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Diversity and altitudinal niche width characteristics for 35 taxa of the Papua New Guinea *Frullania* flora with consideration of sibling pairs

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Abstract. The *Frullania* taxa on Mount Albert Edward, Papua New Guinea, form many associations that suggest a high degree of niche similarity, but at different altitudes, different associations form. The species diversity of the genus is greatest at the middle altitudes and least in the dry lowlands. This altitudinal separation is apparent in the niche widths of the taxa. The members of the four sibling taxa pairs examined exhibit distinct altitudinal niches, suggesting that the sibling taxa are distinct, with different niche optima.

Introduction

Niche theory suggests that when a large number of closely related taxa occur in a small geographic area we should expect to find accompanying niche separations. Inoue's collections of *Frullania* on Mount Albert Edward, Papua New Guinea, revealed 57 *Frullania* taxa, including ten infraspecific taxa pairs (Hattori 1988). These data provide an opportunity to test niche separation in this very common tropical genus.

Hattori and Piippo (1986) have shown that altitudinal distribution differs among taxa of *Frullania*, and Li et al. (1989) have suggested that altitude might be important in separating *Frullania* taxa on ordination axes. Thus, we have indications that for *Frullania*, altitude is an important niche

parameter that can be used as an ecological descriptor.

Diversity is related to niche width, and as fewer niches become available, the diversity diminishes. As the tropical conditions that favor *Frullania* disappear in dry lowlands or cool, exposed alpine areas, we would predict that the diversity would diminish. If this is true, we might expect to find the relationship of altitude to diversity to be influenced by the altitude niche width of individual taxa. The collections of H. Inoue on Mt. Albert Edward permit us to examine these relationships.

Collecting Area

All specimens were collected on Mt. Albert

Edward, Papua New Guinea, by H. Inoue and identified by S. Hattori (Hattori 1988). The collecting areas extend from 40 m to 3700 m altitude (no collections at 500-1000 m). Most of the area above 2900-3000 m is alpine. Below that altitude most, perhaps all, the *Frullania* grow on trees, whereas in the alpine areas taxa may be found on rocks and shrubs.

Data Analysis

Taxa diversity, taxa richness (species and infraspecific taxa), and niche width and overlap were calculated using the program COMMANAL, written by the senior author and available through the International Association of Bryology Software Library. Statistical analyses (Student t test, 95% confidence intervals, Mann-Whitney U test) were done with the microcomputer version of MINITAB.

All 57 taxa were used for the diversity, redundancy, and richness analyses. For the remaining analyses, we used only the 35 taxa with a frequency of 2% or greater.

Total taxa diversity and diversity by altitudinal zone were computed by both the Shannon-Weaver diversity (Shannon & Weaver 1949) and the Stirling approximation of the Brillouin information theory-based diversity (Patten 1962; see Glime et al. 1981), using only presence values. These diversities were nearly identical and only the information theory-based results are presented here. Because the values are presence values, there is little meaning to any statistical comparison of diversity by sample among altitudinal zones. However total diversity based on the summation of these samples in each zone is informative.

Species associations were computed using Sorensen's K (1948) and the program COMMANAL.

$$K = 2C/(A + B)$$

where C = the number of co-occurrences of two species

A = the number of occurrences of species A

B = the number of occurrences of species B

Niche width and overlap were computed by both the Levins formula (Levins 1968) and the Freeman-Tukey formula (Smith 1982). Unlike the Freeman-Tukey formula, the Levins formula does not account for the rarity of the resource itself. This causes the Levins values to be smaller, and these predict the likelihood of encountering a taxon in a given area. The Freeman-Tukey value is related to the likelihood of encountering the taxon in a niche with any given resource state.

In this study, we partitioned the altitude resource into 10 resource states (with only 7 represented) with 500 m intervals. We used presence values, since cover values were not available. Glime et al. (1987), using bryophyte communities along mountain streams, showed that when there are sufficient samples, niche width values using presence are comparable to those of cover. The *Frullania* study was comprised of 648 samples, and this number far exceeds those in the 1987 study.

Results

Taxa diversity

Inoue found 57 taxa (Hattori 1988). Taxa diversity (all 57 taxa), redundancy, and taxa richness are presented in Figure 1. As would be expected (Glime et al. 1981), the Brillouin diversities were all lower than the Shannon diversities, but were nearly identical. The alpine zone (3000 m and above) has the least diversity, greatest redundancy, and smallest number of species. Likewise, few taxa are represented at low altitudes, with only two being collected below 500 m. Redundancy is considerably higher (redundancy = 1) in

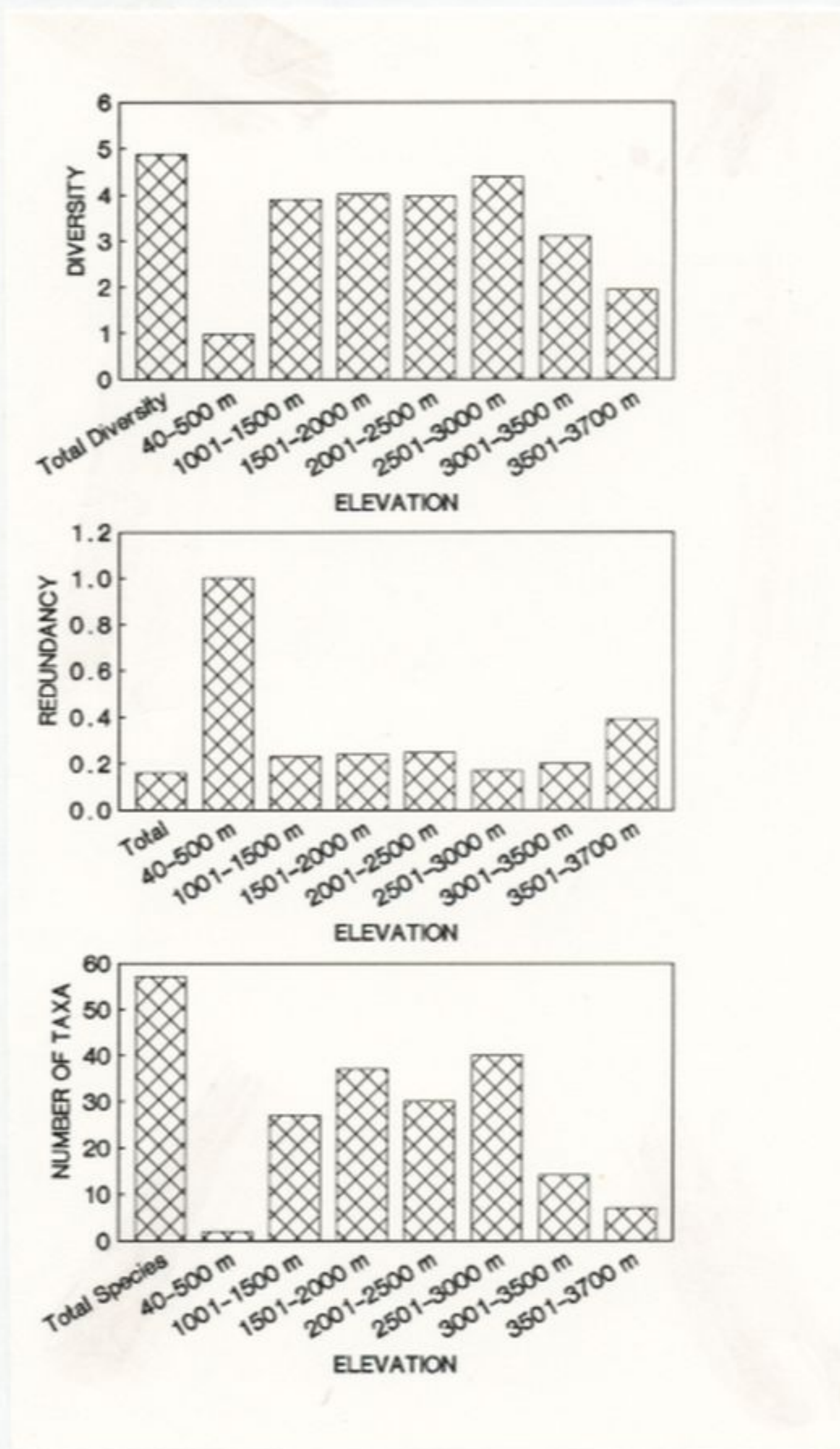


Figure 1. Taxa diversity, redundancy, and number of taxa of *Frullania* (Mt. Albert Edward, Papua New Guinea) in each resource state using altitude as a niche resource. The altitude resource is partitioned into eight states with 500-meter intervals (state 2 has no collection data).

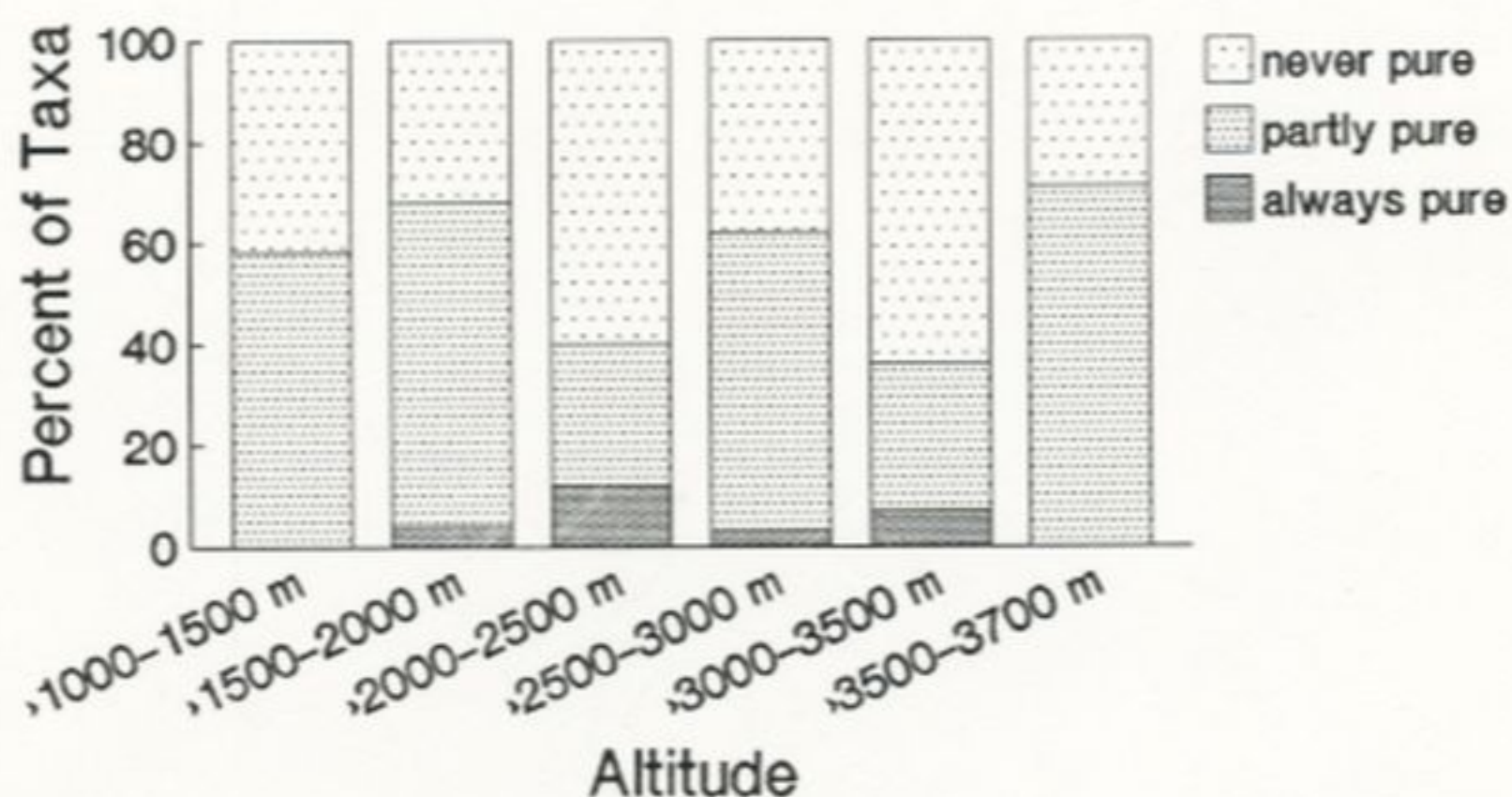


Figure 2. Percentage of taxa (based on 35 taxa with at least 2% frequency) associated with other taxa at each 500-m altitude interval.

of the taxa ever occur all the time in pure collections with no associated taxa at any altitude, and only four (*F. armatifolia*, *F. armitiana* var. *inflexula*, *F. falsisinuata*, and *F. papillata*) occur associated with other taxa in every collection at all altitudes. Instead, most of the taxa occur both as mixed and pure collections, i.e. partly pure.

Table 1 lists the Sorensen's K (1948) value ($\times 100$) of association for the 35 taxa with a frequency of at least 2%. The largest association values are between *F. serrata* var. *hamatispina* and *F. curvistipula* var. *latistipula* (52); *F. serrata* subsp. *spinistipula* and *F. attenuata* (40); *F. serrata* var. *hamatispina* and *F. grolleana* (33); *F. ornithocephala* var. *intermedia* and *F. junghuhniana* var. *tenella* (31); *F. papuana* and *F. junghuhniana* var. *tenella* (30). All other associations have a K value of less than 30.

At each altitudinal level, however, association values may be higher (tables not shown). At 1000-1500 m, *F. grandilobula* shares a K value of 50 with both *F. armitiana* var. *inflexula* and *F. attenuata*. At 1501-2000 m, none of the 28 taxa has a K value greater than 50 with any other taxon. At 2001-2500 m, many associations have K values above 50: *F. armatifolia* and

F. falsisinuata (86), *F. ornithocephala* (50), *F. subdentata* (86); *F. attenuata* with *F. grolleana* (54), *F. macgregorii* (61), *F. schusteriana* (67), and *F. serrata* subsp. *spinistipula* (55); *F. falsisinuata* and *F. subdentata* (100, 3 collections); *F. grolleana* and *F. macgregorii* (57), *F. ornithocephala* var. *intermedia* (50), *F. serrata* subsp. *spinistipula* (50); *F. macgregorii* and *F. schusteriana* (55), *F. serrata* subsp. *spinistipula* (58); *F. serrata* subsp. *spinistipula* and *F. ornithocephala* var. *intermedia* (52), *F. schusteriana* (64). At 2501-3000 m, only the association of *F. curvistipula* var. *latistipula* and *F. serrata* var. *hamatispina* has a K value greater than 50 (59). At 3001-3500 m, only two associations have a K value greater than 50: *F. falsisinuata* and *F. errans* var. *angulistipula* (60), *F. junghuhniana* var. *tenella* (64). In the region above 3500 m, *F. junghuhniana* var. *tenella* and *F. ornithocephala* var. *intermedia* have a K value of 57. *Frullania papuana* and *F. ornithocephala* dominate the collections in this alpine region and have a K value of 46.

Niche width

Niche widths and associated mean altitudes for the 35 taxa with a frequency of 2% or greater are presented in Figure 3. Frequencies of the

spinistipula and *F. ornithocephala* var. *intermedia* (52), *F. schusteriana* (64). At 2501-3000 m, only the association of *F. curvistipula* var. *latistipula* and *F. serrata* var. *hamatispina* has a K value greater than 50 (59). At 3001-3500 m, only two associations have a K value greater than 50: *F. falsisinuata* and *F. errans* var. *angulistipula* (60), *F. junghuhniana* var. *tenella* (64). In the region above 3500 m, *F. junghuhniana* var. *tenella* and *F. ornithocephala* var. *intermedia* have a K value of 57. *Frullania papuana* and *F. ornithocephala* dominate the collections in this alpine region and have a K value of 46.

Niche width

Niche widths and associated mean altitudes for the 35 taxa with a frequency of 2% or greater are presented in Figure 3. Frequencies of the 35 taxa in each altitudinal resource state are presented in Figure 4.

The broadest niches are those of *F. apiculata*, *F. appendistipula* var. *spinifera*, *F. armatifolia*, *F. attenuata*, *F. errans* var. *angulistipula*, *F. gracilis*, *F. ornithocephala*, and *F. ornithocephala* var. *intermedia*.

As predicted, the Freeman-Tukey niche width values are all larger (mean 0.80 \pm 0.04) than those of the Levins formula (mean 0.35 \pm 0.04).

Mean altitudes for the taxa ranged from 1622 m to 3147 m, with only two taxa (*F. papuana* and *F. armitiana*) having a mean altitude above 3000 m. Even so, *F. papuana* was collected once below 1500 m.

Niche overlap

Freeman-Tukey niche overlap values for the 35 taxa with a frequency of 2% or greater are presented in Figure 5. The

mean F-T overlap was 0.65 \pm 0.02 for 595 pairs of taxa; the mean Levins overlap was 0.52 \pm 0.026. Many altitudinal distributions (28%) for the taxa pairs were significantly different ($=$ 0.01, non-parametric Mann-Whitney U test). Using only three states (40-1500 m, 1501-3000 m, and $>$ 3000) instead of 500-m intervals resulted in broader overlaps; the three-state results are not presented here.

Sibling taxa

Niche width and altitudinal range for the four pairs of sibling taxa with a frequency of 2% or greater and frequency values in each of the resource states for altitude for each of these taxa are presented in Figure 6.

In Figure 6, one can easily see that the ranges of the infraspecific taxa differ substantially between siblings. *Frullania armitiana* (mean altitude = 3101 m, F-T width = 0.70) is significantly separated ($=$ 0.05, Mann-Whitney U test) from its variety *F. armitiana* var. *inflexula* (mean altitude = 2600 m, F-T width = 0.80), with an F-T overlap of 0.61. *F. curvistipula* (mean altitude = 2120 m, F-T width = 0.93) is significantly separated from *F. curvistipula* var. *latistipula* (mean altitude = 2717 m, F-T width = 0.67), with an F-T overlap of 0.67. *F. ornithocephala* (mean altitude = 2331 m, F-T width = 0.99) is significantly separated from its variety, *F. ornithocephala* var. *intermedia* (mean altitude = 2730 m, F-T width = 0.95), with an F-T overlap of 0.92. *F. serrata* subsp. *spinistipula* (mean altitude = 1845 m, F-T width = 0.79) is significantly separated from *F. serrata* var. *hamatispina* (mean altitude = 2474 m, F-T width = 0.76) with an F-T overlap of 0.66.

Discussion

Associations

The middle altitudes support more taxa and higher diversity than either the lowland



Figure 3. Levins and Freeman-Tukey niche width values for 35 *Frullania* taxa (Mt. Albert Edward, Papua New Guinea) for the resource altitude. Dendrogram groups refer to those of Li *et al.* (1989) and generally correspond to low (group 2) and high (group 1) altitude groups. *Indicates taxon that belongs to the opposite group from the one where it appears in this figure. Altitude indicates mean altitude of occurrence with 95% confidence interval indicated by brackets. Mean Levins niche width = 0.35 ± 0.041 . Mean Freeman-Tukey niche width = 0.80 ± 0.038 . (Number samples = 648; range of altitude = 40 to 3700 m; altitude is divided into 10 states [with 3 having no collections] with 500 m intervals; only taxa with frequency of 2% or more are included.)

or alpine region (Fig. 1). Likewise, only at the middle altitudes are there taxa that always occur in pure collections (Fig. 2). On the other hand, at 2000-2500 m, we find the highest number of associations with a K value greater than 50, suggesting that at this altitudinal range some benefit might be derived from an association. This K value implies that the taxa are not only associated with other taxa, but that there is a high degree of fidelity in the association.

Several advantages can be gained by an association formed among epiphytic liverworts.

1. Small liverworts can live among larger ones and be protected from high light intensity in the forest canopy or in exposed alpine areas.
2. Associated liverworts can protect each other from drying out by reducing the amount of free space among the branches and leaves.
3. Liverworts that have a poor ability to move water from the substrate or surface of the clump to their own branches can take advantage of the water moved by an associated species.

Although few authors describe such commensal relationships in plants, Rydin (1985) has suggested that they exist among *Sphagnum* species with differential abilities to absorb water in one circumstance and to retain it in another. His conclusions are further supported by the studies of Li (unpublished data) on two additional species of *Sphagnum*.

One must, however, exercise caution in interpreting such circumstantial evidence, for it might merely be ephemeral coexistence manifest at this single point in time. The evidence to refute this statement, however, is the preponderance of taxa that never occur in pure collections (Fig. 2). We must interpret this to mean that the associated taxa are always struggling in a

habitat where no suitable free space exists or that there is in fact some benefit in coexistence.

Niche trends

The distribution of niche widths appears to be related to diversity and sample purity. Taxa at the low and high ends of the altitudinal range tend to have narrower niches than those taxa in the middle. Certainly part of this narrowness results from fewer collections in the low and high altitudes. On the other hand, the smaller number of collections is in turn a result of the reduced availability of *Frullania* to be collected at these altitudes.

The Levins niche widths and Freeman-Tukey niche widths are considerably different, indicating that the niche states (i.e. altitudes) were not equally available among the collections. Because it is sensitive to the availability of the niche, the Levins width tells us how common the taxa might be, compared with other taxa, if we examined the area without regard to altitude. The Freeman-Tukey width, on the other hand, tells us the potential for each taxon if its niche (resource state) were equally available to that of all other resource states. For example, the smallest niche width is that of *F. papillata* (F-T = 0.57), with 95% of its observations expected between 2368 and 2575 m. In fact, we find that it occurs in only two altitude ranges, between 2500 and 3500 m.

We can conclude that most of these *Frullania* taxa could occupy niches in most of the altitudinal ranges, but because of other factors, they are most successful in a relatively narrow range. Several observations support this statement.

When one examines the mean altitudes and 95% confidence intervals for each taxon of *Frullania* (Fig. 3), it is clear that many taxa have rather narrow altitudinal

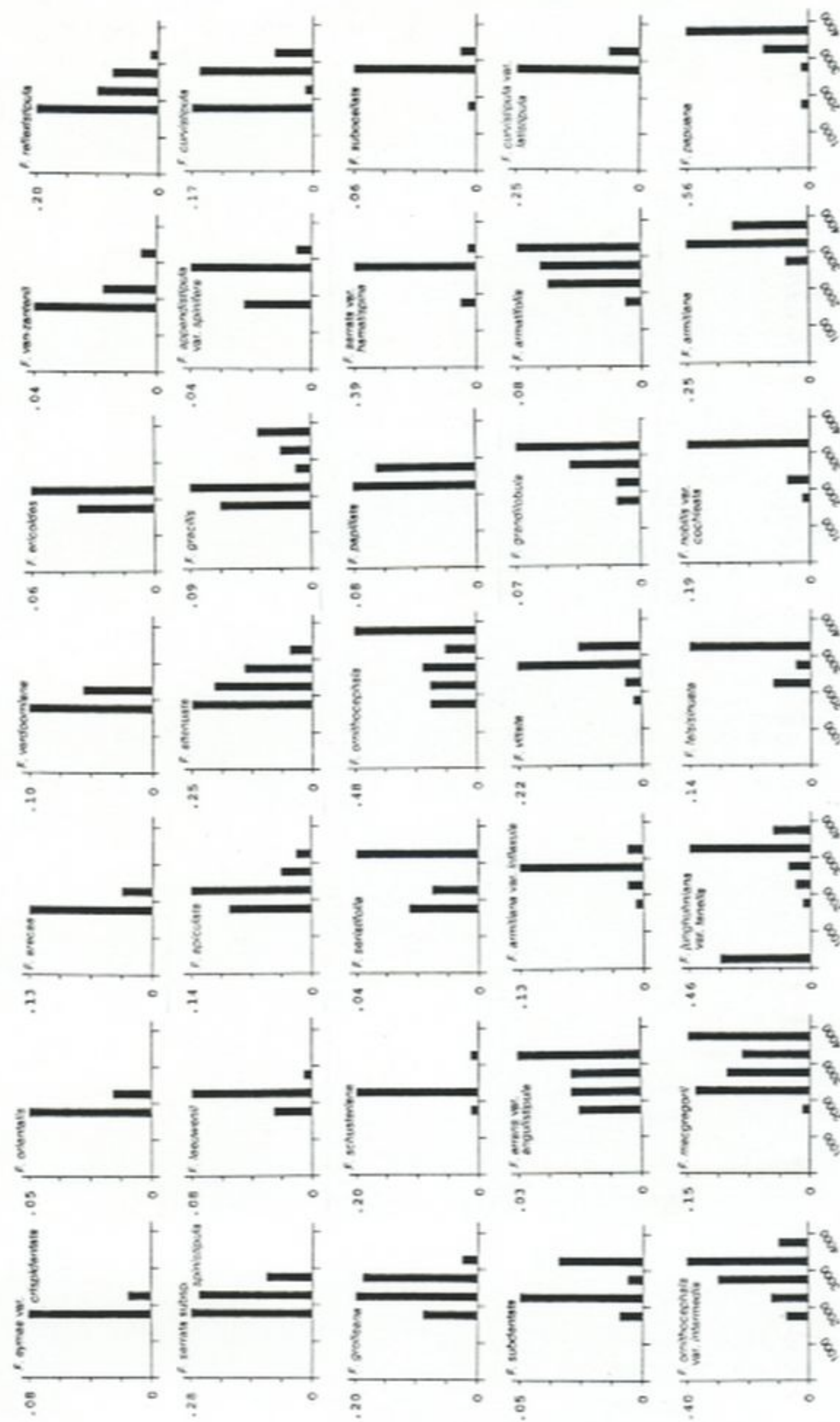


Figure 4. Frequencies of the 35 taxa with frequencies of 2% or more in eight resource states with 500 m intervals, arranged from lowest to highest altitude as shown in Figure 3. (Resource state 2 has no collections.)

preferences, as shown by their narrow 95% confidence ranges (Fig. 3). Such taxa include *F. apiculata*, *F. attenuata*, *F. gracilis*, *F. ornithocephala*, and *F. ornithocephala*.var. *intermedia*.

Among the 35 *Frullania* taxa, 28% of the taxa pairs (Fig. 5) have members that have significantly different altitudes of collection ($\alpha = 0.01$, Mann-Whitney U test), suggesting that the overlap difference is significant. These include taxa that occur in a wide range of altitudes (Fig. 4) and have broad niche widths.

By contrast, *F. errans*.var. *angulistipula* has the widest 95% confidence range about its mean altitude, and a wide niche width (0.96), with no significantly different altitudinal values when compared with any other species at $\alpha = 0.01$.

Li et al. (1989) suggested that these taxa separate into two major groups (dendrogram based on TWINSpan analysis of these data) corresponding to lower and higher altitudes. Likewise, the Li PCA axis three separates the high altitude taxa at one end and the low altitude taxa at the other end. In Figure 3, we have listed the taxa of the dendrogram groups, showing that when the taxa are ordered by their mean altitudes their arrangement corresponds closely with the dendrogram separation. It is noteworthy that those taxa that were not faithful to the appropriate altitudinal branch are those taxa preferring middle altitudes, and we have labelled these the Transition Group. The far ends of Groups 1 and 2 are taxa with relatively narrow niche widths.

Sibling taxa

Landolt (1977) stressed the importance of closely related taxa for the delimitation of phytosociological units. He showed that the sub-classifications of a species can be of particular importance for separating plant associations that contain few species.

Horton (1988) used niche width measurements for soil pH, calcium, and magnesium to support her separation of several questionable taxa of *Encalypta*. Shaw (1981) showed that the morphological variation of two species of *Pohlia* correlated with niche variation, and he concluded that combining taxa based on overlapping form alone can result in the loss of ecological information (Shaw 1985). Landolt (1977) concluded that in places where crucial ecological factors undergo a sudden change, even closely related taxa, not isolated genetically, mutually exclude one another to a large degree. Closely related taxa can thus be considered as very good character- or differential species for describing associations. The present study contains several species that have more than one variety or subspecies present, and provides an interesting comparison of niches for these controversial taxa.

To use niche width as either a taxonomic separator or as an association separator, the data must meet several important criteria:

1. The infraspecific taxa must be consistently identifiable by the person naming the taxa.
2. The niche parameter must have a sufficiently wide range among the samples to provide for a niche separation.
3. There must be sufficient samples throughout that wide range to permit adequate comparison.
4. The parameter for delimiting the niche must differ significantly between the taxa being compared.

Landolt (1977) listed three problems in using infraspecific taxa in phytosociological studies:

1. Few polymorphous species groups have been sufficiently investigated biosystematically to assure conclusive evidence on the value of the taxa involved,

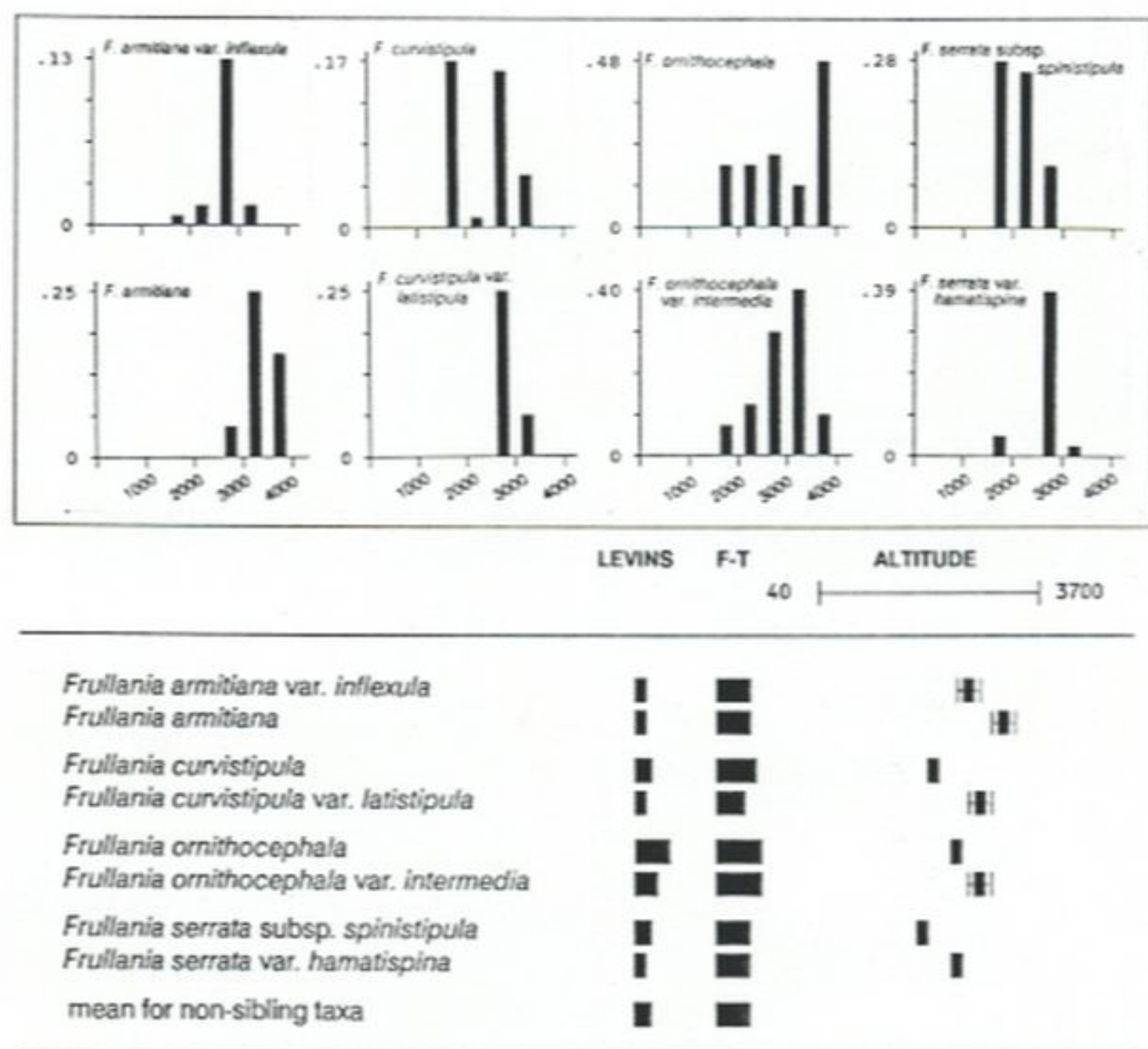


Figure 6. Relationships of four pairs of sibling taxa. Top: Frequencies of taxa in eight altitudinal resource states with 500 m intervals. (No collections were made at 500 - 1000 m.) Bottom: Niche width, mean altitudes, and 95% confidence intervals, illustrating the difference in niches of the two members of sibling pairs.

so that we do not know if the described types are really genetically fixed.

2. It is almost impossible for a phytosociologist to identify these taxa.

3. Taxa occurring within a given group often have a very limited distribution and thus are not identical to similar taxa in other areas.

These problems are essentially eliminated in the present study. Hattori has made a lifelong study of the genus and has identified all the specimens included in the study. Even if they are not true genetic taxa, the naming of the morphotype (whether it be genetic or ecological) provides evidence that can describe an association. All taxa were collected and identified in the laboratory where it was possible to compare specimens and be consistent in naming. The geographic area of concern in this study is a single mountain, so any distributional limitation is irrelevant.

Some interesting differences in altitudinal distribution are present among the sibling taxa of *Frullania* (Fig. 6). The altitudes of collection of the members of all the sibling pairs are significantly different from each other, in spite of rather broad niches, yet only 28% of the 35 taxa analyzed have significantly different altitudes of collection. The very broad niche widths of *F. ornithocephala* and its variety *F. ornithocephala* var. *intermedia* illustrate that even closely related taxa with very wide niches can have different optimal niches. This is best shown in Figure 6, where it is clear that *F. ornithocephala* is dominant in the alpine regions, whereas *F. ornithocephala* var. *intermedia* is dominant below. Likewise, *F. armitiana* is dominant at higher altitudes, whereas *F. armitiana* var. *inflexula* becomes dominant just below, where *F. armitiana* begins to drop out. A similar shift occurs in the infraspecific taxa of *F. serrata*. Such shifts in abundance suggest that other niche parameters serve to separate the members

of these infraspecific taxa pairs when they occur at the same altitudes.

Frullania curvistipula has a bimodal distribution that broadly overlaps *F. curvistipula* var. *latistipula* between 2500 and 3000 m. The variety, on the other hand, is restricted to the upper end of the *F. curvistipula* range. Some environmental factor depresses the population of *F. curvistipula* in the 2000 - 2500 m range, where *F. attenuata*, *F. macgregorii*, *F. serrata* subsp. *spinistipula*, and *F. schusteriana* are dominant. Among these 'competing' taxa, all have broad ranges that overlap the peaks of the *F. curvistipula* range, except for *F. schusteriana*. We can conclude that *F. schusteriana* has probably not competitively replaced *F. curvistipula* in the middle of the *F. curvistipula* range because the former is a slender, pendent species, whereas the latter is a medium-sized, mat-forming species. On the other hand, the presence of pendent forms such as *F. schusteriana* and *F. papillata* suggests that it may have been more moist in the 2000 - 2500 m range. It is therefore interesting that the variety *F. curvistipula* var. *latistipula* is likewise absent in this range, suggesting that it has similar physiological characters that prevent it from occupying this range.

In the present study, we have shown that the members of sibling pairs have different optima for altitude on Mt. Albert Edward and that they rarely were identified together. From these observations, we can conclude one of the following:

1. Investigator bias in identification has resulted in the implied distribution pattern.
 2. The siblings are genetically distinct and mostly allopatric.
- or
3. The siblings are ecological variants induced by altitudinally related factors.

Common garden or transplant tests are

	Sorensen's K x 100
<i>F. armitiana</i> x <i>F. armitiana</i> var. <i>inflexula</i>	0
<i>F. curvistipula</i> x <i>F. curvistipula</i> var. <i>latistipula</i>	2
<i>F. ornithocephala</i> x <i>F. ornithocephala</i> var. <i>intermedia</i>	2
<i>F. serrata</i> subsp. <i>spinistipula</i> x <i>F. serrata</i> var. <i>hamatispina</i>	0

Table 2. Sorensen's K value for sibling pairs.

ferences while having relatively broad overlaps.

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