
Apion sp.1	0	0	0	0	0	1	0	1	1	0	0
Apion sp.2	0	0	1	1	0	1	0	1	0	0	0
Lachnaia paradoxa	0	0	0	0	0	1	0	1	0	0	0
Lachnaia tristigma	0	0	1	1	1	0	0	0	0	0	0
Lachnaia pubescens	0	0	1	1	1	0	0	0	0	0	0
Longitarsus jacobaeae	0	0	0	0	0	0	0	1	0	0	0
Leptomona erythrocephala	0	0	0	0	0	1	0	1	0	0	0
Psylliodes sp.	0	0	0	0	0	1	1	0	0	0	0
Smaragdina sp.	0	0	0	0	0	1	0	1	0	0	0
Cryptocephalus rufipes	0	1	1	1	0	0	0	0	0	0	0
Podagrica fuscicornis	0	0	1	1	0	0	0	0	0	0	0
Tituboea sp.	0	0	1	1	1	0	0	0	0	0	0
Aphthona cyparissiaes	0	0	1	1	1	0	1	0	0	0	0
Chrysomela sp.	0	0	1	1	0	0	0	0	0	0	0
Psylliodes sp.	0	0	1	0	0	0	0	0	0	0	0
Chaetocnema concinna	0	0	1	0	0	0	0	0	0	0	0
Scymnus interruptus	0	0	1	1	0	1	0	0	0	1	0
Scymnus sp.	0	0	0	0	0	1	0	0	0	0	0
Scymnus apetzi	0	0	1	1	0	0	0	0	0	0	0
Coccinella septempunctata	1	0	1	1	0	0	1	1	0	0	0
Clitostethus arcuatus	1	0	1	1	0	1	0	0	0	0	0
Psyllobora vigintiduopunctata	0	0	0	0	0	0	0	0	0	1	0
Adalia decempunctata	0	0	0	0	0	0	1	0	0	0	1
Hippodamia variegata	0	0	0	0	0	0	0	0	0	0	1
Mordella sp.	0	0	0	0	0	1	0	0	0	0	0
Variimorda villosa	0	0	1	1	0	0	0	0	0	0	0
Mordella aculeata	0	0	1	1	0	0	0	0	0	0	0
Variimorda sp.	0	0	1	1	0	1	0	0	0	0	0
Anaspis flava	0	0	0	0	0	1	0	0	0	0	0
Olibrus sp.	0	0	1	1	0	0	0	0	0	0	0
Athous sp.	0	1	1	1	0	0	0	0	0	0	0
Cardiophorus sp.	0	0	0	0	0	0	0	0	0	1	0
Tenebrionidae sp.ind.	0	0	1	0	0	0	0	0	0	0	0
Scaurus tristis	0	0	1	0	0	0	0	0	0	0	0
Opatrum sp.	0	0	0	1	0	0	0	0	0	0	0
Stenosis sp.	0	0	0	0	0	1	1	0	1	0	0
Blaps gigas	0	0	0	0	0	0	0	0	0	0	1
Blaps sp.	0	0	0	0	0	0	0	0	0	0	1
Pimelia sp.	0	0	0	0	0	0	0	0	0	0	1
Heliotaurus ruficollis	0	0	1	1	0	0	0	1	1	0	1
Oedemera femorata	0	0	1	1	1	0	0	0	0	0	0
Oedemera podagrariae	0	0	1	0	0	0	0	0	1	0	0
Oedemera tristis	0	0	1	0	0	1	0	0	0	0	0
Bruchidius villosus	0	0	1	0	0	0	0	0	0	0	0
Pissodes sp.	0	0	1	1	0	0	0	0	0	0	0
Magdalis sp.	0	0	1	0	0	0	0	0	0	0	0
Curculio sp.	0	0	0	0	0	1	0	0	0	0	0
Lixus sp.	0	1	1	1	0	0	0	0	0	0	0
Lixus (*Lixomorphus*) *algirus*	0	0	0	0	0	1	1	0	0	1	0
Agapanthia cardui	0	0	1	0	0	0	0	0	0	0	0
Calamobius filum	0	0	1	0	0	0	0	0	0	0	0
Cerambycidae sp.ind.	0	0	1	0	0	0	0	0	0	1	0
Gyrinus sp.	0	0	1	0	0	0	0	0	0	0	0
Cantharis sp.	0	0	1	0	0	1	0	0	0	0	0
Psilothrix sp.	0	1	1	1	1	1	0	0	1	0	0
Dasytes sp.	0	0	1	1	1	0	0	1	1	1	0
Enicopus sp.	0	1	1	1	1	1	0	1	0	1	0
Thanasimus sp.	0	1	0	0	0	0	0	0	0	0	0
Trachys fabricii	0	0	1	1	1	0	0	1	0	0	0
Trachys pygmaeus	1	0	0	0	0	0	0	0	0	0	0
Anthaxia sp.	0	0	1	1	0	0	0	0	0	1	0
Megatoma undata	0	0	1	1	1	1	1	1	0	0	0
Dermestes sp.	0	0	0	0	0	0	0	0	0	1	0
Byturus sp.	0	0	1	1	1	0	1	0	0	0	0
Cassida viridis	0	0	1	1	0	1	1	0	1	1	0
Cassida sanguinosa	0	0	1	0	0	0	1	0	1	0	0
Anthicus sp.	1	0	0	0	0	0	0	0	0	0	0
Hemiptera											
Heterogaster sp.	0	0	1	1	0	1	1	0	0	1	0
Oxycarenus lavaterae	0	0	0	0	0	1	1	0	0	1	0
Anthocoris nemorum	0	0	1	1	0	0	0	0	0	0	0
Orius niger	0	0	1	1	0	0	0	0	0	0	0
Orius sp.	.0	0	0	0	0	1	0	0	0	0	0
Tingis sp.	0	0	1	1	0	0	0	0	0	0	0
Calocoris sp.1	0	0	1	1	0	0	0	0	0	1	0
Calocoris sp.2	0	0	1	1	0	0	0	0	0	0	0
Deraeocoris sp.	0	0	1	1	0	0	0	0	0	0	0
Adelphocoris sp.	0	0	1	0	0	1	1	0	0	0	0
Anthocoris sp.	0	0	1	0	0	0	0	0	0	0	0
Psallus ambiguus	0	0	1	1	0	1	0	0	0	0	0
Lygus sp.1	0	1	0	0	0	1	1	0	1	0	0
Lygus sp.2	0	0	0	0	0	1	1	0	1	0	0
Lygus sp.3	0	0	0	0	0	1	1	0	1	0	0
Lygus sp.4	0	0	0	0	0	1	0	0	1	0	0
Tuponia sp.	0	0	0	0	0	1	0	0	0	0	0
Plagiotylus sp.	0	1	1	1	0	0	0	0	0	0	0
Closterotomus norvegicus	0	1	0	0	0	0	0	0	0	0	0
Heterotoma sp.	0	0	0	0	0	0	0	0	0	1	0
Geocoris sp.	0	0	0	0	0	0	0	0	0	0	1
Uroleucon sp.	1	0	0	0	0	0	0	0	0	0	0
Issus coleoptratus	0	0	1	1	0	0	0	0	0	0	0
Issus sp.	0	0	1	1	0	0	0	0	0	0	0
Tropiduchidae sp.ind.	0	0	1	0	0	0	0	0	0	0	0
Graphosoma italicum	0	0	1	1	0	0	0	0	0	0	0
Nezara viridula	0	0	1	1	0	1	1	1	1	0	0
Piezodorus lituratus	0	0	1	0	0	0	0	0	0	0	0
Pentatoma rufipes	0	0	1	0	0	0	0	0	0	0	0
Stallia venustissima	0	0	1	1	0	0	0	0	0	0	0
Dolycoris numidicus	0	0	1	0	0	0	0	0	0	0	0
Eurydema sp.	0	0	1	0	0	0	0	0	0	0	0
Dyroderes umbraculatus	0	0	1	1	0	0	0	0	0	0	0
Allygus sp.1	0	0	0	0	0	1	1	1	0	0	0
Allygus sp.2	0	0	0	0	0	1	1	0	0	0	0
Cicadella sp.1	0	1	0	0	0	1	1	1	1	0	0
Cicadella sp.2	0	0	0	0	0	1	1	0	0	0	0
Cicadella sp.3	0	0	0	0	0	0	1	0	0	0	0
Cicadella sp.4	0	0	0	0	0	0	1	0	0	0	0
Agalliota sp.	0	0	0	0	0	0	0	1	0	0	0
Deltocephalinae sp.ind.	0	0	0	0	0	0	0	0	1	0	0
Salda littoralis	0	0	0	0	0	0	0	1	0	0	0
Pyrrhocoris apterus	0	0	1	0	0	1	1	0	0	0	1
Syromastus rhombeus	0	1	1	0	0	0	0	0	0	0	0
Ocypus olens	0	0	0	0	0	0	1	0	0	0	0
Oxytelus sp.1	0	0	0	0	0	1	0	0	0	0	0
Oxytelus sp.2	0	0	0	0	0	1	1	0	0	0	0
Hymenoptera											
Myrmecaelurus sp.1	0	0	1	0	0	0	0	0	0	0	0
Myrmecaelurus trigrammus	0	0	1	0	0	0	0	0	0	0	0
Myrmeleon formicarius	0	0	0	0	0	0	0	0	0	0	1
Chrysopa viridana	0	0	0	0	0	1	0	0	0	0	0
Chrysoperla carnea	1	0	0	0	0	0	0	0	0	1	0
Aulogymnus sp.1	0	0	1	1	0	0	0	0	0	0	0
Aulogymnus sp.2	0	0	1	0	0	0	0	0	0	0	0
Eulophidae sp.ind.	0	0	0	0	0	1	1	1	0	0	0
Ormyrus sp.	0	0	1	1	0	1	1	1	1	0	0
Brachymeria sp.	0	0	0	0	0	0	0	0	1	0	0
Ichneumonidae sp.ind.	0	0	1	0	0	1	1	0	1	0	0
Braconidae sp.1 ind.	0	1	1	0	0	0	0	0	0	0	0
Braconidae sp.2 ind.	0	0	0	0	0	1	1	0	1	0	0
Pteromalus sp.	0	0	0	0	0	1	1	1	1	0	0
Systasis sp.	0	0	0	0	0	0	0	0	1	0	0
Camponotus atlantis	0	0	0	0	0	0	0	1	0	0	0
Camponotus ruber	0	0	0	0	0	0	1	1	0	0	0
Camponotus vagus	0	0	1	1	1	0	0	0	0	0	0
Camponotus sp.	0	0	0	0	1	0	0	0	0	0	0
Cataglyphis bicolor	0	1	1	1	1	1	1	1	1	1	0
Lasius flavus	0	0	0	0	0	0	0	1	0	0	0
Lasius sp.	0	0	0	0	0	0	0	1	0	0	0
Aphaenogaster testaceo pilosa	0	0	1	1	0	0	0	0	0	0	0
Messor barbarus	0	0	1	1	1	0	0	0	0	1	0
Crematogaster scutellaris	0	0	1	1	1	1	0	1	0	1	0
Crematogaster auberti	0	1	1	1	0	1	0	0	0	0	0
Tapinoma simrothi	0	0	1	1	0	0	0	1	1	0	0
Tapinoma magnum	0	1	0	0	0	0	0	1	0	1	0
Pheidole pallidula	0	0	1	1	0	1	0	1	1	0	0
Tetramorium biskrense	1	0	1	1	1	0	1	0	0	0	0
Plagiolipis schmitzii	0	0	0	0	0	0	0	0	1	0	0
Monomorium subopacum	1	0	0	0	0	0	0	0	0	0	0
Pompilus sp.1	0	0	1	1	0	0	0	0	0	0	0
Pompilus sp.2	0	0	1	0	0	0	0	0	0	0	0
Pompilidae sp.ind.	0	0	1	1	0	0	0	0	0	0	0
Anoplius sp.	0	0	0	1	0	0	0	0	0	0	0
Halictus intumescens	0	0	1	1	1	0	0	0	0	0	0
Halictus quadricinctus	0	0	1	1	1	0	0	1	0	0	0
Halictus sp.	1	0	0	0	1	1	1	0	0	0	0
Hylaeus sp.	0	0	1	1	1	0	0	0	0	0	0
Colletes sp.	0	1	0	0	0	0	0	0	0	0	0
Ceratina cyanea	0	0	1	1	1	0	0	0	0	1	0
Andrena sp.	0	0	1	1	1	0	0	0	0	0	0
Sphex sp.	0	1	0	0	0	0	0	0	0	0	0
Trypoxylon figulus	0	0	1	0	0	0	0	0	0	0	0
Vespula germanica	0	0	0	0	0	1	0	1	1	0	0
Bombus sp.	0	1	0	0	0	0	0	0	0	0	0
Apis mellifera	1	0	1	1	1	1	1	1	1	1	1
Diptera											
Calliphora sp.1	0	1	1	1	0	1	1	1	0	1	1
Calliphora sp.2	0	0	1	0	0	1	0	0	0	0	0
Lucilia sp.1	0	0	1	1	1	1	1	1	1	0	1
Lucilia sp.2	0	0	1	1	0	0	0	0	0	0	0
Lonchaeidae sp.1 ind.	0	0	0	0	0	1	0	0	0	0	0
Lonchaeidae sp.2 ind.	0	0	0	0	0	1	0	0	0	0	0
Sciara sp.	0	1	0	0	0	0	0	0	0	0	0
Liancalus sp.	0	1	0	0	0	0	0	0	0	0	0
Otites sp.	0	0	1	1	0	0	0	0	0	0	0
Pegomya sp.	0	0	1	0	0	1	1	0	0	0	0
Delia sp.	0	0	1	1	0	1	1	0	1	0	0
Anthomyia sp.1	0	0	1	1	0	0	0	0	0	0	0
Anthomyia sp.2	0	0	0	0	0	1	1	0	0	0	0
Musca domestica	0	0	1	1	1	1	1	1	1	0	0
Musca sp.	0	0	1	0	0	0	0	0	0	0	0
Muscidae sp.ind.	0	0	1	0	0	0	0	0	0	1	0
Tephritis sp.1	0	0	0	0	0	1	1	0	1	0	0
Tephritis sp.2	0	0	0	0	0	1	1	0	0	0	0
Meromyza sp.	0	0	0	0	0	1	1	0	0	0	0
Thaumatomyia notata	0	1	0	0	0	0	0	0	0	0	0
Thereva sp.	0	0	1	0	0	0	0	0	0	0	0
Villa modesta	0	0	1	0	0	0	0	0	0	0	0
Exoprosopa jacchus	0	0	1	1	0	0	0	0	0	0	0
Philonicus albiceps	0	0	1	0	0	0	0	0	0	0	0
Sarcophaga sp.	1	1	1	1	1	1	0	1	0	1	1
Miltogramma sp.	0	0	1	0	0	0	0	0	0	0	0
Nowickia sp.	0	0	1	0	0	0	0	0	0	0	0
Cylindromyia auriceps	0	0	1	1	0	0	0	0	0	0	0
Exorista sp.1	0	0	1	1	1	0	0	0	0	0	0
Exorista sp.2	0	0	1	0	0	0	1	1	0	0	0
Fannia sp.	0	0	1	1	0	1	1	1	0	0	0
Tipula sp.1	0	0	1	1	0	0	0	0	0	0	0
Tipula sp.2	0	0	1	0	0	0	0	0	0	0	0
Chloromyia formosa	0	0	1	1	0	1	0	0	0	0	0
Episyrphus balteatus	0	0	1	0	0	0	0	0	0	0	1
Eupeodes corollae	0	1	0	0	0	0	0	0	0	0	0
Lepidoptera											
Zerynthia rumina	0	0	1	1	0	0	0	0	0	0	0
Pieris rapae	1	0	1	1	0	1	1	1	1	0	1
Colias croceus	0	0	1	1	0	0	0	0	0	0	0
Gonepteryx cleopatra	0	0	1	1	0	0	0	0	0	0	0
Lampides boeticus	0	0	1	0	0	0	1	0	1	0	1
Polyommatus icarus	0	0	1	1	0	0	1	0	1	0	0
Lycaena phlaeas	0	0	1	1	0	0	1	0	0	0	0
Vanessa atalanta	0	0	1	1	1	1	0	0	0	0	0
Cynthia cardui	0	0	1	0	0	0	0	0	0	0	0
Rhodometra sacraria	0	1	1	1	0	0	0	0	0	0	0
Utetheisa pulchella	0	0	1	1	0	1	1	0	0	0	1
Autographa gamma	0	0	1	1	0	0	0	0	0	0	0
Heliothis peltigera	0	0	1	0	0	0	0	0	0	0	0
Acontia lucida	0	0	1	1	0	0	0	0	0	0	0
Grammodes stolida	1	0	0	0	0	0	0	0	0	0	0
Noctuidae sp.ind.1	0	0	0	0	0	0	1	0	0	0	1