Effects of natural phenomena and human activity on the species richness of endemic and non–endemic Heteroptera in the Canary Islands

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Abstract

Effects of natural phenomena and human activity on the species richness of endemic and non–endemic Heteroptera in the Canary Islands.— The geographical patterns of Heteroptera species diversity in the Canary Islands were analysed, and endemic and non–endemic species were studied both together and separately. Causal processes most likely controlling these patterns, as well as the theory of island biogeography, hypotheses about evolutionary time, habitat heterogeneity, climatic stability, intermediate disturbances, energy, environmental favourableness–severity, productivity and human influence were investigated. The combination of habitat heterogeneity and human influence accounted for the total number of species. However, when endemic and non–endemic species were analysed separately, habitat heterogeneity and favourableness–severity explained the richness of endemic species, whereas habitat heterogeneity and human influence explained that of non–endemic species.

Key words: Canary Islands, Heteroptera, Species richness, Biogeography.

Resumen

Efectos de los fenómenos naturales y la actividad humana sobre la riqueza específica de heterópteros endémicos y no endémicos de las Islas Canarias.— En el presente trabajo se analiza la distribución geográfica de los heterópteros en las Islas Canarias, tomando en consideración las especies endémicas y no endémicas juntas y por separado. Asimismo se investigan los procesos causales que con mayor probabilidad controlan los patrones de distribución resultantes, poniendo a prueba la teoría de la biogeografía insular y las hipótesis del tiempo evolutivo, de la heterogeneidad de hábitats, de la estabilidad climática, de las perturbaciones a escala intermedia, de la energía, de la favorabilidad–severidad ambiental, de la productividad y de la influencia humana. El número total de especies sobre las islas queda explicado por una combinación de la heterogeneidad de hábitats y de la influencia humana. Sin embargo, cuando se analizan las especies endémicas y no endémicas por separado, la heterogeneidad de hábitats y la favorabilidad–severidad explican la riqueza específica de las endémicas mientras que la heterogeneidad de hábitats y la influencia humana explican la riqueza específica de las especies no endémicas.

Palabras clave: Islas Canarias, Heteroptera, Riqueza específica, Biogeografía.

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Introduction

The description and analysis of the geographical trends in species diversity and the testing of explanatory hypotheses are of major concern when assessing the biodiversity of an area. Several practical and philosophical problems must be solved to approach these analyses adequately. Regarding insular faunas, most studies about species diversity are based on the theory of island biogeography of MacArthur & Wilson (1967) which considers area and isolation as the determinant factors of the number of species that inhabit the islands (see, for example, Sfenthourakis, 1996; Dennis & Shreeve, 1997; Hanski & Gyllenberg, 1997). However, Williamson (1989) encouraged the search for explanations of biodiversity patterns beyond the theory of MacArthur and Wilson. Haila (1990) and Fox & Fox (2000), for example, suggested that a realistic vision of insular ecology should include the development of alternative hypotheses about the dynamics that may have an important role in the system studied. Some authors, such as Brown & Lomolino (2000), consider that a new paradigm shift is currently in the making regarding island biogeography (Lomolino, 2000).

Human presence is prevalent in nearly all islands, and biogeographical interpretations and conservation efforts must take into account that the interconnection between human activity and natural phenomena explains the current patterns of insular biodiversity (Chown et al., 1998). Insular biotas are more vulnerable to human influence than those of continental regions, as the proportion of endemic species, with small distribution areas, is higher in the islands (Sadler, 1999). Kitchener (1982) showed that the best predictors for species richness might differ for endemic species when compared to the predictors for introduced species (see also Chown et al., 1998; Fox & Fox, 2000). The concept of native species is ambiguous, as ecologists do not use this term consistently (Callicott et al., 1999; Shrader–Frechette, 2001). In islands which have been inhabited by humans for a long time it is almost impossible, given the scarcity of palaeoecological data, to distinguish between non–endemic native species and those species introduced by humans (Willerslev et al., 2002). Particularly in oceanic islands, the only operational distinction is between endemic species, which are generally native, and non–endemic species, which are generally colonizers. Human impact on islands tends to jeopardize endemic species while providing new habitats and means of dispersion for colonizers (Sadler, 1999). Therefore, it is necessary to consider endemic and non–endemic species separately when assessing the influence of human activity on species richness in islands.

Heteroptera of the Canary Islands are well recollected and understood taxonomically (Heiss & Báez, 1990; Heiss & Ribes, 1992; Ribes & Ribes, 1997; Heiss, 1997). The Canary Islands are characterized by a rather diverse fauna of Heteroptera, which comprises more than 350 species, over 25% of which are endemic to the archipelago (Ribes & Ribes, 1997). Becker (1992) analysed the number of species of Heteroptera in the Canary Islands, but did not take into account the influence of human activity or consider endemic species separately.

In this paper, geographical patterns of heteropterous species diversity in the Canary Islands are identified, and endemic and non–endemic species are studied together and separately, in an attempt to detect the causal processes, whether natural or human–induced, that most likely control those patterns.

Material and methods

Study area

The Canary Islands, constituted by seven major islands and a set of small islets, are located off the north–western coast of Africa. Along with the archipelagos of Azores and Hawaii, they are one of the largest strings of volcanic islands worldwide (Schmincke, 1976). Although the genesis of the Canary Islands is similar to that of other oceanic islands, their eruptive history has been longer and more complex, comprising a time span of more than 20 m.y. in contrast with the few million years of other island groups (López–Ruíz, 1985). As a result, endemic species and genera make up a significant proportion of their biota.

The Canary Islands have a heterogeneous climate which, according to the bioclimatic classification of Rivas–Martínez (1993), belongs to the Mediterranean macrobioclimate, showing at least two months of aridity after the summer solstice. Precipitation tends to decrease from north to south and from west to east, increasing considerably with elevation (Vega, 1992).

The variables and hypotheses

Table 1 shows the list of variables used and their sources. The numbers of species of Heteroptera (total and endemic) for the Canary Islands were taken from Heiss & Báez (1990), Heiss & Ribes (1992), Ribes & Ribes (1997), Heiss (1997), and Báez & Zurita (2001). There are a total of 363 heteropterous species in the archipelago, 105 of which are endemic.

The following explanatory hypotheses were tested:

Evolutionary time (Pianka, 1966; Rohde, 1992)

A new habitat or niche that becomes available, not used previously by any species, will be occupied if there is sufficient time for a suitable species to evolve. Older islands are more likely to have undergone a more complex history (Margalef, 1963). The history of volcanic islands has a special influence on the evolution of insular fauna;

Table 1. List of variables and their sources. Sources: Juan et al., 2000 (1); Servicio Geográfico del Ejército, 1975 (2); Quirantes–González & Pérez–González, 1991 (3); Rivas–Martínez, 1987 (4); Instituto Nacional de Meteorología, 2000 (5); Font, 1983 (6); Vega, 1992 (7); Coma, 1979 (8); Instituto Canario de Estadística, 1995 (9); Martín et al., 2001 (10).

Tabla 1. Listado de variables y su procedencia. (Ver arriba.)

Variables
Geological Age (1)
Elevation range–*ER* (2)
Distance to the continent (2)
Minimum distance between islands (2)
Surface area (2)
Number of ecosystems–*NE* (3)
Number of phytoclimatic regions–*PR* (4)
Number of successional vegetation series–*VS* (4)
Number of bioclimatic elevation belts–*BB* (4)
Temperature range (5)
Precipitation range (5)
Maximum precipitation recorded in 24 hours (5)
January temperature (5)
July temperature (5)

Variables
January humidity (5)
July humidity (5)
Mean annual days with precipitation–*DP* (6)
Hours of sunshine (6)
Potential evapotranspiration (6)
Number of days with fog–*DF* (6)
Mean Annual Temperatures ((7)
Mean Annual Precipitation (7)
Actual evapotranspiration (8)
Number of inhabitants–*NI* (9)
Population density (9)
Cropland surface percentage (9)
Total cropland surface–*CS* (9)
Number of plant species–*NP* (10)

some islands could have begun as smaller isles and later joined, and eruptions may have divided an island into isolated parts which might favour the allopatric differentiation of vagile species (Machado, 1992). A direct relationship between the number of endemic species and the geological age of each island is expected according to this hypothesis.

Habitat heterogeneity (Pianka, 1966)

The more heterogeneous and complex the physical environment, the more complex and diverse the animal communities that inhabit it. This hypothesis predicts direct relationships between species richness and number of plant species, elevation range, number of ecosystems on each island, number of phytoclimatic regions, number of ecological successions of vegetation, and number of bioclimatic elevation belts, as these variables indicate different levels of habitat heterogeneity.

Climatic stability (Klopfer, 1959)

A climatically stable environment allows the existence of more niches with predictable resources on which rare species can specialize, thus favouring an increase in faunal diversity. On the contrary, a fluctuating environment may increase the extinction rate in the island or preclude specialization, thereby decreasing the species richness of the island (Brown & Lomolino, 1998). According to this hypothesis, inverse relationships between the number of species and temperature range and precipitation range are expected.

Intermediate disturbances (Connell, 1978)

Disturbances of intermediate magnitudes and frequencies maintain higher levels of diversity. The maximum precipitation recorded in 24 hours, as an estimate of the intensity of floods, and the maximum precipitation recorded in 24 hours/mean annual days with precipitation, as an estimate of their severity, are variables related to disturbances. The relationship between species richness and the associated variables could be direct, inverse or unimodal.

Energy

Hutchinson (1959) proposed that energy might determine the species richness of an area. This idea was further developed by Connell & Orias (1964), Brown (1981), and Wright (1983). The main argument is that a population requires a minimum amount of energy to subsist. In this way, the energy available limits the number of populations that may share this energy in a specific region. This hypothesis may be tested by searching for direct relationships between the number of species and certain variables related to solar energy, such as mean annual temperature, annual hours of sunshine, potential evapotranspiration, January temperature, and July temperature.

Environmental favourableness–severity (Richerson & Lum, 1980)

When the environmental parameters are close to optimal values for the physiological requirements of the species, organisms may specialize with respect to more physical gradients, and may use a higher amount of energy, matter, and genome to make co–adaptive adjustments to other species. The mean values of the environmental variables are suitable indices to test this hypothesis (Richerson & Lum, 1980). Direct, inverse or unimodal responses of species richness are expected with respect to mean annual days with precipitation, number of days with fog, January humidity, and July humidity; inverse or unimodal responses are expected with respect to the variables related to energy, namely mean annual temperature, annual potential evapotranspiration, annual number of sunshine hours, January temperature, and July temperature.

Productivity hypothesis of Tilman (1982)

Over a range of resources that goes from extremely poor to low, the greater the availability of resources, the higher the number of species. In a moderate range of resources the species richness will be maximum, and it will decrease as the resources become more abundant. Annual precipitation and evapotranspiration have been used as predictors of productivity (see Rosenzweig, 1968; Leith, 1975). According to Mittelbach et al. (2001), species richness is expected to show direct, inverse or unimodal responses to the associated variables.

Island biogeography theory (MacArthur & Wilson, 1967)

The number of species is directly related to the surface area and inversely to the degree of isolation of the islands. The distance to the continent, the minimum distance between islands, and the surface area of each island were used to test this hypothesis.

Human influence (Simberloff, 1986)

Human presence and activity may jeopardize the survival of some species but may favour others by providing suitable habitats for them. In particular, agricultural systems often consist of many species of introduced plants that constitute new habitats for phytophagous insects, which, in turn, constitute new habitats for entomophages. In this study, the number of heteropterous species, as well as the number of endemic and non–endemic species separately, was related to the number of inhabitants, population density, cropland surface percentage, and total cropland surface of each island. Direct or inverse relationships would be in accordance with the hypothesis.

Statistical analyses

The total number of heteropterous species, the number of heteropterous species endemic to the archipelago, and the total number of non–endemic heteropterous species were analysed separately.

The normality of the variables was tested by means of the Kolmogorov–Smirnov test. Each hypothesis was studied separately relying on bivariate analyses as stepwise variable selection techniques make some questionable assumptions and their results may be of doubtful biological validity (James & McCulloch, 1990; Chown et al., 1998). Linear regressions to detect monotonic responses (either direct or inverse) of the species richness to each variable analysed, and second–degree polynomial regressions to detect unimodal responses were performed. To prevent the increase of the error type II that may be caused by testing several hypotheses simultaneously, the Bonferroni sequential test was used (Rice, 1989), starting with a significance level $\alpha = 0.05$ divided by the number of hypotheses.

A stepwise multiple regression of the species richness was performed to explain species richness (*S*) by a combination of several hypotheses only on the variables that remained significant after applying the Bonferroni test in the bivariate analysis (James & McCulloch, 1990). The variables selected by the multiple regression in the variance partitioning procedure called partial regression analysis (Legendre, 1993) were then used. The part of the variance in species richness explained by the multiple regression (R_{T}^{2}) that is due to each selected hypothesis exclusively (R_{Hi}^{2}) and the part due to the shared action of different hypotheses (R_{Iij}^{2}) was thus specified. To do this, each selected environmental variable related to a hypothesis was regressed in turn onto the subset of selected variables related to other hypotheses, and only the regression residuals, which represent the part of the variation that is not explained by other hypotheses, were retained. The pure effect of each hypothesis (R_{Hi}^{2}) was assessed by regressing *S* on the residuals of the variables related to the hypothesis. The variation due to the sharedaction of two hypotheses was obtained by subtracting from (R_{T}^{2}) the pure effect of the two hypotheses involved ($R_{Hi}^{2}+R_{Hj}^{2}$).The unexplained variation of *S* was $1-R_{T}^{2}$.

Results

Total number of heteropterous species

Significant linear regressions of the number of heteropterous species (*S*) on nine variables were found. However, only four remained significant after applying the Bonferroni sequential test. The variables involved were, in decreasing order of explanatory power, the number of plant species (*NP*), the number of inhabitants (*NI*), total cropland surface (*CS*), and number of natural ecosystems (*NE*), all directly related with the number of species (fig. 1). These relations were predicted by the hypotheses of habitat heterogeneity and human influence.

According to the Bonferroni test, the number of species of heteroptera (*S*) followed a lineal regresión with *NP, NI, CS* and *NE* (directly related)

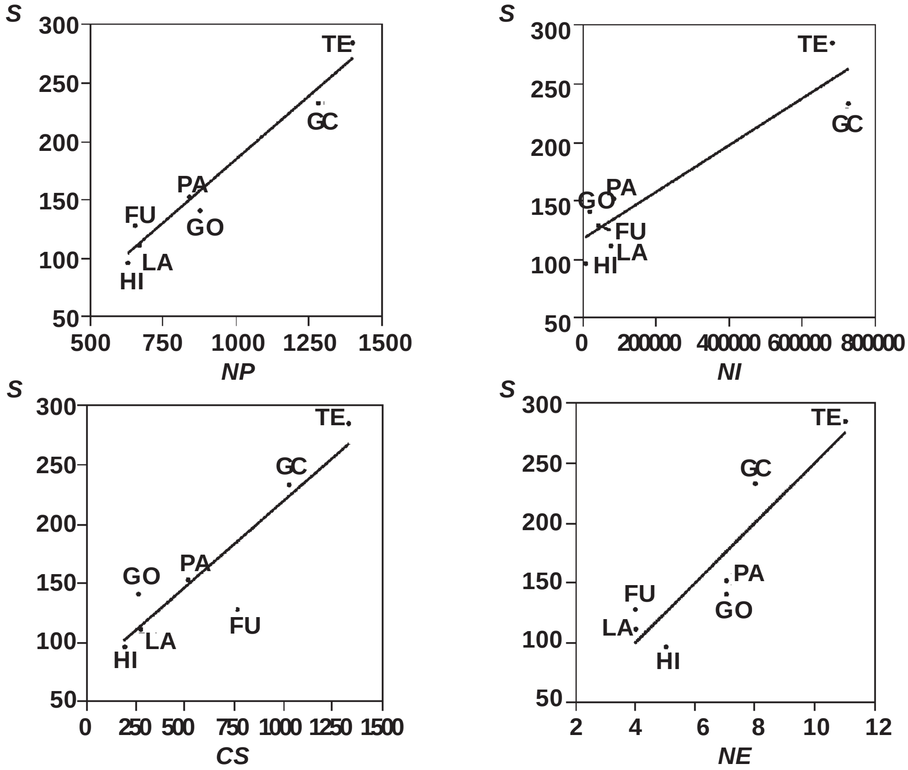

Fig. 1. Bivariate linear regressions of the number of heteropterous species (*S*) on environmental variables that remained significant after applying Bonferroni's sequential test. (Abbreviations of environmental variables as in table 1; FU. Fuerteventura; GC. Gran Canaria; GO. Gomera; HI. El Hierro; LA. Lanzarote; PA. La Palma; TE. Tenerife.)

*Fig. 1. Regresiones lineales bivariantes del número de especies de heterópteros (*S*) sobre las variables ambientales que permanecieron significativas tras aplicar la prueba secuencial de Bonferroni. (Abreviaturas de las variables ambientales como en la tabla 1; FU. Fuerteventura; GC. Gran Canaria; GO. Gomera; HI. El Hierro; LA. Lanzarote; PA. La Palma; TE. Tenerife.)*

according to the test of the following paragraph (stepwise multiple regression) the number of species of heteroptera (*S*) on the Canary Islands depends directly on the combination of *NE* and *CS* according to the equation.

Using stepwise multiple regression, the number of heteroptera species (*S*) was significantly explained by the combination of the number of natural ecosystems (*NE*) and the total cropland surface (*CS*), which are included in the model in this order, according to the following equation:

$$S = 0.158021 \times NP + 0.049346 \times CS - 9.152072$$
$$R^2 = 0.99342; \; p = 0.00001$$

The hypotheses of habitat heterogeneity and human influence are not therefore mutually exclusive, but they combine to explain the species richness of Heteroptera in the Canary Islands.

Partial regression analysis showed the following partition of the variance of *S*:

Part of variance explained exclusively by *NP*: $R_{NP^2} = 0.14838$;

Part of variance explained exclusively by *CS*: $R_{CS^2} = 0.02798$;

Part of variance explained by the SharedAction of *NP* and *CS*: $R_{NP\text{-}CS^2} = 0.81706$;

Unexplained variance: $1 - R^2 = 0.00658$.

Endemic heteroptera species

Linear regressions of the number of heteroptera species endemic to the Canary Islands (*ES*) were significant with twelve variables, although only eight of these passed the Bonferroni sequential test, namely, in decreasing order of explained variance, number of natural ecosystems (*NE*), elevation range (*ER*), number of plant species (*NP*) number of days with fog (*DF*), number of ecological successions of vegetation (*VS*), number of bioclimatic elevation belts (*BB*), number of phytoclimatic regions (*PR*) and mean annual days with precipitation (*DP*) (fig. 2), all directly related with the number of endemic species. No significant unimodal model was obtained. The hypotheses selected were therefore those of habitat heterogeneity and environmental favourableness–severity, with six and two variables involved, respectively.

Using stepwise multiple regression the number of endemic heteropterous species (*ES*) was significantly explained by the combination of the number of natural ecosystems (*NE*), and number of days with fog (*DF*), which are included in the model in this order, according to the following equation:

$$ES = 4.973214 \times NE + 2.294643 \times DF - 13.491071$$
$$R^2 = 0.99038;\ p < 0.0001$$

The hypotheses of habitat heterogeneity and environmental favourableness–severity were not thus mutually exclusive, but when combined they accounted for the species richness of endemic Heteroptera species in the Canary Islands.

The result of the partial regression analysis showed the following partition of the *ES* variance:

Part of variance explained exclusively by *NE*: $R_{NE^2} = 0.13463$;

Part of variance explained exclusively by *DF*: $R_{DF^2} = 0.03561$;

Part of variance explained by the sharedaction of *NE* and *DF*: $R_{NP\text{-}DF^2} = 0.82014$;

Unexplained variance: $1 - R^2 = 0.00962$.

Non–endemic heteropterous species

Linear regressions of the number of non–endemic heteropterous species (*NES*) were found for nine variables, although only three remained significant after applying the Bonferroni test, namely number of plant species (*NP*), number of inhabitants (*NI*), and total cropland surface (*CS*), all directly related to the number of species (fig. 3). These relations were predicted by the habitat heterogeneity hypothesis and the human influence hypothesis.

Using stepwise multiple regression, the number of non–endemic heteropterous species was significantly explained by the combination of the number of plant species (*NP*), and the total cropland surface (*CS*), which is included in the model according to the following equation:

$$NES = 0.100187 \times NP + 0.051906 \times CS + 8.349266$$
$$R^2 = 0.98473;\ p = 0.0002$$

The hypotheses of habitat heterogeneity and human influence were not mutually exclusive, but in combination they explained the species richness of Heteroptera in the Canary Islands.

The result of the partial regression analysis showed the following partition of the variance of *NES*:

Part of variance explained exclusively by *NP*: $R_{NP^2} = 0.10333$;

Part of variance explained exclusively by *CS*: $R_{CS^2} = 0.05364$;

Part of variance explained by the sharedaction of *NP* and CS: $R_{NP\text{-}CS^2} = 0.82776$;

Unexplained variance: $1 - R^2 = 0.01527$.

Discussion

Different processes for endemic and non–endemic species

Results from the present study show that factors accounting for the richness of endemic and non-endemic Hereroptera species differ. Becker (1992) found that the species richness of both predatory and herbivore Heteroptera in the Canary Islands was significantly related to plant species richness. However, Becker (1992) did not distinguish between endemic and non–endemic species in Heteroptera. Our results show that, although both groups of species are related to vegetation, endemic species respond to natural habitat heterogeneity while non–endemic species respond to the number of plant species, which included introduced plant species, and to the availability of new habitats due to agricultural activity. This is consistent with the results of Kitchener (1982), who showed that for some groups of vertebrates, the best predictors for species richness were different for those species recorded only in natural vegetation when compared to those for species found in disturbed situations.

The variance partitioning analysis revealed a high proportion of sharedaction of the cropland surface of the islands and the number of natural ecosystems or the number of plant species. This may be due to the effect of area, because larger islands support more diverse ecosystems, more plant species and larger cropland surface. This would be consistent with the finding of Becker (1992) that the number of species of predatory Heteroptera in the Canary Islands was significantly related to the area of the islands. However, after taking into account the effect of habitat heterogeneity and human activity, the effect of area is negligible. This might be a rather common pattern for insects. Abbott (1974), for example, found that area was of minor importance in explaining insect species richness on the southern ocean islands while plant species richness accounted for most variation in insect species richness, and Williams (1982) found that plant species richness was an important predictor of insect richness but that area was less important.

The role of habitat heterogeneity

Insular habitat heterogeneity has been reported to have an effect on species richness for other groups of arthropods as well. Owen & Smith (1993) found that the total number of species and the number of endemic species of lepidoptera in the Canary Islands, Azores and Madeira were significantly cor-

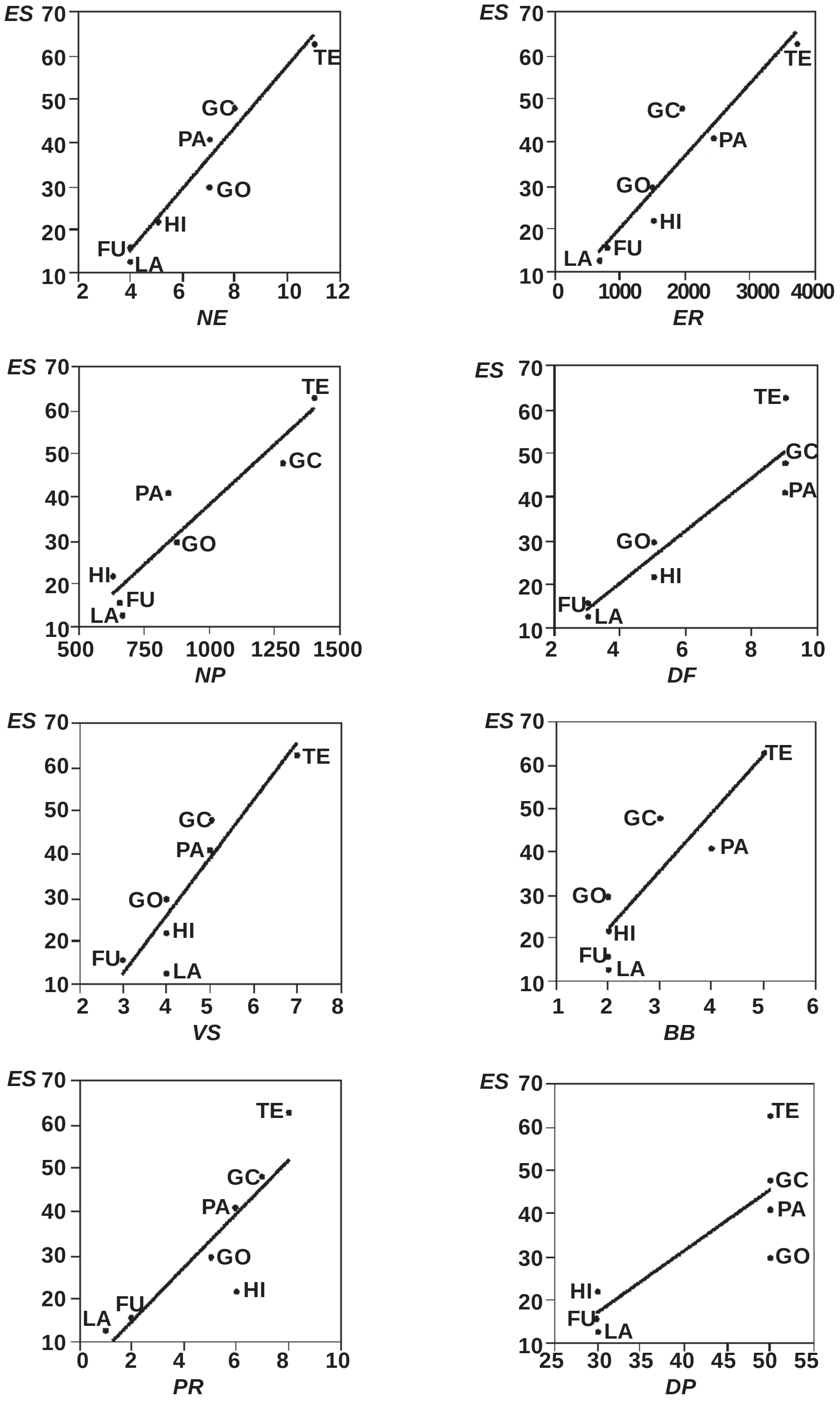

Fig. 2. Bivariate linear regressions of the number of endemic heteropterous species (*ES*) on environmental variables that remained significant after applying the Bonferroni sequential test. (For abbreviations of environmental variables see table 1, for other abbreviations see figure 1.)

*Fig. 2. Regresiones lineales bivariantes del número de especies de heterópteros endémicos (*ES*) sobre las variables ambientales que permanecieron significativas tras aplicar la prueba secuencial de Bonferroni. (Para las abreviaturas de las variables ambientales ver tabla 1, para otras abreviaturas ver figura 1.)*

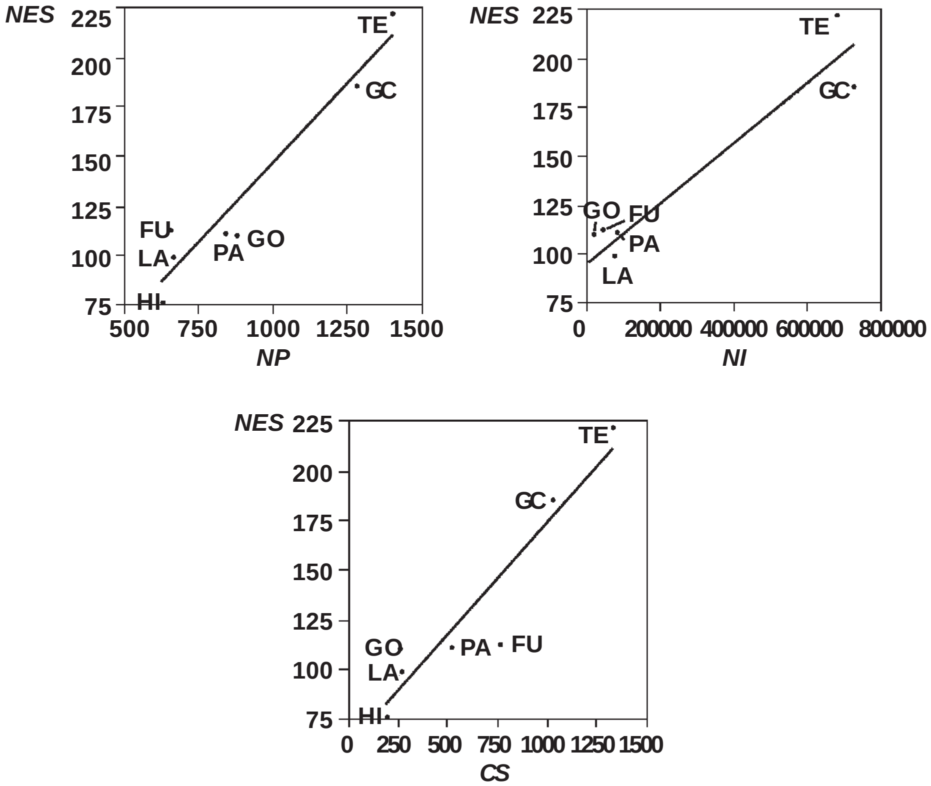

Fig. 3. Bivariate linear regressions of the number of non–endemic heteropterous species (*NES*) on environmental variables that remained significant after applying the Bonferroni sequential test. (For abbreviations of environmental variables see table 1, for other abbreviations see figure 1.)

*Fig. 3. Regresiones lineales bivariantes del número de especies de heterópteros no endémicos (*NES*) sobre las variables ambientales que permanecieron significativas tras aplicar la prueba secuencial de Bonferroni. (Para las abreviaturas de las variables ambientales ver tabla 1, para otras abreviaturas ver figura 1.)*

related with vegetation diversity, and Sfenthourakis (1996) considered that habitat diversity was the most important factor determining terrestrial isopod species richness in the Aegean archipelago.

Natural habitat heterogeneity also plays a role for non–endemic Heteroptera. Such a role has been reported for other groups of species; Chown et al. (1998), for instance, found that indigenous vascular plant species richness was important in determining alien insect species richness in southern ocean islands, although this relationship was modified by the extent of human activity, as an increase in both plant species richness and human activity provoked an increase in alien insect species richness.

The role of human activity on non–endemic species

Invading species have been shown to be more successful in habitats altered by human activities than in undisturbed habitats inhabited by locally adapted native species (Elton, 1958; Sax & Brown, 2000). Simberloff (1986) suggested that new plants introduced into islands constitute food or shelter for new insects, and some of these new insects become prey species for yet other predatory and parasitic insects. In this way, habitat change in islands, such as those created by agriculture, may increase the probabilities of success for many alien species.

In natural ecosystems the resident insect community may present predatory or competitive resistance to alien invasions that are not exerted in agricultural systems, which are novel for native species. Notwithstanding this, the presence of introduced species in natural ecosystems could be of concern for the conservation of endemic fauna, since Fox & Fox (2000) considered the presence of invasive species as a form of disturbance for indigenous species (see also Fox & Fox, 1986).

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