

Area and habitat relationships in island land snail faunas: an Aegean case study exploring the choros model

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Abstract – In the present paper we study the biogeography of land snails in the Skyros archipelago (central Aegean) using both conventional species-area analysis and the newly-developed choros model. The choros model is a simple mathematical relationship, which analyses species richness as a function of area and of environmental heterogeneity, quantified by assessing the number of defined habitats present on each island. We surveyed land snails on 12 islands of the archipelago of Skyros in the central Aegean Sea (Greece). The different types of habitats were defined based on the ecology and biology of each species distributed in the archipelago. Forty-two land snail species were recorded living in 11 different habitat types. The z-values from both models, the choros and the classic species-area relationship, place the archipelago in the “within biogeographic province” category, mainly due to the recent formation of the archipelago. This recent formation resulted in a group of small islands still behaving as parts of a continuous landmass. The recorded extinction of land snails in the archipelago follows the general pattern of extinctions of this animal group in the Aegean area. The choros model gave a better fit to the data than the classic species-area model, indicating that the range of habitats available plays a significant role in determining faunal diversity independently of area. The availability of knowledge on the ecology of each species in most islands of the Aegean enabled us to recognise the key environmental features on which we based the definition of the habitat types. Such background knowledge is essential if island studies are to progress beyond the simple demonstration of a species/area relationship.

Key words Aegean Sea, choros model, habitat diversity, land snails, species-area, species richness.

INTRODUCTION

The species-area relationship not only is one of ecology's few laws but it is also one of the longest known. There is more evidence for the generality of this pattern than of any other described in ecology, but scientists are still not sure of its theoretical base and its actual shape (Rosenzweig, 1995; Lomolino and Weiser, 2001). Rosenzweig (1995; 2003) showed that the processes determining species diversity produce logarithmic species-area relationships with z-values (slopes) that vary within a specific range. For sample-area (intraprovincial) species-area relationships z varies between 0.1–0.2, for archipelagic ones it tends to have values of 0.25–0.55 and for the interprovincial species-area relationships it begins at 0.6 and ranges upwards, with most about 0.9 to 1 or even higher (Rosenzweig 1995; 2003). These empirical differences suggest a different balance of causes in

each case, and provide a starting point for more detailed analyses.

The two major mechanisms proposed to account for these species-area relationships are the habitat hypothesis and the area *per se* hypothesis (Connor and McCoy, 1979). Although there have been many attempts to establish the superiority of one hypothesis over the other, it is generally acknowledged that habitat diversity and area *per se* are not mutually exclusive mechanisms but supplementary and may operate individually or in combination (Connor and McCoy, 1979; 2000; Kohn and Walsh, 1994; Rosenzweig, 1995; Ricklefs and Lovette, 1999). Hence, at least four models have been developed combining the effects of area and habitat diversity on species richness (for a review see Triantis *et al.*, 2003). The choros model was introduced to reflect the actual ability of a region to maintain a particular number of species in a certain

higher taxon (Triantis *et al.*, 2003). The choros value (K), is the result of the multiplication of the total area (A) of the region or island by the number of the different habitat types found within it (H); thus $K=H \times A$. Species richness (S) of the region is expressed as a power function of the choros (K), namely $S = cK^Z$, which is analogous to $S = cAZ$ proposed by Arrhenius (1921), by substituting area (A) with choros (K).

In the present paper we study the biogeography of land snails in the Skyros archipelago using both the species-area relationship and the choros model, we evaluate the behaviour of the choros model, and we analyse categorisation of habitats for the land snails in the archipelago.

METHODS

Study area

The Skyros island group lies in the central part of the Aegean Sea (Figure 1). The largest island of the archipelago is Skyros, which lies 19 miles east of Evvoia Island and is the ninth largest island of the Aegean Sea with a total area of 208 km². More than 20 small islets are situated around the island of

Skyros, all inside the isobath of 200 meters. Man has inhabited Skyros since the Neolithic (Patton, 1996) but this island lies away from the main trading routes of the Aegean. For, at least, the last 200 years the total population of the island has never exceeded 4,000 inhabitants.

The geological formations of the island of Skyros itself consist mainly of limestone (66%), schist (22%) and neogene formations (7%) (Melentis, 1973). The substrate of the neighbouring islets is mainly limestone (Melentis, 1973). Only the islet of Exo Diavatis does not consist of a calcareous substrate, but of semimetamorphic clastic formations (mainly gneiss) (personal field observations).

The isolation of the Aegean landmass, including Skyros, occurred 4.5 million years ago, but the formation of the archipelago, by further fragmentation, is supposed to have occurred by early Holocene (Van Andel and Shackleton, 1982; Perissoratis and Conispoliatis, 2003).

The climate of the area is characterized as thermo-mediterranean with a quite long dry period, beginning at the end of April and ending in early October (Andreakos, 1978).

The southeast part of Skyros island is mountainous and rocky covered by degraded

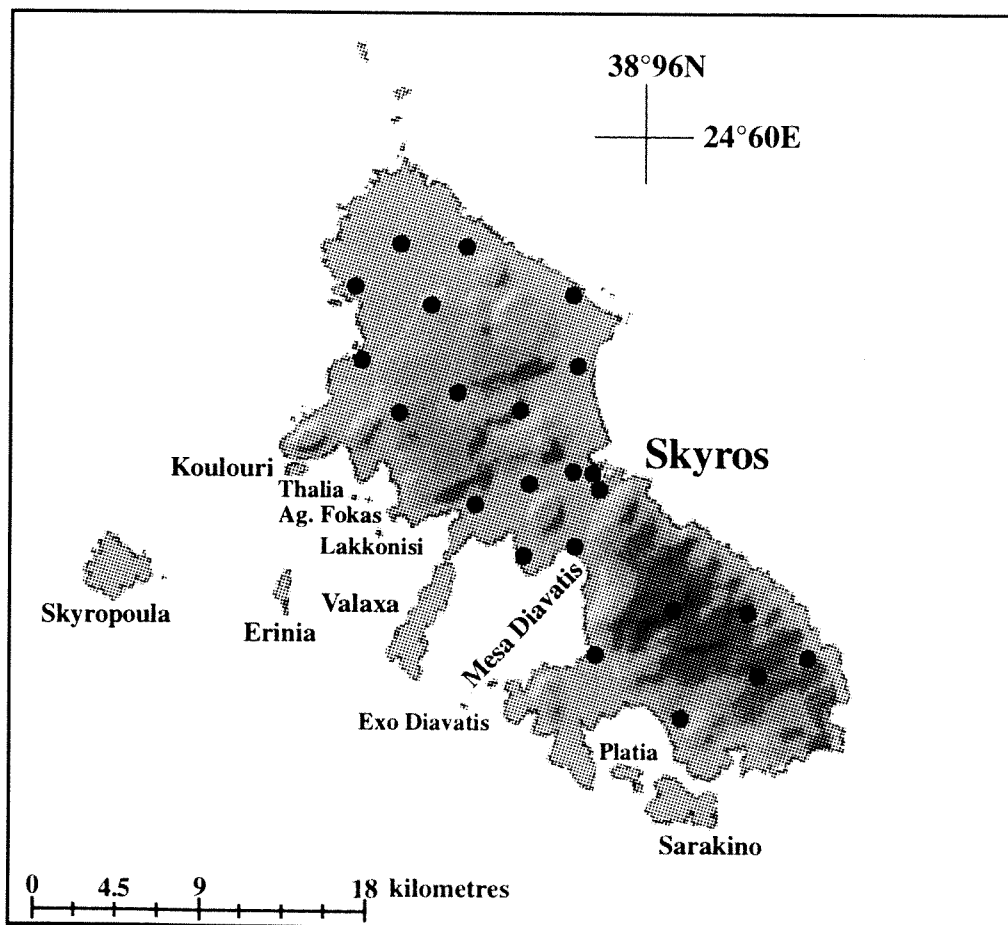


Figure 1 Map of Skyros' archipelago with the islands included in this study and the sites surveyed.

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

Island	Area (km ²)	No of species	No of habitats
1. Skyros (Skr)	208	42	11
2. Valaxa (Val)	4.33	21	7
3. Skyropoula (Sky)	3.83	20	8
4. Sarakino (Sar)	3.34	16	8
5. Platia (Pla)	0.62	15	8
6. Erineia (Eri)	0.53	14	5
7. Koulouri (Kou)	0.29	14	6
8. Mesa Diavatis (MeD)	0.039	10	4
9. Exo Diavatis (ExD)	0.018	4	2
10. Lakkonisi (Lak)	0.016	7	4
11. Agios Fokas (AgF)	0.003	7	4
12. Thalia (Thl)	0.002	6	4

maquis dominated mainly by *Quercus coccifera*, and phrygana. By contrast, forests of *Pinus halepensis*, maquis mainly with *Juniperus phoenicea* and lush vegetation cover the northwest part. Maquis, phrygana and perennials dominate the other islands of the group (Dafis *et al.*, 1996; personal field observations).

We visited the archipelago of Skyros during late June 2001 but mainly in early January and late April 2002. We collected land snail species from 23 different sites all over the island of Skyros and from 11 smaller islands of the archipelago (Figure 1; Table 1). On the smaller islands the land snails were sampled from the whole area of the island. Litter and soil were removed from each site, taken from patches likely to yield small species. All the material collected is deposited in the collections of the Natural History Museum of Crete.

Habitat diversity

Habitat types were defined according to the biology of each species inhabiting the archipelago, based on the proposed definition of Looijen (1995, 1998) and we avoided defining habitat types *a priori*, based for example on the different vegetation types of the islands. Looijen (1995, 1998) proposed that biotope should be defined as "an area (topographic unit) characterized by distinct, more or less uniform biotic and/or abiotic conditions" and (realized) habitat as "the set of environments in which a species lives". Habitat is assigned to the species concept and biotope to the community concept.

For the definition of habitats, apart from our own research and observations on the biology of each land snail species inhabiting the archipelago of Skyros, we also considered a significant amount of data accumulated during the last decades on the natural history of the land snail species distributed in the Aegean Sea (see Mylonas, 1982, 1985; Riedel,

1992; Vardinoyannis, 1994; Mylonas *et al.*, 1995; Botsaris, 1996; Wiktor, 2001; Triantis *et al.*, 2004). For each species, we first recorded the biotope the species was found in, forest, phrygana, maquis, meadows, settlements or buildings (recent and abandoned), sandy and pebbly beaches, cultivations (recent and abandoned), and salt-marshes. Then, we recorded the precise location of each species in the biotope (rocks, stones, pile of stones, litter) (Table 2). For the definition of habitat types we combined the above data with the special characteristics of the biology of each species, and the presence of limestone since the majority of land snails depend on it (Heller, 1982; Mylonas, 1982; Goodfriend, 1986). Our approach to defining and classifying land molluscan habitats attempts to identify the specific requirements of each species, based on our observations of the ecology of each species in the archipelago and also on the available knowledge of its ecology in the Aegean islands overall. In order to have a simple, parsimonious and ecologically realistic approach to habitat types we used the key environmental features recognized by our observations and the available knowledge from the Aegean islands (Table 2). The procedure for the determination of the habitat types in the archipelago starts from specialist species towards the more generalist species. Based on each specialized species a distinct habitat type was recognized, except of course in the cases where two or more specialized species occupy highly overlapping habitats. Then, based on the species that occupy a restricted set of environments, additional key environmental features were considered for the definition of new habitat types. This procedure was repeated till the most generalist species were included, so as to include all the different habitats occupied by the land snails of the region. With the above procedure, some species, specialists, are restricted to a particular habitat type; others are present on some of them and a number of species are present in all the habitat types recognized. The key environmental features used may differ on scale depending on the biological requirements of each species.

According to our approach, the (realized) habitat of a species can be a specific "standing place", independent of the biotope(s) the habitat is found in. Thus, we do not use forest as habitat, since our study revealed that the presence of no land snail species depends on forests. On the contrary, specific components of a biotope, such as stones or litter, which also may occur elsewhere, are crucial for the presence of a species. For example, the presence of *Pyramidula chorismenostoma*, *Rupestrella philippii* and *R. rhodia* is determined entirely by the presence of calcareous rocks, and not by the biotope in which these rocks occur. The same stands for *Idyla bicristata* whose presence depends exclusively on

the existence of stones (calcareous and/or non-calcareous) regardless of the biotope. In other cases, however, a species may occur in a variety of "standing places", but it is always confined to a particular biotope. For example, *Theba pisana* is restricted to sandy beaches, and within this biotope, it can be found almost everywhere, on plants, under stones, etc. In this case, habitat and biotope coincide, not as ecological terms but more or less as topographical areas. Similarly, anthropophilous species, such as *Limax flavus*, are strongly associated with settlements, where it can be found under stones, in the soil, under rotting wood or debris. In this case, settlements are the appropriate habitat category. Maquis and phrygana are considered as one habitat type "shrublands", since certain species such as *Helix cincta*, *Helicella sp.*, and *Oxychilus hydatinus* are strongly associated with both of them. Moreover, in maquis and phrygana the same species were found without any differentiation (Table 2).

Assembling the information for each species (Table 2) distributed in the island group, we defined 11 different habitat types that describe the environmental heterogeneity of the area under study, in respect to land snails.

Statistical Methods

Because both species-area relationship and choros model are power functions, by using the logarithm of the choros equation and the classic species-area equation we obtain linear relations of $\log(S)$ with $\log(K)$ and $\log(A)$, $\log(S) = a + b\log(K)$ (eqn 1) and $\log(S) = c + z\log(A)$ (eqn 2), respectively. We use these conventional logarithmic transformations to estimate the parameters z and c for purposes of comparison, since linear regression is the classic method used (Rosenzweig, 1995). All regressions and the estimations of parameters were carried out with STATISTICA 5 (StatSoft, Inc. Tulsa, U.K). We also performed a Student's test to check for statistical differences between the slopes of the equations (Zar, 1984). The Pearson product-moment correlation coefficient (R^2) was used for the comparison of the two models.

Results

Forty-four species of land snails were found on the surveyed islands; 42 of them are extant, belonging to 33 genera, and two extinct. We did not locate any living individuals of *Pomatias elegans* but only two subfossil shells on Skyros Island. Thus, we consider that *P. elegans* has become extinct from the island group. Though during our three surveys we searched intensively in all the areas from which *Helix figulina* was reported in the past (Liebegott, 1986) and also in all the potential places for the species to occur, no live animal was collected, but only a huge number of empty shells. We believe that this indicates its recent extinction in the island group. We have excluded both species from our analyses. In total we made 21 new records for the island group and one new for Greece (*Lehmannia valentiana*).

In total we defined 11 different habitat types (Table 3). The distinction between the two habitat types "calcareous stones" and "non-calcareous stones" was made since a significant number of species was found under stones in areas of Skyros Island where limestone was absent. The same was not observed for the rocks or the piles of stones, so these two habitat types are strongly related with the presence of limestone. The number of habitat types in each island was positively related with the area, $\log(H) = 0.80 + 0.11\log(A)$ ($R^2 = 0.69$, $P < 0.001$).

Simple linear regression of $\log(S)$ as a function of $\log(K)$ and $\log(A)$ respectively, gives:

$$\text{(eqn 1) } \log(S) = 1.06 + 0.16\log(K) \quad (R^2 = 0.91, P < 0.001)$$

$$\text{(eqn 2) } \log(S) = 1.19 + 0.18\log(A) \quad (R^2 = 0.88, P < 0.001)$$

The R^2 value of the choros model is higher compared to the R^2 of the classic species-area model, indicating the better fit of the choros model. The estimate of the slope for the choros model was lower than for the classic model, but no significant statistical difference was found ($P > 0.05$).

DISCUSSION

Approaching habitat diversity

Scientists have long noted the significant

Table 3 Habitat types used in this study and the islands where each habitat type is present.

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| 1. | Calcareous stones: Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl |
| 2. | Shrublands: Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl, ExD |
| 3. | Noncalcareous stones: Skr, ExD |
| 4. | Piles of stones: Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl |
| 5. | Rocks: Skr, Val, Sky, Sar, Pla, Eri, Kou |
| 6. | Litter: Skr, Val, Sky, Sar, Pla, Eri, Kou, MeD, Lak, AgF, Thl |
| 7. | Cultivations: Skr, Val, Sky, Sar, Pla, Kou |
| 8. | Settlements or buildings: Skr, Val, Sky, Sar, Pla |
| 9. | Sandy beaches: Skr, Sar |
| 10. | Pebbly beaches: Skr, Sky, Pla |
| 11. | Salt marshes: Skr |

contribution of habitat diversity to species richness (MacArthur and Wilson, 1967; Rosenzweig, 1995; Ricklefs and Lovette, 1999; Triantis *et al.*, 2003; Tews *et al.*, 2004). Despite this, the lack of a common language among scientists on what habitat is and on how we can measure it in a comparable way causes much confusion.

Definitions of "habitat" in the ecological literature refer to at least seven different concepts (Looijen, 1995; 1998; Hall *et al.*, 1997; Dennis *et al.*, 2003). Thus, practical guidance to the recognition of an organism's habitat is lacking and consequently, habitats are described with a lack of precision (Rosenzweig, 1995). As Watt (1971) wrote "if we do not develop a strong theoretical core that will bring all parts of ecology back together, we shall all be washed out to sea in an immense tide of unrelated information". The establishment of this common language can be accomplished only by having unambiguous and mutually exclusive definitions of terms.

Even if the definitions proposed by Looijen (1995, 1998) resolve the problematic use of the concepts of habitat and biotope, defining the habitat types for a certain taxonomic group in a region remains a very laborious procedure. The difficulty originates from the fact that the biogeographer and the ecologist have to pass from the level of the simple species list to detailed knowledge of the ecology of every species present in the area under study.

The first effort of defining and classifying land snail habitats in a region is that of Boycott (1934), who studied the land snails of Britain. His approach was based on specific characteristics of the ecology of each species such as food, life history, dispersal and competition, but the habitats he presented were closer to the term "biotope" than to "habitat", as a result of the fuzziness in the use of these terms. He noted, however, that many species occupied a wide range of biotopes, which contained the same microenvironments. He also pointed out that a collation of data from the adjacent regions was needed for the definition and classification of habitats of the land snails in a region.

In our small data-set, it is evident that area and the number of habitats are correlated. The effect of habitat independent of area can be seen most clearly on Exo Diavatis, the only non-calcareous island of the archipelago. Exo Diavatis showed the lowest habitat diversity, and had the smallest fauna, despite having a larger area than three other islands studied. It is worth noting that an *a priori* habitat classification based, for example, on standard plant communities, would not have exposed such a relationship between species richness and habitat diversity.

In some studies (e.g. Ricklefs and Lovette, 1999; Fox and Fox, 2000) a habitat diversity index (HD) has been used taking into account the relative areas

of each habitat present. We have not used this approach, and have simply enumerated the habitat types present on each island. This partially reflects the impossibility of an accurate assessment of the areas involved, but as in some other studies (MacArthur, 1958; Solem *et al.*, 1981), it also reflects the fact that measures other than area (height of foliage, depth of litter, size of rocks) may be equally or even more significant. Moreover, in some of these cases the measure of the area that a habitat type occupies is meaningless.

The choros model and the biogeography of the land snails in the island group

In general, the choros model exhibits similar behaviour to the classic species-area relationship (Triantis *et al.*, 2003). In the case of the archipelago of Skyros, both z-values of choros (0.16) and species-area (0.18) models, place the archipelago in the within biogeographic province category (intraprovincial) as proposed by Rosenzweig (1995). Similar z values are found when we compare the diversities of different sized pieces of a province. They result from the accumulation of habitat heterogeneity within a province as we sample larger and larger fractions of it. The main differentiation between the intraprovincial and the archipelagic category is that in the latter, local extinctions cannot easily be replaced, and the smaller the area of the island, the greater the chance that such extinction will happen, and the z-value will become steeper (Rosenzweig 1995; 2003).

The low z-values for both choros and species-area models for the land snails of the archipelago of Skyros are the anticipated result of the "recent" formation of the archipelago (Van Andel and Shackleton, 1982; Dermitzakis, 1990; Perissoratis and Conispoliatis, 2003). This "recent" formation results in small islands that still behave as parts of a continuous land mass, and consequently, the reduction of area has not yet led to a significant loss of species (Terborgh and Winter, 1980; Karr, 1982), with small islands exhibiting high number of species. Species such as *Helix cincta* are exceptionally present on these small islets whereas usually they are absent (Vardinoyannis and Botsaris, 1990). Characteristic is the case of Mesa Diavatis, which holds both *Helix cincta* and *H. aspersa*. The presence of two *Helix* species in such a small island is reported here for the first time from the Aegean. Short distances between the islets and the long presence of man contribute to this, as the probability of new immigrants reaching the islands is high, despite the low dispersal ability of land snails. Hence, z values remain in the intraprovincial, rather than the inter-island range.

The probable extinction of *Pomatias elegans* and *Helix figulina* is indicative of the general pattern of extinctions of land snails in the Aegean islands,

from Pleistocene to present. In general local extinctions have been reported from islands or even islands groups, but these taxa are still present in other islands within the Aegean (Mylonas, 1982; Botsaris, 1996). According to Mylonas (1982; 1984), in the Aegean there is only one case of the total extinction of a land snail species, that of *Zonites siphnicus*. Subfossils of *Z. siphnicus* are found, in large numbers on the islands of Siphnos, Sikinos and Folegandros in Cyclades and its extinction is situated within historical times (Mylonas, 1982). This resistant character of Aegean malacofaunas seems to be the result of two factors: The effective adaptation of the species to their natural environment, which retained a wide range of refugia that offered successful protection from the Pleistocene climatic fluctuations, and the man-made alterations and the spread of introduced species (Mylonas, 1984).

The work of Rosenzweig (1995, 2003) introduced and demonstrated the macroecological nature of the species-area relationship and especially of the biological meaning of the values of the z parameter. The value of z is not just an indication of the isolation of the island group under study but consists of a macroscopic description of the dominant process or processes establishing biodiversity and the time scale at which that these processes act. The similar behaviour of the choros model slope with the slope of the classic species-area relationship allows us to ascribe and use the slope of the choros model as a macroscopic description of the dominant process or processes establishing biodiversity and the time scale at which that these processes act, as proposed by Rosenzweig (1995; 2003)

The importance of the choros model is not just the better fit of data in most cases compared to the Arrhenius species-area relationship (Triantis *et al.*, 2003), but relies on the fact that for the first time a mathematical model that describes species richness and includes habitat diversity is simple and effective. Our current study demonstrates that, although the relationship between species and area is high, the choros model offers, as in other cases, a further improvement of fit. This means that the variation in species richness is better explained by choros (K) rather than area alone, even though the habitats supporting the most species are available on most of the islands studied. Where this is not the case, choros can be expected to account either for an exceptionally high value of z where the number of habitats is highly correlated with size of island, as in the Scilly Islands, south west of Britain (Holyoak *et al.*, in press), or where there is no, or even a negative correlation, and z of the species/area relationship is not significantly different from zero, as in the Canary Islands (Ibanez, 1994; Cameron, 2004).

CONCLUSIONS

One of the primary difficulties in the assessment of the relative importance of area and habitat diversity in explaining the species-area relationships is the inadequacy of the existing definitions of the term "habitat". We are proposing that a simple, parsimonious and ecologically realistic approach should be applied in order to quantify the way that each species responds to the environmental heterogeneity in a specific area. It is our belief that this method of defining habitat diversity can contribute to answering questions related to biodiversity, even though our identification of habitat types is, as yet, rather crude and unrefined. Our goal is to refine and standardize the categorisation of habitats still further.

Use of the choros model combined with a more ecologically realistic consideration of environmental diversity will contribute towards the answering of basic questions of conservation biology, such as the estimation of the number of species to be expected, and extinction and successful immigration rates resulting from anthropogenic activities (Simberloff and Abele, 1976; Brooks, Pimm and Collar, 1997) and the design of nature reserves (Diamond, 1972; Soulé and Wilcox, 1980; Robinson and Quinn 1992). Habitat requirements and the biological knowledge on the species to be conserved have been acknowledged as necessary for the effective application of island biogeography theory to conservation (Zimmerman and Bierregaard, 1986; Devy *et al.*, 1998, Whittaker, 1998). According to Devy *et al.* (1998) "for the conservation and management of biodiversity, especially in island ecosystems, the effects of area and habitat characteristics in influencing species numbers need to be determined".

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