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Diversity of Indonesian gall-forming herbivores along altitudinal gradients

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Abstract. We tested the hypothesis of an inverse relationship between gall-forming species diversity and altitude in the Old World Tropics. We extracted a list of the galling fauna of the Indonesian Islands from previous published work on galls sampled from sea level (0m) to 3400m above sea level.

Diversity of Indonesian galling species was strongly correlated with altitudinal variations. The diversity of gall formers in all taxa combined (insects and mites) increased with decreasing altitude ($r^2=0.76$). Diversity of gall-forming herbivores increased with decreasing altitude for the Cecidomyiidae ($r^2=0.76$), Thysanoptera ($r^2=0.61$), Psyllidae ($r^2=0.61$), Hymenoptera ($r^2=0.54$), Lepidoptera ($r^2=0.54$), Tephritidae ($r^2=0.44$), Aphididae ($r^2=0.31$), Coccoidea ($r^2=0.21$), and Coleoptera ($r^2=0.21$). The diversity of gall-forming mites (Acarina) also increased with decreasing altitude ($r^2=0.78$). Increased diversity of galling species with decreasing altitude may be a global phenomenon. Galls are most abundant at lower altitudes in the Temperate region, the New World Tropics, and the Old World Tropics (this study). Nevertheless, more precise understanding of the pattern of biodiversity in gall-forming herbivores requires studies on the mechanisms that produce them.

Key words. Altitudinal gradients, diversity, herbivory, gall-forming herbivores, Indonesia, insect galls.

INTRODUCTION

Researchers working on the distribution of species have contended that, in general, diversity increases with decreasing latitude (e.g. Dobzhansky, 1950; Kuznezov, 1957; Fischer, 1960; McCoy, 1990; Price, 1991; Rhode, 1992). This pattern has been well documented (e.g. Williams, 1964), although there are exceptions (Eastop, 1972, 1978; Michener, 1979; Janzen, 1981; Dixon et al., 1987). A similar inverse relationship has been shown for diversity along altitudinal gradients (e.g. Holdridge, 1967; Holdridge et al., 1971; Lawton, Mcgarvin & Heads, 1987; Wolda, 1987; Fernandes & Price, 1988).

For North and South American gall-forming insect species, negative correlations between diversity and altitudinal gradients were described by Fernandes & Price (1988, 1991). Galliform insects have been useful in ecological studies due to the sessile habits of the larvae. Galls are often conspicuous, making them easy to count. Furthermore, many evolutionary studies are possible due to their host plant-specificity, diversity and abundance (Fernandes & Price, 1992).

We recompiled data on the gall-forming insects and mites of Indonesia from Docters van Leeuwen-Reijnvaan & Docters van Leeuwen (1926) to test the proposed, inverse relationship between gall-forming species diversity and altitude in the Old World Tropics. Verification of the pattern in Indonesia may be crucial to expand the hypothesis to other biogeographical regions, and to construct a global scenario where the hypothesis can be tested in a mechanistic manner.

MATERIAL AND METHODS

We extracted a list of the galling fauna of the Indonesian Islands from the work of Docters van Leeuwen-Reijnvaan & Docters van Leeuwen (1926). Their work may represent the most comprehensive survey of insect and mite galls in the tropics. They had collected galls over an 18-year period (1908–1926), recording 1536 galling species. The data were exceptionally well-suited for our analysis, because the altitude had been recorded for all galls found. Galls were sampled from sea level (0m) to 3400 m above sea
level. We divided the altitudinal gradient into 100 m intervals. Galls found between intervals were moved to the nearest altitude, e.g. those found at 1020 m were placed in the 1000 m interval, and galls at 870 m were placed in the 900 m interval. Illustrations for most of the galls were provided (see Figs 1 and 2) as well as records of the gall formers and their host plants.

We used a simple linear regression to test whether the proposed pattern existed for the Indonesian islands. The data was transformed into logarithm (S + 1), where S is the number of species. This transformation yielded a significant increase in the amount of variation explained by the model (Snedecor & Cochran, 1980).

RESULTS

Diversity of Indonesian galling species was strongly correlated with altitudinal variations. The diversity of gall formers in all taxa combined (insects and mites) increased with decreasing altitude ($r^2=0.76$, $F_{1,31}=97.698$, $P<0.0001$, $Y=2.6332-0.0007X$, Fig. 3). Diversity of galling species increased with decreasing altitude for the Cecidomyiidae (Diptera) ($r^2=0.76$, $F_{1,31}=120.394$, $P<0.0001$, $Y=2.2348-0.0007X$, Fig. 3), Thysanoptera ($r^2=0.61$, $F_{1,31}=47.426$, $P<0.0001$, $Y=1.4354-0.0004X$, Fig. 4), Psyllidae (Homoptera) ($r^2=0.61$, $F_{1,31}=47.872$, $P<0.0001$, $Y=1.3150-0.0004X$, Fig. 4), Hymenoptera ($r^2=0.54$, $F_{1,31}=36.197$, $P<0.0001$, $Y=0.6373-0.0002X$, Fig. 5), and Lepidoptera ($r^2=0.54$, $F_{1,31}=35.8097$, $P<0.0001$, $Y=0.8994-0.0003X$, Fig. 5). Variations in altitude influenced less than 50% of the richness of galling species in other taxa, including the Tephritidae (Diptera) ($r^2=0.44$, $F_{1,31}=24.072$, $P<0.0001$, $Y=0.4286-0.0001X$), Aphididae (Homoptera) ($r^2=0.31$, $F_{1,31}=13.943$, $P<0.0004$, $Y=2.5498-0.001X$), Coccoidea (Homoptera) ($r^2=0.21$, $F_{1,31}=7.984$, $P<0.004$, $Y=0.776-0.0003X$), and Coleoptera ($r^2=0.21$, $F_{1,31}=7.984$, $P<0.004$, $Y=0.776-0.0003X$). The diversity of gall-forming mites (Acarina) also increased with decreasing altitude ($r^2=0.78$, $F_{1,31}=111.018$, $P<0.0001$, $Y=2.9768-0.0007X$, Fig. 6).

Fig. 1. Semi-spheroid galls caused by an undescribed species of Cecidomyiidae (Diptera) on the stems and buds of Clerodendron inerme Gaertn. (Verbenaceae) from several localities in Java, Krakatau, and Salajar Island (3x enlarged).

Fig. 2. Spheroid galls caused by an undescribed species of Cecidomyiidae (Diptera) on the stems and leaves of Elatostema sessile Forst. (Urticaceae) from Mount Salak, Java (3x enlarged).
Fig. 3. Diversity of gall-forming species along altitudinal gradients of the Indonesian Islands in all taxa combined (insects and mites), and Cecidomyiidae (Diptera).

DISCUSSION

Increased diversity of galling species with decreasing altitude may be a global phenomenon. Galls are most abundant at lower altitudes in the Temperate region (North America), the New World Tropics (Brazil) (Fernandes & Price 1988, 1991), and the Old World Tropics (Indonesia) (this study). Fernandes & Price (1991) argued that the negative correlation between diversity of galling species and altitude is due to harsher environmental conditions at lower altitudes. Gall formation enables the organisms to achieve greater success than free living herbivores in more stressful, harsher environments (see Fernandes, 1990).

The data collected at the beginning of this century by Docters van Leeuwen-Reijnvaan & Docters van Leeuwen (1926) was re-analysed here, allowing us,
for the first time, to check whether the pattern (see Fernandes & Price 1988, 1991) would hold true if the category 'all taxa' is broken down into various components of galling taxa. Most of the variation in gall diversity in the most abundant and diverse galling taxa (e.g. gall midges, mites, thrips, psyllids, wasps, and lepidopterans) (see Mani, 1964; Gagné, 1989) was accounted for by altitudinal variations. Correlations between altitude and gall diversity for other galling taxa can be associated with many variables, including specific adaptations and habitat specialization. The patterns are only now starting to emerge (see Fernandes, 1992); hence more detailed studies are necessary.

Fig. 4. Diversity of gall-forming species along altitudinal gradients of the Indonesian Islands of Thysanoptera and Psyllidae (Homoptera).
Fig. 5. Diversity of gall-forming species along altitudinal gradients of the Indonesian Islands of Hymenoptera and Lepidoptera.

The trends seen appear strong (see Figs 3–6), and, coupled with the works of Fernandes & Price (1988, 1991, 1992), indicate a global pattern. The complete understanding of this pattern of diversity in galling species requires knowledge of the mechanisms that produce them. We can now proceed to experimental studies of the diversity of galling herbivores, where the mechanisms that influence the patterns can be described and tested in the field.

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Fig. 6. Diversity of gall-forming species along altitudinal gradients of the Indonesian Islands of the Acarina.

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