Preservation of Our World in the Wake of Change, Vol. VI A/B
ISEEQS Pub. Jerusalem, Israel, 1996. Editor: Y. Steinberger

PERIPHERALITY AND REGIONAL RARITY ARE POSITIVELY CORRELATED: QUANTITATIVE EVIDENCE FROM THE UPPER GALILEE FLORA (NORTH ISRAEL)

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INTRODUCTION

Darwin's (1859) statement that "rarity is the precursor of extinction" has been widely confirmed (Fiedler and Ahouse, 1992). In order to maintain biological diversity, conservation efforts are largely focused on rare species. However, species rarity has broad ecological meaning, and can be interpreted in a variety of ways (Harper, 1981; Rabinowitz, 1981; Gaston, 1994). Many species are rare at the periphery of their geographic distribution (Hengeveld and Haeck, 1982; Brown, 1984). Rabinowitz (1981) has referred these cases as *pseudo-rarity* and exclude them from her well-known scheme of classifying rare species. We suggest the term *peripheral rarity*; it corresponds to Schoener's (1987) *diffusive rarity*, i.e., species that are rare in particular locations, but common elsewhere. For the Australian birds, Schoener (1987) concluded that *diffusive rarity* is very common, but later he found that technical misinterpretation invalidates this conclusion (Schoener, 1990). The question, how important is *peripheral rarity*, remains open. In the present paper, based on the flora of Upper Galilee (north Israel), we quantitatively address this question, and, more generally, the relationships between peripherality and regional rarity.

METHODS

The Israeli Rotem database (Shmida and Ritman, 1985; Shmida, 1994) consists of more than 400,000 field observations and 4,000 herbarium sheets on 2,399 plant species. The Upper Galilee, a mountainous region of ca. 700 km^2 at the north of Israel (33°N; 35°E), is the most intensively studied region in Israel, comprising a rich flora of more than 1,100 species. The rare plants of the Upper Galilee have been quantitatively monitored since 1989 by the Israeli Plant Information Center and the Authority of Nature Reserve (Cohen and Shmida, 1992; Shmida, 1994).

We exclude from the analysis 32 species that are endemic to Israel, Lebanon and Jordan and Sinai, since for species with a narrow distribution, any location might be regarded as peripheral. Introduced and cultivated species were also excluded. The remaining 1,065 species were classified into "rare" and "non-rare" categories. Schoener (1987) distinguished between two measures of rarity: *occurrence rarity* is when a species occurs in few localities and *abundance rarity* is when the absolute population size in these localities is small. It is very difficult, and, in some cases, practically impossible, to obtain data on the *abundance rarity* of plants at a regional or even at a local level. Therefore, we use *occurrence rarity* to define the rare species assemblage of the Upper Galilee. Rare species are defined as those recorded from ten or less 1-km^2 square cells within the area, regardless of their abundance within the squares. Peripherality was quantified by an Index of Peripherality (*IP*) (Nathan et al., 1996), which ranges from one (extremely peripheral) to zero (extremely non-peripheral). It was used to measure peripherality within a rectangular frame of 40° x 40°, between 53°N and 13°N and 15°E and 55°E, with the study area (33°N, 35°E) at its center. The method is described in detail in Nathan et al. (1996). Data used to calculate *IP* values were obtained from the regional floras, especially the Conspectus Flora Orientalis (Heller and Heym, 1980-1994).

Arcsine transformation was used to normalize the distribution of the *IP* values. This enables performing a *T*-test for the comparison between *IP* values of rare versus non-rare species. In order to examine the relationships between peripherality and

rarity, the Chi-square test for 2x2 contingency tables was calculated. The level of significance was set at $\alpha = 0.05$ for all tests (two-tailed).

RESULTS

Among 1,065 plant species of the Upper Galilee, 226 (21%) were classified as rare and 839 (79%) as non-rare (Table 1). Rare species are significantly more peripheral than non-rare species ($T = 8.01$; $df = 1063$; $P < 0.0001$). Seventy-five species (7%) are at the most extreme periphery of their distribution ($IP = 1$); 53 of them are rare (23% of all rare species) and only 22 are non-rare (3% of all non-rare species) (Table 1). The tendency these extremely peripheral species to be rare and non-extreme peripheral species ($IP < 1$) to be non-rare is highly significant ($\chi^2 = 118.0$; $P < 0.0001$).

Table 1. Classification of rarity for non-endemic plants of the Upper Galilee with statistics of peripherality index (*IP*): mean, standard deviation (SD), frequencies in relation to some critical values and position of periphery*.

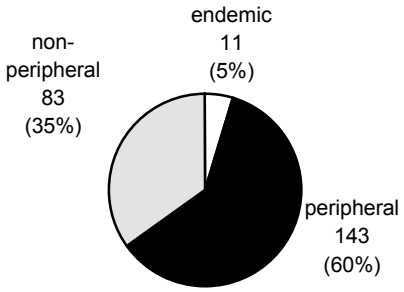
Rarity:	Rare	Non-rare	Total
No. of species	226	839	1065
IP: mean	0.82	0.68	0.71
SD	0.28	0.33	0.32
No. of cases			
$IP = 1.0$	53	22	75
$IP < 1.0$	173	817	990
$IP > 0.9$	143	274	417
$IP \leq 0.9$	83	565	648
Periphery*			
Northern	9	0	9
Eastern	2	8	10
Southern	127	262	389
Western	5	4	9

* Location of periphery in relation to the geographic range of the 417 peripheral ($IP > 0.9$) species.

An *IP* value of 0.9 indicates that the Upper Galilee population is 2° (ca. 180 km) close to the species' extreme periphery. The extreme southern periphery of an $IP = 0.9$ Mediterranean species, for example, is at the northern Negev desert of Israel (31°N). Four hundred and seventeen species (39%) are more peripheral than that level (i.e., $IP > 0.9$); 143 of them are rare (63% of all rare species) and 274 are non-rare (33% of all non-rare species) (Table 1). The tendency of these peripheral species to be rare and of less peripheral species ($IP \leq 0.9$) to be non-rare is also highly significant ($\chi^2 = 70.1$; $P < 0.0001$). Most (93%) of the highly peripheral ($IP > 0.9$) species reach the Upper Galilee at their southern periphery (Table 1). All 9 species that reach it at their northern periphery are rare (Table 1).

Taking a criterion of $IP > 0.9$ to define peripherality, most (63%; Table 1) of 226 rare species are peripheral. If rare endemics are also considered (11 out of the 32 endemic species that occur in Upper Galilee, which were excluded from the analysis), we can divide the 237 rare species of Upper Galilee into three categories: 11 (5%) endemics; 83 (35%) non-peripheral; and 143 (60%) peripheral species (Fig. 1). *Peripheral rarity* is therefore the most common type of rarity in Upper Galilee plants.

Figure 1. Classification of the rare plant species of Upper Galilee into endemic (restricted to Israel, Sinai, Jordan and Lebanon), peripheral ($IP > 0.9$) and non-peripheral ($IP \leq 0.9$) rare species.



DISCUSSION

The relationship between peripherality and regional rarity was found to be positive, highly significant and reciprocal: rare species are more peripheral, and peripheral species are more likely to be rare. A positive correlation between rarity and peripherality is assumed in many studies of abundance and distribution of species (e.g., Brown, 1984), but so far no firm quantitative support was available.

Carter and Prince (1988) argued that while there are many examples of peripheral populations' tendency

to exhibit *occurrence rarity* (i.e., peripheral populations occur less frequently than non-peripheral ones), no examples were found regarding their *abundance rarity* (i.e., peripheral populations are not smaller in size). *Occurrence rarity* was measured in our analysis and our conclusion was similar to that of Carter and Prince (1988). However, while their conclusion is based on several within-species examples (a comparison between peripheral and non-peripheral populations of the same species), our conclusion is based on many between-species comparisons (between peripheral and non-peripheral populations of different species that occur in the same region; see Nathan et al. (1996) for a discussion of these two approaches). Since *abundance rarity* was not measured in our analysis, a between-species comparison is not possible. Using a within-species approach, it seems that, unlike Carter and Prince (1988), most peripheral populations of the Upper Galilee plants are considerably smaller than less-peripheral populations of the same species. For example, all 9 species that reach their northern periphery in (or close to) the Upper Galilee, that were considered rare in terms of *occurrence rarity* (Table 1), are also rare in terms of *abundance rarity*. Four of these species (*Rumex cyprius, Commicarpus plumbagineus, Reichardia tingitana, Tricholaena teneriffae*) are very common and even dominant in southern parts of Israel. Four additional species (*Ephedra aphylla, Kickxia aegyptiaca, Pennisetum ciliare, Saccharum spontaneum*) are locally less common in southern Israel, but occur in higher densities than in the Upper Galilee. Only one species (*Orobanche palaestina*) occurs in low densities all over its distribution.

The importance of peripherality as a key characteristic of most Israeli plants (Zohary, 1973) and animals (Yom-Tov and Tchernov, 1988), due to the unique geographical disposition of Israel, is supported by a quantitative analysis in this study. Many plants of Upper Galilee are at or close to the periphery of their species' distribution, mostly the southern one. A similar conclusion was found for the Israeli breeding birds (Nathan et al., 1996). Thus, Israel offers an excellent opportunity for exploring hypotheses concerning different aspects of peripherality.

Our study shows that *peripheral rarity* is the most common type of rarity in the Upper Galilee plants: 3 of every 5 rare species are peripheral. This finding should lead to a reconsideration of setting priorities in conservation of biodiversity in Israel. It should be clear that conservation of rare plant species in Israel is mainly a conservation of peripheral populations. A peripheral rare species is expected to be more vulnerable than a non-peripheral rare species (Nathan et al., 1996). This may be is because geographically peripheral populations are more likely to occur at ecologically marginal "sink" habitats, being maintained only by immigration from large, self-maintaining population of "source" habitats in the more central part of the species' distribution (Brown and Kodric-Brown, 1977; Pulliam, 1988). This implies that the persistence of a peripheral population is dependent upon its remoteness (defined as a factor combining the effects of geographical isolation and dispersal ability of the species). However, the applicability of this source-sink mechanism to the maintenance of peripheral population is scale-dependent. In local spatial scales (meters to hundreds of meters), sink-source mechanism can be very effective (Shmida and Wilson, 1985). In larger spatial scales, the rate of propagule recruitment may be too low, and a model of extinction-immigration dynamics (MacArthur and Wilson, 1967) more applicable. It is not clear whether the peripheral populations of the Upper Galilee are maintained by a source-sink mechanism or whether they are more likely to become extinct (and possibly re-established) as a result of extinction-immigration dynamics. In both cases, the fate of the most peripheral populations in the Upper Galilee may be subject to the fate of neighboring populations in the Levant north of Israel. The degree of remoteness and the status of these species in Lebanon and Syria must be assessed, in order to evaluate their status and conservation needs.

Although most rare species are peripheral, most conservation efforts are typically given to endemic species, even if they are less rare (Shmida, 1984) and therefore less vulnerable to extinction. There is a low level of endemism in the Israeli flora (Shmida, 1984). Given that most of the rare endemic species are already being managed, the conservation dilemma is whether to preserve peripheral or non-peripheral rare species. If there is no different in attractivity or functional roles within the local ecosystem, etc., it is reasonable to prefer the non-peripheral species which are less vulnerable, thus less difficult to preserve. However, there are different arguments for assigning high conservation priority to peripheral populations (Lesica and Allendorf, 1995; Nathan et al., 1996). Peripheral populations, being ecologically and genetically dissimilar from each other and from more central

ones, constitute a valuable asset as "engines of speciation" and sources of pre-adaptations to support populations in other sections of the species range. In conclusion, peripheral rare species, an important sector of the Upper Galilee flora, are inherently at risk, and their conservation should be assigned high priority.

ACKNOWLEDGMENTS

We thank Batya Levinson, David Heller, and Adi Ben-Nun for technical assistance, Nechama Ben-Eliahu for reading the ms, and many Rotem members who spent many days in the field in searching for rare plants and monitoring them quantitatively.

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