



# Species richness, environmental heterogeneity and area: a case study based on land snails in Skyros archipelago (Aegean Sea, Greece)

K. A. Triantis<sup>1,2\*</sup>, M. Mylonas<sup>1,2</sup>, M. D. Weiser<sup>3</sup>, K. Lika<sup>2</sup>  
and K. Vardinoyannis<sup>1</sup>

<sup>1</sup>Natural History Museum of Crete, University of Crete, Irakleio, <sup>2</sup>Department of Biology, University of Crete, Irakleio, Greece and <sup>3</sup>Department of Ecology and Evolutionary Biology, University of Arizona, 1041 East Lowell Street, USA

## ABSTRACT

**Aim** To test the performance of the *choros* model in an archipelago using two measures of environmental heterogeneity. The *choros* model is a simple, easy-to-use mathematical relationship which approaches species richness as a combined function of area and environmental heterogeneity.

**Location** The archipelago of Skyros in the central Aegean Sea (Greece).

**Methods** We surveyed land snails on 12 islands of the archipelago. We informed the *choros* model with habitat data based on natural history information from the land snail species assemblage. We contrast this with habitat information taken from traditional vegetation classification to study the behaviour of *choros* with different measures of environmental heterogeneity.  $R^2$  values and Akaike's information criterion (AIC) were used to compare the *choros* model and the Arrhenius species–area model. Path analysis was used to evaluate the variance in species richness explained by area and habitat diversity.

**Results** Forty-two land snail species were recorded, living in 33 different habitat types. The *choros* model with habitat types had more explanatory power than the classic species–area model and the *choros* model using vegetation types. This was true for all islands of the archipelago, as well as for the small islands alone. Combined effects of area and habitat diversity primarily explain species richness in the archipelago, but there is a decline when only small islands are considered. The effects of area are very low both for all the islands of the archipelago, and for the small islands alone. The variance explained by habitat diversity is low for the island group as a whole, but significantly increases for the small islands.

**Main conclusions** The *choros* model is effective in describing species–richness patterns of land snails in the Skyros Archipelago, incorporating ecologically relevant information on habitat occupancy and area. The *choros* model is more effective in explaining richness patterns on small islands. When using traditional vegetation types, the *choros* model performs worse than the classic species–area relationship, indicating that use of proxies for habitat diversity may be problematic. The slopes for *choros* and Arrhenius models both assert that, for land snails, the Skyros Archipelago is a portion of a larger biogeographical province. The *choros* model, informed by ecologically relevant habitat measures, in conjunction with path analysis points to the importance of habitat diversity in island species richness.

## Keywords

Aegean Sea, *choros* model, environmental heterogeneity, habitat diversity, land snails, small islands, species–area relationship, species richness, vegetation types.

\*Correspondence: K. A. Triantis, Natural History Museum of Crete, University of Crete, PO Box 2208, 71409 Knossou Av., Irakleio, Crete, Greece. E-mail: kostas@nhmc.uoc.gr

## INTRODUCTION

A fundamental goal of ecology and biogeography is to identify and understand the factors that enhance or constrain species richness. The best known pattern in species diversity is the species–area relationship: the increase in species richness with increasing area. While the species–area relationship is one of biogeography’s best documented patterns, questions remain about its theoretical basis and empirical shape (Rosenzweig, 1995; Lomolino & Weiser, 2001).

There have been many attempts to identify and measure the factors that contribute to the strikingly orderly relationship between area and species diversity (e.g. MacArthur & Wilson, 1967; Rosenzweig, 1995). Many mechanisms have been proposed to account for species–area relationships (e.g. Whittaker, 1998; Connor & McCoy, 2000), but the two most widely accepted are the habitat diversity hypothesis (Williams, 1964) and the area *per se* hypothesis (Preston, 1962a,b; Simberloff, 1976; Rosenzweig, 1995). Despite attempts to establish the primacy of one over the other, habitat diversity and area *per se* are not mutually exclusive mechanisms. They are supplementary, and may operate individually or in combination to drive species–area relationships (Connor & McCoy, 1979, 2000; Kohn & Walsh, 1994; Rosenzweig, 1995; Ricklefs & Lovette, 1999). Therefore the goal should be to understand how area and habitat diversity interact to create patterns of richness. At least four models have been proposed that attempt to combine the effects of area and habitat diversity on species richness (Buckley, 1982; Rafe *et al.*, 1985; Tjørve, 2002; Triantis *et al.*, 2003). The two first models have generally been neglected, mainly due to their tenuous assumptions and degrees of complexity. Here we investigate further the relatively simpler *choros* model of Triantis *et al.* (2003).

The *choros* model posits that overall area and habitat complexity interact multiplicatively to predict species richness better than is predicted by area alone (Triantis *et al.*, 2003). The term *choros* ( $K$ ) is simply the total area ( $A$ ) of a region multiplied by the number of habitat types ( $H$ ) within that region:  $K = A \times H$ . The species richness ( $S$ ) of the region is then expressed as a power function, such that  $S = c(A \times H)^z = cK^z$ . This relationship is an extension of the simpler species–area relationship  $S = cA^z$  (Arrhenius, 1921). The structure of the *choros* model is similar to the ‘species–energy’ relationship proposed by Wright (1983) and Wright *et al.* (1993), who used a multiplicative formula of area and actual evapotranspiration (AET), area  $\times$  AET, to estimate the energetic resources available.

A comparison of fit of the *choros* model and the classic species–area relationship showed that *choros* was more effective in 20 of 22 cases. Thus, the species richness in each case study is better explained by area  $\times$  habitat (the *choros*  $K$ ) rather than area alone (Triantis *et al.*, 2003). The *choros* model also shows improved prediction for other systems (Watson, 1964; Sillen & Solbreck, 1977; Cowie, 1995;

Lawesson *et al.*, 1998; Medail & Vidal, 1998; Perry *et al.*, 1998; Steadman & Freifeld, 1998; Granados *et al.*, 2001; Watson, 2003; K.A.T., unpubl. data).

Here we compare directly the explanatory performance of the *choros* and area models. We incorporate and evaluate the performance of two measures of habitat diversity ( $H$ ): one based on the observed ecology of land snails; the other based on traditional vegetation types. Additionally, we focus on the performance of the *choros* model in describing species richness on small islands.

## METHODS

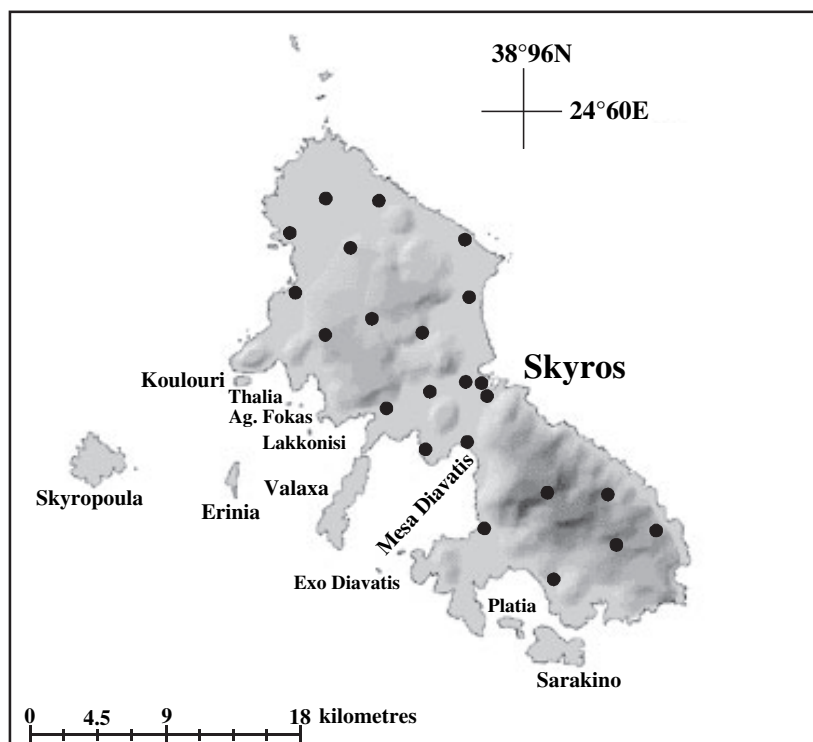
### Study area

The archipelago of Skyros lies in the central Aegean Sea. The largest island of the archipelago is Skyros, with a total area of 208 km<sup>2</sup> which rises to an elevation of 792 m. About 20 small islets are found within the isobath of 200 m around the island of Skyros (Fig. 1).

The geological formations of Skyros consist mainly of limestone (66%), schist (22%) and neogene formations (7%) (Melentis, 1973). Islets are mainly limestone (Melentis, 1973). Only the islet of Exo Diavatis does not consist of a calcareous substrate, but of semi-metamorphic clastic formations (mainly gneiss; M.M., pers. obs.). The climate is characterized as thermo-mediterranean, with a long, dry period beginning at the end of April and ending in early October. The mean annual rainfall is 543 mm and the mean annual temperature is 18.1 °C (Andreakos, 1978).

Pine forests with *Pinus halepensis* Miller, maquis with *Juniperus phoenicea* L., and lush vegetation cover the north-west part of Skyros. In contrast, south-east Skyros is rocky and mountainous; covered by phrygana and degraded maquis with *Quercus coccifera* L. (Dafis *et al.*, 1996). Maquis, phrygana and grasses dominate the remaining islands of the archipelago.

We visited the archipelago of Skyros during late June 2001, early January and late April 2002. Land snails in the Aegean exhibit varying biological cycles (Mylonas & Vardinoyannis, 2001; Parmakelis & Mylonas, 2002). Thus the three different sampling periods give relatively complete knowledge of habitat preference. We collected land snail species by hand from 12 islands of the group (Fig. 1; Table 1). We surveyed 23 sites on Skyros, spread throughout the island, aiming at sampling all different biotopes present (Fig. 1). On the smaller islands, the land snails were sampled from the whole area of the island. Each locality was sampled by at least three experts until no new species were found. Approximately 3 L of litter and topsoil were removed from each locality, taken from patches likely to yield litter-dwelling micro-snails. The litter and topsoil samples were sieved and searched in the laboratory, discarding material passing through a 0.4-mm mesh. The presence of species at each locality was recorded, but abundance was not estimated. All collections are deposited in the Natural History Museum of Crete.



**Figure 1** Map of the Skyros archipelago, showing the islands included in this study and the sites surveyed (black dots).

**Table 1** Area, number of species and number of habitat types for islands of the Skyros archipelago included in this analysis

Island	Area (km <sup>2</sup> )	Species	Number of habitat types	Number of vegetation types
Skyros (Skr)	208	42	33	7
Valaxa (Val)	4.33	21	18	4
Skyropoula (Sky)	3.83	20	22	5
Sarakino (Sar)	3.34	16	22	5
Platia (Pla)	0.62	15	18	4
Erineia (Eri)	0.53	14	11	3
Koulouri (Kou)	0.29	14	9	3
Mesa Diavatis (MeD)	0.039	10	5	2
Exo Diavatis (ExD)	0.018	4	2	4
Lakkonisi (Lak)	0.016	7	5	2
Agios Fokas (AgF)	0.003	7	5	1
Thalia (Thl)	0.002	6	5	1

### Habitat diversity

We used two measures of habitat diversity. The first is informed by the ecology and biology of land snails; the second is based on traditional vegetation types commonly used in ecological studies (Nilsson *et al.*, 1988; Ricklefs & Lovette, 1999; Davidar *et al.*, 2001).

First, we defined habitats using a habitat matrix with eight different biotopes in the vertical axis (pine forest, shrublands, meadow, cultivation, settlements, salt marsh, pebbly beach, sandy beach) and six elements of the biotopes in the horizontal

**Table 2** Habitat matrix used to describe habitat types occupied by land snails in the Skyros archipelago

Biotope	Elements of biotope					
	Stones	Pile of stones	Rock	Bush or plant	Soil	Litter
Pine forest						
Shrubland						
Meadow						
Cultivation						
Settlements						
Salt march						
Pebbly beach						
Sandy beach						

axis (stones, pile of stones, rock, soil, bush or plant, litter). Thus there are 48 possible combinations of biotope and element (Table 2). For each collection, we recorded biotope and element.

Seven different vegetation types were defined for the island group (generally following Dafis *et al.*, 1996): pine forest, maquis, phrygana, cultivation, coastal vegetation, riparian vegetation and grassland.

### Statistical methods

*Choros* was estimated for habitat types ( $K_H$ ) (using the habitat matrix) and for vegetation types ( $K_V$ ). Since the *choros* equation and the classic species–area equation are both power functions, by using the logarithm of the two models we obtain

linear relations of  $\log(S)$  and  $\log(A)$ ,  $\log(K_V)$  and  $\log(K_H)$ , respectively:

$$\log(S) = \log(c) + z \log(A) \quad (1)$$

and

$$\log(S) = \log(c) + z \log(K_V) \quad (2)$$

and

$$\log(S) = \log(c) + z \log(K_H) \quad (3)$$

We used the conventional logarithmic transformations for purposes of comparison. All regressions and estimations of parameters were carried out following Sincich *et al.* (1999). We used Student's test to check for differences between the slopes of the three equations (Zar, 1984).

For comparison of the models, as a measure of goodness of fit we used the  $R^2$  values and the more general Akaike's information criterion (AIC). As the models have the same number of fitted parameters,  $R^2$  values are comparable without any modification (Kvalseth, 1985; Loehle, 1990). The difference in AIC values ( $\Delta AIC = AIC_i - AIC_j$ ) indicates the best model, since the model with the lowest AIC value is considered to be better (Sakamoto *et al.*, 1986; Burnham & Anderson, 2002). We also performed a comparison of the *choros* model with the classic equation for the small islands ( $<1 \text{ km}^2$ ) of the archipelago.

Path analysis with correlated causes (Li, 1975; Sokal & Rohlf, 1981; Grace & Pugsek, 1997, 1998; Legendre & Legendre, 1998) is used to assess the relative direct and indirect effects of predictor or causal variables, according to an *a priori* model. Path analysis is useful for distinguishing the role of multiple collinear variables (e.g. area and habitat diversity) in respect of various response variables. In general, we follow the approach of Kohn & Walsh (1994). According to the model used, habitats directly affect species richness, while area affects species richness in two ways: directly, as a straightforward factor; and indirectly, through habitats (Fig. 5 of Kohn & Walsh, 1994). In this path model the explained variance of species richness is of three types: (1) variance in species richness that is associated only with area (area's unique variance explanation); (2) variance in species richness that is associated only with habitat diversity (habitat diversity's unique variance explanation); and (3) variance in species richness that is explained by both area and habitat diversity. This sum yields the  $R^2$  of the multiple regression (Li, 1975). The magnitude of the shared variance is proportional to the magnitude of correlation between area and habitat diversity (Li, 1975; Legendre & Legendre, 1998; J.B. Grace, pers. comm.).

## RESULTS

In total, 42 land snail species were collected from the 12 islands examined. Island size ranged from 0.002 to 208  $\text{km}^2$ . Species richness by island ranged from four to 42 species (Table 1). Land snails occupied 33 of the 48 possible biotope/element combinations in the habitat matrix, which are considered as the habitat types (Table 3). All 42 species, seven vegetation

types (Table 4), and the 33 habitat types (biotope/element combinations) were found on the largest island, Skyros. The smallest islands (Agios Fokas and Thalia) had a single vegetation type (phrygana) and five habitat types.

For all islands, area alone was highly correlated with species richness (equation 1a), for islands  $<1.0 \text{ km}^2$ , this correlation was also significant, but with reduced fit (equation 1b):

$$\log(S_{\text{all}}) = 1.19 + 0.18 \log(A) (R^2 = 0.88, P < 0.001) \quad (1a)$$

$$\log(S_{\text{small}}) = 1.19 + 0.17 \log(A) (R^2 = 0.67, P < 0.05) \quad (1b)$$

The *choros* model using traditional vegetation types ( $K_V$ ) was less predictive than area alone:

$$\log(S_{\text{all}}) = 1.10 + 0.15 \log(K_V) (R^2 = 0.83, P < 0.001) \quad (2a)$$

$$\log(S_{\text{small}}) = 1.09 + 0.13 \log(K_V) (R^2 = 0.55, P < 0.05) \quad (2b)$$

The *choros* model using biotope/element combinations ( $K_H$ ) was a better predictor of species richness than area ( $A$ ) and *choros* with vegetation types ( $K_V$ ), both for all the islands of the archipelago (equation 3a) and the small islands alone (equation 3b):

$$\log(S_{\text{all}}) = 1.03 + 0.15 \log(K_H) (R^2 = 0.91, P < 0.001) \quad (3a)$$

$$\log(S_{\text{small}}) = 1.04 + 0.15 \log(K_H) (R^2 = 0.79, P < 0.001) \quad (3b)$$

The AIC values were lower for the *choros* model with habitat types ( $K_H$ ) than with traditional vegetation types ( $K_V$ ) and for area alone ( $A$ ), indicating the better fit of the *choros* model with habitat types ( $K_H$ ) (Table 5).

For the data sets analysed here, the slope estimates for the two *choros* versions were lower than those for area alone, but no significant statistical differences were found.

The number of habitat types in each island was positively correlated with the area:  $\log(H) = 1.11 + 0.22 \log(A)$ , ( $R^2 = 0.79$ ,  $P < 0.001$ ). The correlation between vegetation types and area was also positive, with a lower correlation coefficient,  $\log(V) = 0.16 + 0.55 \log(A)$ , ( $R^2 = 0.74$ ,  $P < 0.001$ ).

Path analysis was used to evaluate the effects of area and habitat diversity on variation in species richness. For all islands of the archipelago, we calculated that 4% of species richness is associated only with area; 6% with habitat diversity; 84% is explained by both area and habitat diversity; and 6% of the variance remains unexplained. Thus, due to the strong correlation of area with habitat diversity, the magnitude of the shared variance is very high.

For the small islands, 5% of the species richness is associated only with area; 24% with habitat diversity; and 62% is explained by both area and habitat diversity. The unexplained variance for the small islands is 9%.

## DISCUSSION

Knowledge of how species interact with their environment is of obvious importance to understanding large-scale patterns of

**Table 3** Habitat types used in this study, and the islands where each is present

Habitat	Islands*
Stones in forest	Skr
Stones in shrublands	Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl, ExD
Stones in meadows	Skr, Val, Sky, Sar, Eri
Stones in cultivation	Skr, Val, Sky, Sar, Pla, Kou
Stones in settlement	Skr, Val, Sky, Sar, Pla
Stones in salt march	Skr
Stones in sandy beach	Skr, Sar
Stones in pebbly beach	Skr, Sky, Pla
Pile of stones in forest	Skr
Pile of stones in shrublands	Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl
Pile of stones in meadows	Skr, Val, Sky, Sar, Eri
Pile of stones in cultivation	Skr, Val, Sky, Sar, Pla, Kou
Pile of stones in sandy beach	Skr, Sar
Pile of stones in pebbly beach	Skr, Sky, Pla
Rock in forest	Skr
Rock in shrublands	Skr, Val, Sky, Sar, Pla, Eri, Kou
Rock in meadow	Skr, Val, Sky, Sar, Eri
Bushes or plants in forest	Skr
Bushes or plants in shrublands	Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl
Bushes or plants meadows	Skr, Val, Sky, Sar, Eri
Bushes or plants in cultivation	Skr, Val, Sky, Sar, Pla, Kou
Bushes or plants in settlement	Skr, Val, Sky, Sar, Pla
Bushes or plants in sandy beach	Skr, Sar
Bushes or plants in pebbly beach	Skr, Sky, Pla
Soil in forest	Skr
Soil in shrublands	Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl, ExD
Soil in meadow	Skr, Val, Sky, Sar, Eri
Soil in cultivation	Skr, Val, Sky, Sar, Pla, Kou
Soil in settlement	Skr, Val, Sky, Sar, Pla
Soil in sandy beach	Skr, Sar
Soil in pebbly beach	Skr, Sky, Pla
Litter in forest	Skr
Litter in shrublands	Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl

\*See Table 1 for island codes.

**Table 4** Vegetation types used in this study, and the islands where each is present

Vegetation	Islands*
Pine forest	Skr
Maquis	Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, ExD
Phrygana	Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl, ExD
Cultivation	Skr, Val, Sky, Sar, Pla, Kou
Coastal vegetation	Skr, Sky, Sar, Pla, ExD
Riparian vegetation	Skr
Grassland	Skr, Val, Sky, Sar, Eri, ExD

\*See Table 1 for island codes.

diversity as well as more local ecological patterns (Watson, 1964; Brown, 1995; Rosenzweig, 1995; Gaston, 2000). Our results offer several lines of evidence that environmental heterogeneity, studied through the habitat types occupied by land snails, is central to patterns of land snail species richness on

**Table 5** Slope and AIC values for equations 1–3

Data set	Model	Slope value	$\Delta$ AIC
All islands	Species area (equation 1a)	0.18	-52.64
	<i>Choros</i> model ( $K_V$ , equation 2a)	0.15	-48.67
	<i>Choros</i> model ( $K_H$ , equation 3a)	0.15	-56.28
Small islands	Species area (equation 1b)	0.17	-31.06
	<i>Choros</i> model ( $K_V$ , equation 2b)	0.13	-28.42
	<i>Choros</i> model ( $K_H$ , equation 3b)	0.16	-33.91

the Skyros archipelago. The *choros* model has more explanatory power than area alone. While the increase in fit ( $R^2$  and AIC) is not great between area alone and *choros*, these results, together with the findings of Triantis *et al.* (2003), show that the increased fit of *choros* over area alone is relatively consistent.

Area and number of habitats are strongly interconnected (Harner & Harper, 1976; Rafe *et al.*, 1985; Gibson, 1986; Rosenzweig, 1995). The strong intercorrelation of area and habitat diversity probably results from the interdependence of

area and the presence of specific habitat types (Whitehead & Jones, 1969; Kohn & Walsh, 1994). Certain habitat types (in our case the habitat types related to salt marshes and pine forests) occur only on the largest island, Skyros. Other habitats, such as those associated with beaches and anthropogenic biotopes (cultivation, settlement), are not found on the smaller islands. The results of path analysis indicate that the variance in species richness explained by the intercorrelation of area and habitat diversity, and habitat diversity alone, is dramatically higher compared with the variance explained by area alone, for both small islands and the archipelago as a whole.

The increase in fit of the *choros* model over area alone is more apparent in the subset of small islands. As the contribution of habitat diversity is more intense at finer scales (Schmida & Wilson, 1985), diversity on small islands may be influenced by habitat diversity more than larger islands. On small islands, an increase in species number, along with the increase in area, is usually not observed or is very erratic (the 'small-island effect': Niering, 1963; MacArthur & Wilson, 1967; Whitehead & Jones, 1969; Woodroffe, 1986; Lomolino, 2000; Lomolino & Weiser, 2001; Williamson *et al.*, 2001). Environmental heterogeneity then becomes one of the main determinants of how many species will maintain populations (Botsaris, 1996; Losos, 1996; Whittaker, 1998; Lomolino & Weiser, 2001). Our path analysis showed that the effects of area were low, and that habitat diversity effects were greater on small islands than in the archipelago as a whole. Moreover, the variance explained by both area and habitat diversity on small islands was lower than for all the islands of the archipelago. At this scale, as environmental heterogeneity becomes one of the main determinants of species persistence, and as area and available habitats become increasingly decoupled, area alone cannot efficiently express the total effects of habitat diversity and island size on species richness, and the *choros* model is more effective at explaining patterns of diversity on small islands.

Inclusion of habitat diversity in models attempting to explain variation in species richness is not new (Buckley, 1982; Rafe *et al.*, 1985; Deshayes & Morisset, 1988; Kohn & Walsh, 1994; Tjørve, 2002). The utility and novelty of the *choros* model are not necessarily due to the better fit to observed data, but arise from the relative simplicity of the technique, as well as the increased explanatory power of the model. *Choros* is a concept that holds not only quantitative but also qualitative information for the area under study, facilitating a more appropriate approach to mechanisms responsible for the establishment of species richness.

The results of Triantis *et al.* (2003) indicate that the inclusion of a measure of environmental heterogeneity in the *choros* model across 22 studies of disparate taxa (notwithstanding that habitat types were defined differently by ecologists) leads to a more effective description of species richness compared with the classic species–area relationship, in 91% of the cases. However, the results of this study argue that using habitat diversity measures informed by the natural history of the focal taxon should act to increase the explanatory

power (fit) of the *choros* model. In the present work, inclusion of vegetation types as the measure of habitat diversity in the *choros* model ( $K_V$ ) fitted the data less well than area alone. That is in accordance with an extensive literature indicating that the occurrence of land snail species is not related to the vegetation types of an area (e.g., Cain, 1983; Heller, 1988). Thus, using habitat diversity measures not informed by the natural history of the focal taxon (e.g. traditional vegetation types as habitat diversity for snails) should be undertaken with caution. Nevertheless, for some animal taxa, vegetation types appear to reflect the habitat diversity experienced by these groups (Tews *et al.*, 2004).

Within the present data set, the island Exo Diavatis demonstrates the importance of using ecologically relevant measures of habitat diversity. Exo Diavatis had the lowest species richness and the lowest habitat diversity, despite being larger and having more vegetation types than several other islands (Lakkonisi, Agios Fokas and Thalia). Exo Diavatis is the only island in the archipelago without limestone, an important resource for many land snails (Mylonas, 1982; Tompa, 1984; Goodfriend, 1986). Thus, the use of vegetation types fails to describe the ecologically relevant habitat diversity for land snails.

A major obstacle for the broader study of habitat diversity effects has been the disparity between how organisms experience habitat, and how ecologists have operationally defined habitat. This has led to multiple meanings of 'habitat' to ecologists (Hall *et al.*, 1997; Dennis *et al.*, 2003). Thus practical guidance to the recognition of habitat is lacking, and consequently habitats are described with a lack of precision (Rosenzweig, 1995). Additionally, habitat specialization and differentiation within the focal taxon is inexorably linked to the influence of habitat diversity on richness patterns. If organisms randomly occupy habitats as defined by ecologists, the assumption that the habitats have meaning to the taxon is invalid. Accurate description of habitat is essential, as the influence of habitat on richness is dependent on the degree of habitat specialization and differentiation (Hart & Horwitz, 1991; Ricklefs & Lovette, 1999). Greater habitat specialization within the focal taxon will increase the influence of habitat diversity on richness. We have estimated that 12 of the 42 land snail species in the Skyros archipelago are habitat specialists (Triantis, 2002). Greater similarity between inferred habitat definitions and organisms' perceptions of habitat should increase the ability to detect the signal of habitat diversity.

As far as the  $z$  values are concerned, the *choros* model exhibits similar behaviour to the classic species–area relationship (Triantis *et al.*, 2003). The slopes ( $z$  values) of the area–richness and *choros*–richness models are 0.18 and 0.16, respectively; and both place the Skyros archipelago land snails in the 'within biogeographical province' (intraprovincial) category (Rosenzweig, 1995, 2004). While we present an explanatory model of species richness, the typical goal of such analyses is to create predictive models of species richness, avoiding the need to collect exhaustive natural history and habitat occupancy data. Further tests of the predictive ability of

the *choros* model would be to look at other archipelagos within the biotic province, such as the Northern Sporades or Euboean Islands, using the *z* and *c* values estimated from the island group of Skyros.

MacArthur & Wilson (1967) pointed out that 'in the absence of good information on diversity of habitats, we first turn to island areas'. Thirty-eight years later, habitat diversity is still difficult to assess in a standardized way, while easily measured parameters such as island area, elevation and distance from the mainland are predominantly used. Here we offer a method of examining the importance of habitat diversity to island species richness. The *choros* model, informed by ecologically relevant habitat measures, in conjunction with path analysis, points to the importance of environmental heterogeneity in island species richness. Nevertheless, this analysis suggests caution in the use of proxy measures of habitat diversity. Further development of these methods should focus on developing tests of the assumptions underlying how species and ecologists 'perceive' habitats (K.A.T. and co-workers, unpubl. data).

## ACKNOWLEDGEMENTS

We are grateful to our colleagues P. Lymberakis, A. Parmakelis, M. Iovic, A. Kagiampaki, E. Tsolaki, A. J. Kerckhoff, and especially to R. A. D. Cameron and S. Sfenthourakis for their comments on earlier versions of the manuscript. R. J. Whittaker and two anonymous referees provided valuable and constructive comments. We would like also to thank Professor A. Wiktor for his valuable help in the identification of slug species. J. B. Grace kindly made available relevant chapters of his unpublished book on path analysis. Part of the present study was funded by the Natural History Museum of Crete. K.A.T. received the Manasaki Scholarship. The University of Arizona, Department of Ecology and Evolutionary Biology supported M.D.W.

## REFERENCES

- Andreakos, K. (1978) *Climatic elements of the Greek Network (1930–1975) (in Greek)*. Climate Department, Ministry of Defence, Athens.
- Arrhenius, O. (1921) Species and area. *Journal of Ecology*, **9**, 95–99.
- Botsaris, I. (1996) *The biogeography of terrestrial molluscs on the islands and islets of Saronikos Gulf (in Greek)*. PhD thesis, University of Athens, Athens.
- Brown, J.H. (1995) *Macroecology*. University of Chicago Press, Chicago, IL, USA.
- Buckley, R. (1982) The habitat-unit model of island biogeography. *Journal of Biogeography*, **9**, 339–344.
- Burnham, K.P. & Anderson, D.R. (2002) *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Cain, A.J. (1983) Ecology and ecogenetics of terrestrial molluscan populations. *The mollusca*, Vol. 6. *Ecology* (ed. by W.D. Russell-Hunter), pp. 597–647. Academic Press, New York.
- Connor, E.F. & McCoy, E.D. (1979) The statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.
- Connor, E.F. & McCoy, E.D. (2000) Species–area relationships. *Encyclopedia of biodiversity*, Vol. 5 (ed. by S.A. Levin), pp. 397–412. Academic Press, New York.
- Cowie, R.H. (1995) Variation in species diversity and shell shape in Hawaiian land snails: *in situ* speciation and ecological relationships. *Evolution*, **49**, 1191–1201.
- Dafis, S., Papastergiadou, E., Georghiou, K., Babalonas, D., Georgiadis, T., Papageorgiou, M., Lazaridou, T. & Tsiaoussi, V. (1996) *The Greek 'habitat' project NATURA 2000: an overview*. Commission of the European Communities DG XI. Directive 92/43/EEC. Greek Biotope/Wetland Center, Goulandris Natural History Museum, Thessaloniki, Greece.
- Davidar, P., Yoganand, K. & Ganesh, T. (2001) Distribution of forest birds in the Andaman Islands: importance of key habitats. *Journal of Biogeography*, **28**, 663–672.
- Dennis, R.L.H., Shreeve, T.G. & Van Dyck, H. (2003) Towards a functional resource-based concept for habitat: a butterfly biology viewpoint. *Oikos*, **102**, 417–426.
- Deshaye, J. & Morisset, P. (1988) Floristic richness, area, and habitat diversity in a hemiarctic archipelago. *Journal of Biogeography*, **15**, 747–757.
- Gaston, K.J. (2000) Global patterns in biodiversity. *Science*, **405**, 220–227.
- Gibson, C.W.D. (1986) Management history in relation to changes in the flora of different habitats on an Oxfordshire estate, England. *Biological Conservation*, **38**, 217–232.
- Goodfriend, G.A. (1986) Variation in land-snail shell form and size and its causes: a review. *Systematic Zoology*, **35**, 204–223.
- Grace, J.B. & Pugsek, B.H. (1997) A structural equation model of plant species richness and its application to a coastal wetland. *American Naturalist*, **149**, 436–460.
- Grace, J.B. & Pugsek, B.H. (1998) On the use of path analysis and related procedures for the investigation of ecological problems. *American Naturalist*, **152**, 151–159.
- Granados, M., O'Kennon, R.J. & Benz, B.F. (2001) Plant species–area relationships in ten central Texas protected natural areas. *SIDA*, **19**, 1061–1072.
- Hall, L.S., Krausman, P.R. & Morrison, M.L. (1997) The habitat concept and a plea for standard terminology. *Wildlife Society Bulletin*, **25**, 173–182.
- Harner, R.F. & Harper, K.T. (1976) The role of area, heterogeneity, and favorability in plant species diversity of pinyon–juniper ecosystems. *Ecology*, **57**, 1254–1263.
- Hart, D.D. & Horwitz, R.J. (1991) Habitat diversity and the species–area relationship: alternative models and tests. Habitat Structure. *The physical arrangement of objects in space* (ed. by S.S. Bell, E.D. McCoy and H.R. Mushinsky), pp. 47–68. Chapman & Hall, London.
- Heller, J. (1988) The biogeography of the land snails of Israel. *The zoogeography of Israel* (ed. by T.Y. Yom and E. Tcher-

- nov), pp. 325–354. Dr Junk Publishers, Dordrecht, the Netherlands.
- Kohn, D.D. & Walsh, D.M. (1994) Plant species richness the effect of island size and habitat diversity. *Journal of Ecology*, **82**, 367–377.
- Kvalseth, T.O. (1985) Cautionary note R2. *American Statistician*, **39**, 279–285.
- Lawesson, J.E., De Blust, G., Grashof, C., Firkbank, L., Honnay, O., Hermy, M., Hobitz, P. & Jensen, L.M. (1998) Species diversity and area-relationships in Danish beech forests. *Forest Ecology and Management*, **106**, 235–245.
- Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd edn. Elsevier, Amsterdam.
- Li, C.C. (1975) *Path analysis: a primer*. Boxwood Press, Pacific Grove, CA, USA.
- Loehle, C. (1990) Proper statistical treatment of species–area data. *Oikos*, **57**, 143–146.
- Lomolino, M.V. (2000) Ecology's most general, yet protean pattern: the species–area relationship. *Journal of Biogeography*, **27**, 17–26.
- Lomolino, M.V. & Weiser, M.D. (2001) Towards a more general species–area relationship: diversity on all islands, great and small. *Journal of Biogeography*, **28**, 431–445.
- Losos, J.B. (1996) Ecological and evolutionary determinants of the species–area relation in Caribbean anoline lizards. *Philosophical Transactions of the Royal Society of London B*, **351**, 847–854.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ, USA.
- Medail, F. & Vidal, E. (1998) Patterns of plant richness and composition on western Mediterranean islands (off the southeast coast of France). *Canadian Journal of Botany*, **76**, 321–331.
- Melentis, I. (1973) The geology of the island of Skyros (in Greek). *Bulletin of the Geological Society of Greece*, **10**, 298–322.
- Mylonas, M. (1982) *The zoogeography and ecology of the terrestrial mollusks of Cyclades (in Greek)*. PhD Thesis, University of Athens, Athens.
- Mylonas, M. & Vardinoyannis, K. (2001) Life cycle strategies of land snails in central and southern Greece. *Abstracts of 14th World Congress of Malacology* (ed. by P.-L. Salvini, J. Volzow, H. Sattmann and G. Steiner), pp. 374. Unitas Malacologica, Vienna.
- Niering, W.A. (1963) Terrestrial ecology of Kapingamarangi Atoll, Caroline Islands. *Ecological Monographs*, **33**, 131–160.
- Nilsson, S.G., Bengtsson, J. & Ås, S. (1988) Habitat diversity or area *per se*? Species richness of woody plants, carabid beetles and land snails on islands. *Journal of Animal Ecology*, **57**, 685–704.
- Parmakelis, A. & Mylonas, M. (2002) Aspects of the reproduction and activity of two sympatric *Mastus* species (Gastropoda: Pulmonata: Buliminidae). *Journal of Molluscan Studies*, **68**, 225–234.
- Perry, G., Rodda, G.H., Fritts, T.H. & Sharp, T.R. (1998) The lizard fauna of Guam's fringing islets: island biogeography, phylogenetic history, and conservation implications. *Global Ecology and Biogeography Letters*, **7**, 353–365.
- Preston, F.W. (1962a) The canonical distribution of commonness and rarity: Part I. *Ecology*, **43**, 185–215.
- Preston, F.W. (1962b) The canonical distribution of commonness and rarity: Part II. *Ecology*, **43**, 410–432.
- Rafe, R.W., Usher, M.B. & Jefferson, R.G. (1985) Birds on reserves: the influence of area and habitat on species richness. *Journal of Applied Ecology*, **22**, 327–335.
- Ricklefs, R.E. & Lovette, I.J. (1999) The roles of island area *per se* and habitat diversity in the species–area relationships of four Lesser Antillean faunal groups. *Ecology*, **68**, 1142–1160.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Rosenzweig, M.L. (2004) Applying species–area relationships to the conservation of species diversity. *Frontiers of biogeography: new directions in the geography of nature* (ed. by M.V. Lomolino and L.R. Heaney), pp. 325–343. Sinauer Associates, Sunderland, MA, USA.
- Sakamoto, Y., Ishiguro, M. & Kitagawa, G. (1986) *Akaike information criterion statistics*. KTK Scientific Publishers, Tokyo.
- Schmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.
- Sillen, B. & Solbreck, C. (1977) Effects of area and habitat diversity on bird species richness in lakes. *Ornis Scandinavica*, **8**, 185–192.
- Simberloff, D.S. (1976) Experimental zoogeography of islands: effects of island size. *Ecology*, **57**, 629–648.
- Sincich, T., Levine, D.M. & Stephan, D. (1999) *Practical statistics by example using Microsoft® Excel*. Prentice Hall, Upper Saddle River, NJ, USA.
- Sokal, R.R. & Rohlf, F.J. (1981) *Biometry*, 2nd edn. WH Freeman, New York.
- Steadman, D.W. & Freifeld, H. (1998) Distribution and relative abundance of landbirds in the Vava'u Group, Kingdom of Tonga. *Condor*, **100**, 609–628.
- Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M. & Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*, **31**, 79–92.
- Tjørve, E. (2002) Habitat size and number in multi-habitat landscape: a model approach based on species–area curves. *Ecography*, **25**, 17–24.
- Tompa, A.S. (1984) Land snails (Stylommatophora). *The mollusca, Vol. 7, Reproduction* (ed. by A.S. Tompa, N.H. Verdonk and J.A.M. van den Biggelaar), pp. 47–140. Academic Press, London.
- Triantis, K.A. (2002) *Biogeography, systematics and ecology of the land snails in the archipelago of Skyros (in Greek)*. MSc Thesis, University of Crete, Iraklion.
- Triantis, K.A., Mylonas, M., Lika, K. & Vardinoyannis, K. (2003) A model for species–area–habitat relationship. *Journal of Biogeography*, **30**, 19–27.

- Watson, G.E. (1964) *Ecology and evolution of passerine birds on the islands of the Aegean Sea*. PhD Thesis, Yale University, New Haven, CT, USA.
- Watson, D.M. (2003) Long-term consequences of habitat fragmentation: highland birds in Oaxaca, Mexico. *Biological Conservation*, **111**, 283–303.
- Whitehead, D.R. & Jones, C.E. (1969) Small islands and the equilibrium theory of insular biogeography. *Evolution*, **23**, 171–179.
- Whittaker, R.J. (1998) *Island biogeography, ecology, evolution, and conservation*. Oxford University Press, Oxford, UK.
- Williams, C.B. (1964) *Patterns in the balance of nature and related problems in quantitative biology*. Academic Press, New York.
- Williamson, M., Gaston, K.J. & Lonsdale, W.M. (2001) The species–area relationship does not have an asymptote. *Journal of Biogeography*, **28**, 827–830.
- Woodroffe, C.D. (1986) Vascular plant species–area relationships on Nui Atoll, Tuvalu, central Pacific: a reassessment of the small island effect. *Australian Journal of Ecology*, **11**, 21–31.
- Wright, D.H. (1983) Species–energy theory, an extension of species–area theory. *Oikos*, **41**, 495–506.
- Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 66–76. University of Chicago Press, Chicago/London.
- Zar, H.J. (1984) *Biostatistical analysis*, 2nd edn. Prentice Hall, Upper Saddle River, NJ, USA.

## BIOSKETCHES

**Kostas Triantis** is a PhD student in the Department of Biology at the University of Crete. He is studying patterns of biogeography in the Aegean Sea and the relationship between environmental heterogeneity and species richness. He is interested in island biogeography and macro-ecology.

**Moisis Mylonas** is Associate Professor in the Department of Biology of the University of Crete. He is mainly interested in evolutionary island ecology and conservation ecology.

**Michael Weiser** is a graduate student in the University of Arizona, Department of Ecology and Evolutionary Biology. He is interested in regional- to continental-scale patterns of diversity, and is a co-founder and data base manager of the SALVIAS network (<http://www.salvias.net>).

**Konstadia Lika** is studying different aspects of mathematical ecology and ecological modelling.

**Katerina Vardinoyannis** is currently the curator of the Invertebrate (excluding arthropods) Department of the Natural History Museum of Crete. She is mainly interested in systematics and biogeography of land snails, and island biogeography.

---

Editor: Robert Whittaker