

## Effects of area, environmental status and environmental variation on species richness per unit area in Mediterranean wetlands

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**Abstract.** We propose a mechanistic model to relate  $\alpha$ - and  $\gamma$ -diversity to area *per se*, moisture status and environmental variation (local and total), and explored the effects these abiotic variables have on species richness per unit area ( $\alpha$ -diversity) for plant communities in a network of wetland habitats located in a Mediterranean mountainous region of central Spain. In this study, environmental status is measured as actual evapotranspiration (as an expression of energy), slope and soil wetness, and environmental variation refers to slope variation and soil wetness variation. Species richness per unit area was related to soil wetness, soil wetness variation, ground slope and ground slope variation. There were also positive correlations among moisture status and environmental variation variables. There is a joint effect of slope and soil wetness variation in explaining species richness per unit area of these wetland habitats, but area effects and energy are relatively unimportant. We conclude that species richness per unit area of wetland vegetation can be explained by moisture status and local environmental variation, and that habitat area may not have an important effect. Area could affect  $\gamma$ -diversity directly through random sampling and/or indirectly through increasing  $\beta$ -diversity, and energy may be important in areas with larger energy ranges. Complete surveys of environmental status, local and total environmental variation, and their associated species assemblages are needed to explain the processes that give rise to the rule that larger areas have larger species richness.

**Keywords:** Diversity pattern; Energy; Montane; Slope; Soil wetness; Species-area relationship.

### Introduction

MacArthur (1972) defined ecology as a search for repeated patterns. One of the most commonly observed patterns in ecology is the positive (non-linear) relationship between the number of species and the area where they are encountered. Arrhenius (1921) quantified this relationship through the equation  $S = cA^z$ , which can be interpreted so that the increase in species richness ( $S$ ) decreases if the area ( $A$ ) increases if  $z < 1$ , which is

usually the case. The species-area relationship is supported by empirical data concerning the local flora of areas (as in the case of Arrhenius), and of islands of 'similar' habitats found in a more continuous matrix of a 'different' habitat type (Schoener 1988).

How to explain this simple relationship has been much debated (e.g. Connor & McCoy 1979; McGuinness 1984; Case & Cody 1987; Schoener 1988; Williamson 1988), and further theoretical and empirical studies have been suggested (e.g. Wu & Vankat 1991; Holt 1992). There are two major groups of effects that explain this relationship: (1) area effects and (2) habitat variation effects. Several reviews have acknowledged their probable joint importance, but fewer studies have considered the two effects simultaneously (e.g. Buckley 1985; Nilsson et al. 1988; Kohn & Walsh 1994; van der Maarel 1997).

The processes underlying the species-area relationship and those linked to these two groups of effects have been summarized in at least four classic hypotheses:

1. The Habitat Diversity Hypothesis (HDH) (Williams 1943, 1964) maintains that the effect of area on species richness is solely through habitat diversity, larger areas being more diverse because they contain more habitat types. In this paper we will refer to this effect as environmental variation.

2. The Random Sampling Hypothesis (RSH) (Connor & McCoy 1979; Coleman 1981) regards an island's biota as a random sample of a larger community, larger islands constituting larger samples and thus containing more species.

3. The Dynamic Equilibrium Hypothesis (DEH), often referred to as the *area per se* hypothesis, was independently formulated by MacArthur & Wilson (1963, 1967) and others (see Brown & Lomolino 1989 and Wilkinson 1993). It considers the number of species on an island as a dynamic equilibrium between immigration and extinction rates; these rates depend upon the degree of isolation and the area of the islands. Both RSH and DEH predict an area effect that is independent of environmental

variation. Actually, RSH is included in a later modification of MacArthur-Wilson's (1967) theory, the 'target effect' (Gotelli 1995).

4. The Species-Energy Hypothesis (SEH) (Wright 1983), an extension of the species-area relationship, claims that larger areas are more diverse because they receive more energy ( $S = kE^z$ , where  $E = rA$  and  $r$  is the available energy per unit area). The basis of this hypothesis is that more energy will translate into more individuals that represent a larger species pool.

As they were formulated, these hypotheses apply to the total number of species in a larger area –  $\gamma$ -diversity. However, a certain level of  $\gamma$ -diversity can be reached through different paths. We propose the model in Fig. 1 to highlight the possible links that affect  $\gamma$ -diversity, though only the effects of area, environmental status and local environmental variation on species richness per unit area ( $\alpha$ -diversity) will be addressed in this study. We considered energy per unit area as part of the environmental status of the community. We did not explore the effects of total environmental variation on  $\beta$ -diversity because we did not have enough samples per wetland to satisfactorily measure it. Neither did we address the issue of  $\gamma$ -diversity because we did not have complete species lists for the wetlands. Clearly, the relationship between local and regional species pool is a further factor in determining species richness (e.g. Cornell 1993; Duncan et al. 1998).

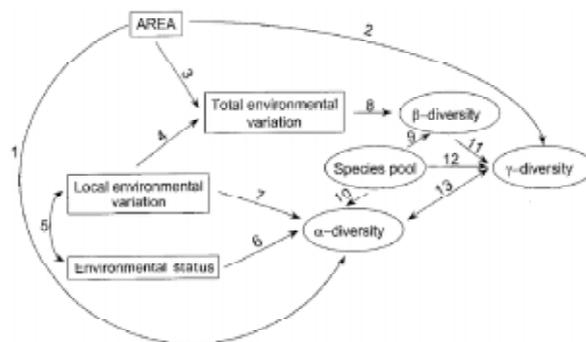
The basic difference between the wetland habitats under study and the surrounding land is a moister environment due to groundwater outcropping. Local soil moisture levels are mirrored in a change of soil features and plant community composition compared to areas outside the influence of groundwater seepage (Rey Benayas et al. 1990; Bernáldez & Rey Benayas 1992).

## Methods

### Survey of the 'habitat island' system

The study area is located at the southern side of the Sierra de Guadarrama mountain range, central Spain. Latitudinal and longitudinal ranges are 40°22' to 41°09' N, and 3°31' and 4°12' W, encompassing an area of 2069 km<sup>2</sup> (Fig. 2). The climate is Mediterranean. Elevation ranges between 560 and 2430 m a.s.l. Between sites, mean annual temperature ranges are 12.4 to 6.3 °C and total annual precipitation ranges from 456 to 1331 mm. The parent material is mostly granite.

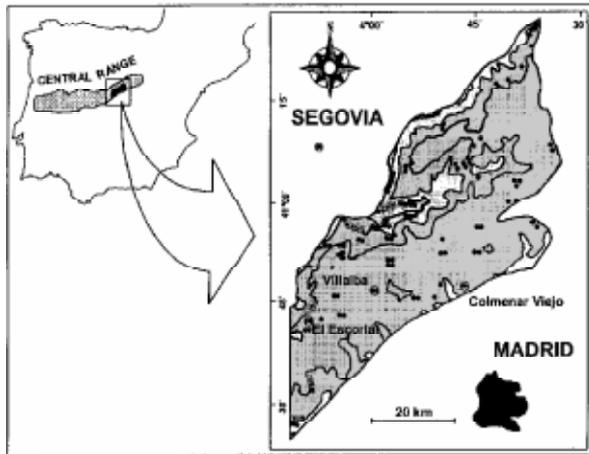
We used panchromatic aerial photographs to map the network of wetland habitats in the study area. The differences between these habitats and non-wetland habitats are most conspicuous in the dry season, when patches



**Fig. 1.** A general model that explains the links between area, environmental status, environmental variation (total and local) and diversity. Total species richness ( $\gamma$ -diversity) is viewed as a function of within patches diversity (species richness per unit area or  $\alpha$ -diversity) among patches diversity ( $\beta$ -diversity) and the species pool (links 11–13) (Whittaker 1972). The direct effect of area on  $\gamma$ -diversity is the random sampling (link 2).  $\alpha$ -diversity can be affected by area (link 1), 'environmental status', meaning moisture status in this case (link 6), local environmental variation (link 7) and the species pool (link 10).  $\beta$ -diversity is related to total environmental variation and the species pool (links 8 and 9, respectively). The model also considers relationships between environmental status and its local variation (link 5) and between area and local environmental variation with total environmental variation (links 3 and 4, respectively).

of green, wet meadow vegetation dominated by *Juncus*, *Carex* and hygrophyte graminoid species are highlighted in a yellow-brown matrix of senescent annual grasses. Thus we selected recent, 1:20 000 scale stereopairs taken in summer to generate an updated, accurate map of the wetlands. The photo-interpretation results were scanned to measure the area of the individual wetlands by means of a Tamaya Digitizing Area-Line Meter. Wetlands were surveyed for perennial vascular plants in the summers of 1993 and 1994. The preliminary results of the survey in the first season helped us to include the whole wetland vegetation spectrum in the region. A total of 92 100-m<sup>2</sup> plots belonging to 66 individual wetlands were sampled, and 237 different species were found. This plot size provided a representative sample of the flora in similar ecosystems (Fernández 1991; Bernáldez & Rey Benayas 1992; Rey Benayas & Scheiner 1993). It also coincided with the area of the smallest wetlands – the size of the wetlands ranged from 100 m<sup>2</sup> to 34 572 m<sup>2</sup>. Species richness per plot ranged from 2 to 44 species (mean species richness  $\pm$  SD = 23.9  $\pm$  6.2 species).

We measured two environmental variables in the field and determined their variation data on a plot basis: soil wetness and slope (microtopography). Soil wetness variation was estimated as the number of different 'hygrotypes' that was encountered in five 20-cm deep



**Fig. 2.** Location of the study area and the 66 surveyed wetland habitats in the Sierra de Guadarrama mountain range.

soil samples that were regularly distributed within the plots. The hygrotypes ranged from 1 (dry soils) to 7, (flooded soils); their number ranged from 1 to 3 per plot (mean  $\pm$  SD =  $1.39 \pm 0.57$ ); across all plots, mean hygrotype  $\pm$  SD =  $4.62 \pm 2.16$ . This and other similar semi-quantitative indices have been proved to be useful estimates of soil wetness (Walbridge 1994; Rey Benayas 1995; Colomer 1999). The plots had a variable topography; some of them had a very uniform slope and others included different slope classes – a slope class being defined by exposition and steepness. Topographic variation was estimated as the number of switches in slope class within the plots in diagonal directions, and ranged from 1 to 3 per plot (mean  $\pm$  SD =  $0.54 \pm 0.8$ ); across all plots, mean slope  $\pm$  SD was =  $6.17^\circ \pm 6.21^\circ$ . Energy was measured as actual evapotranspiration (AET) based upon Monteith's method (1965). AET combines information on temperature, precipitation, radiation, humidity, wind speed and soil water holding capacity. AET across plots was  $431 \pm 25 \text{ mm m}^{-2} \text{ yr}^{-1}$ , and ranged from 389 to 487  $\text{mm m}^{-2} \text{ yr}^{-1}$ .

### Data analysis

Ideally, we should include habitats which vary in the three main variables chosen: (1) area, (2) moisture status and (3) environmental variation. In addition, a fixed unit area allows discrimination between effects of area *per se* and the effects of environmental variation (Kelly et al. 1989). To explore the data we used simple regressions and correlation analyses, multiple regression with standardized partial regression coefficients to understand the relative importance of various independent variables considered simultaneously and path analysis. Number of species per unit area was used as the dependent variable in the regressions and  $\log$ -[wetland area]

and the two measures of environmental variation (number of hygrotypes and number of topographic slope switches) and moisture status (AET, mean hygrotype and slope) were used as independent variables. Since not all wetlands contained the same number of plots, statistical analyses were run on a plot basis ( $n = 92$ ) using SAS (Anon. 1989).

### Results and Discussion

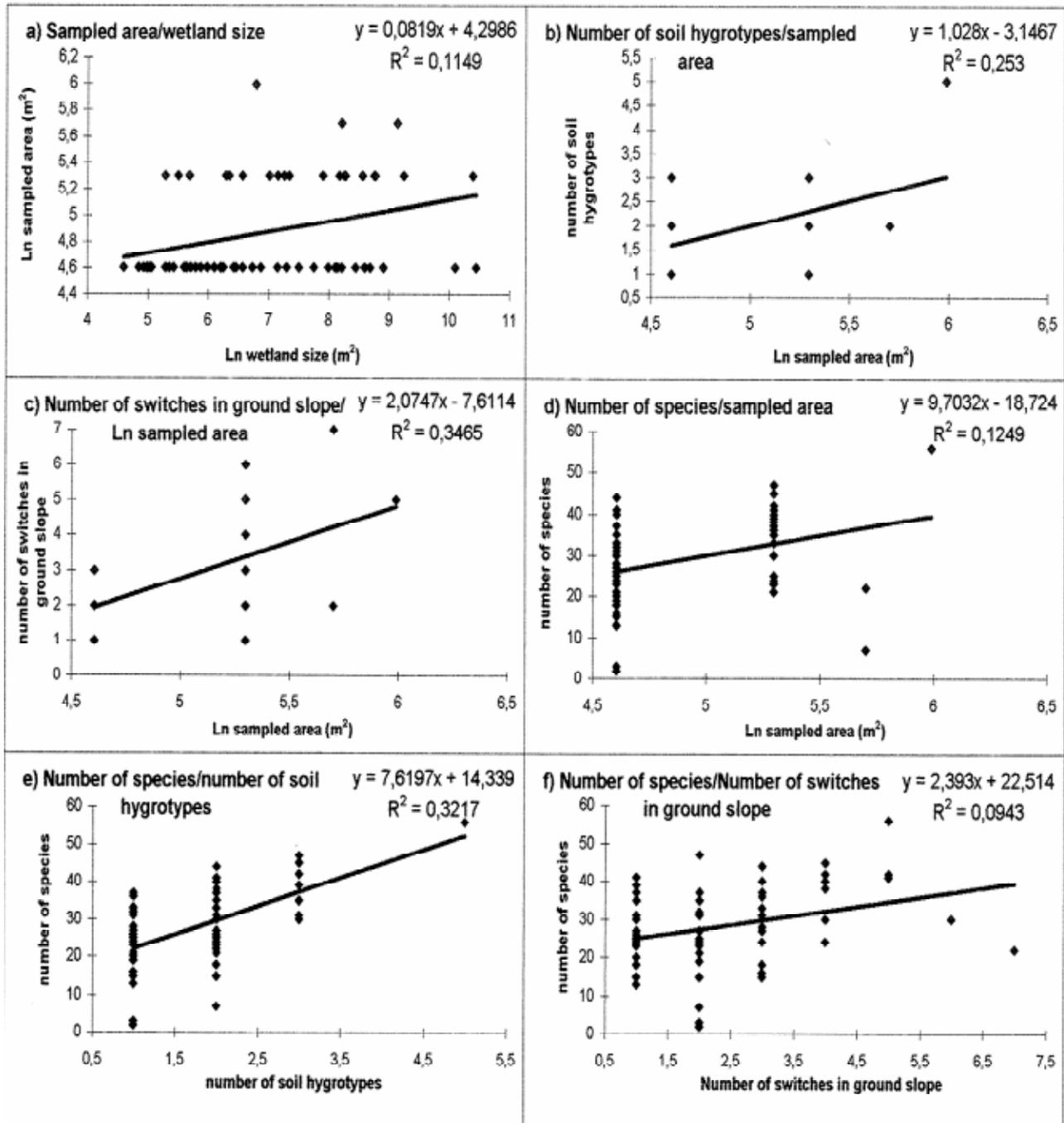
We first explored the pair-wise relationships among species richness per unit area, wetland area, environmental quality and environmental variation. Species richness per unit area was positively related to soil wetness, soil wetness variation, topographic slope and topographic variation (Fig. 3c - f). However, species richness per unit area was not related to wetland area and actual evapotranspiration (Fig. 3a, b). For the same variables, moisture status and environmental variation were correlated (for soil wetness,  $r = 0.25$ ,  $P < 0.02$ ; for slope,  $r_s = 0.43$ ,  $P < 0.0001$ ). Soil wetness and slope were correlated ( $r = 0.31$ ,  $P < 0.003$ ), but their variations were not.

Secondly, we looked at the multiple regression model for species richness per unit area vs. wetland area, moisture status and environmental variation. Only slope (as a measure of moisture status) and number of hygrotypes (a measure of environmental variation) were significant results in this model (Table 1).

This study shows the joint effect of moisture status and environmental variation in explaining species richness per unit area of wetland habitats in the Sierra de Guadarrama and the minor effect of area. First, species richness per unit area was not significantly related to wetland area – the standardized species-area curve (Fig. 3a). The species-area curve may provide evidence for area *per se* effects (Westman 1983; Holt 1992; Kohn & Walsh 1994). Second, the model including wetland area and other environmental variables

**Table 1.** Results of the application of the model based on standardized partial regression coefficients (STB) that simultaneously included the effects of wetland area, moisture status and environmental variation on species richness per unit area. \* = significant at  $P < 0.05$ ; for the model,  $R^2 = 0.23$  and  $P < 0.0009$ . SE = Standard error.

	STB	SE
Wetland area (log)	-0.06	0.59
Actual evapotranspiration	0.04	0.04
Slope	0.26 *	0.17
Slope variation	0.07	1.2
Soil wetness	0.15	0.48
Soil wetness variation	0.21 *	1.65



**Fig. 3.** Relationships of species richness per unit area with **a.** wetland area; **b.** actual evapotranspiration; **c.** slope; **d.** soil wetness; **e.** number of switches in slope; **f.** number of soil hygrotypes ( $n = 92$ ). Relationships in Fig. 3a and b are not significant. Relationships in figures 3c - f are significant at  $P < 0.0001$ ,  $P < 0.01$ ,  $P < 0.03$ , and  $P < 0.007$ , respectively. We evaluated the relationships in Fig. 3d and e using non-parametric correlations ( $r_s = 0.35$  and  $0.23$ , respectively).

provided standardized partial regression coefficients non-significant for wetland area. However, a measure of environmental status (ground slope) and a measure of environmental variation (number of soil hygrotypes) had a significant result, and slope had an indirect effect on species richness per unit area through soil wetness variation. Energy as measured by AET was found not to affect species richness per unit area; we attribute this to the small range of AET values in our study (Rosenzweig 1968, 1995; Wright et al. 1993). Montalvo & Herrera (1993) and Rey Benayas & Scheiner (1993) have documented strong effects of soil salinity and pH on herb species richness in wetland networks located in relatively large and flat detritic basins adjacent to our study area.

Holt (1992) also found for vascular plant species in Kansas that there was no relationship between species number and log sampled quadrat area, while Westman (1983) found that the number of species was independent of island area in standardized samples of xeric shrubs on the California Channel Islands. In a vascular plant study, Kelly et al. (1989) found a non-significant positive partial regression coefficient for island area. They attributed this result to the 'Small Island Habitat' effect: it is possible that habitats exist on small islands that are absent on large ones. This would lead to positive species-area relationships if the habitats of the large areas were more 'favourable' and hence supported more species. Conversely, Kohn & Walsh (1994) found a significant positive correlation between number of vascular plant species per unit area and area for the Shetland Islands. They described significant effects of island area and habitat diversity within multiple models and a total effect of island area on species richness that was twice as great as the direct effect of island area in habitat variation. van der Maarel (1997) mentioned similar cases and confirmed that island area and habitat diversity operate independently.

We conclude that species richness per unit area of wetland vegetation can be explained by moisture status and local environmental variation and that habitat area may not have an important effect. Area could affect  $\gamma$ -diversity directly through the 'random sampling effect' or indirectly through increasing  $\beta$ -diversity in this study (Fig. 1) and energy may be important in areas with larger energy ranges. Complete surveys of environmental status and local and total environmental variation and their associated flora are needed to explain the processes that give rise to the regularity that larger areas have larger species richness.

The effects of the local and regional species pool could not be evaluated in this study but other studies (in particular Zobel 1997; Zobel et al. 1998) have elucidated their importance.

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