Plant communities of the Pro-Namib Desert

Swakop River Catchment, Namibia

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Abstract

Plant assemblages were studied in the Pro-Namib Desert Swakop River catchment in Namibia (southern Africa), in order to investigate patterns of community classification. Two surveys were conducted; a stratified survey of desert and dry river bed vegetation and a grid-based survey of desert vegetation alone. In the first survey, trees (plants >150cm height) were recorded using eight 50 x 50m quadrats in each of four habitats. In the second survey, all plants except grasses were recorded using 25 quadrats on five 2.4km transects (one per 600m of transect) placed in parallel 2km apart (where minimum quadrat size was determined by the nested quadrats method; for herbs: 2 x 4m; and shrubs: 20 x 20m). The data from both surveys were analyzed using standard classification (TWINSPAN) and ordination (DECORANA) techniques. These analyses were conducted for species and quadrats, both (1) with and without outliers (both cases), and (2) with and without downweighting of rare species (species only). However, the ecological interpretation of the results remained consistent throughout. The results from the stratified survey revealed distinct plant communities; (1) riparian forest characterized by *Prosopis glandulosa* and *Salvadora persica,* and (2) desert scrub characterized by *Acacia reficiens*, *Commiphora glaucescans* and *C. virgata*. Sub-communities in desert scrub were also recognized; these were plain and hill assemblages, distinguised by the presence or absence of *Phaeoptilum spinosum*, respectively. These communities match geomophological features of the desert landscape and may reflect differences in the availability of water. However, these communities were largely undetectable in the analyses of the grid-based survey dataset, which suggests that the scale of that survey was inadequate for the purpose of classification, despite the attainment of plateaus on the species-area curves. These results therefore draw attention to the problems of rarity and scale in the study of desert plant communities.

Keywords: Namib, desert, plant community, classification, ordination.

Introduction

In habitats where only a relatively small number of species exist, it would seem, intuitively, that community classification and an understanding of the ecological processes involved would be easier to achieve than in areas of high diversity and complexity. However, plant communities in arid environments are often more difficult to define or classify than those in more species-rich habitats (e.g. Dasti & Agnew 1994). This is particularly true for ephemeral species, whose presence is highly dependent on the irregular and unpredictable nature of physical conditions in nonequilibrium arid land ecosystems (see Wiens 1984, deAngelis & Waterhouse 1987). Walter (1986) has consequently argued that the classification of desert ecosystems may be more effectively achieved through geomorphological features rather than through vegetation. However, perennial desert species are longer-lived and appear to exist in relatively stable communities (e.g. Vasek 1980, Goldberg & Turner 1986), thus providing the foundation for a classification of the vegetation communities themselves. Nevertheless, the water requirements of these species and their ability to compete for soil moisture (e.g. Fowler 1986, Yeasler & Esler 1990) may yet lead to a correlation between particular species and geomorphological features of different water-retaining characteristics.

The purpose of this study is to explore plant assemblage definition in an area of the Pro-Namib Desert Swakop River catchment in Namibia. Its main aim is to describe the plant communities which are present, and thereby provide an initial basis for the future study and perhaps also management of the ecological processes of this area. In addition, the opportunity to consider the connection between species and geomorphological features will be briefly explored. Finally, this analysis provides a salutary reminder of the problems of rarity and scale in the analysis of desert plant communities.

The Namib desert is a narrow strip of land between 80-150km wide which stretches for almost 2000km along the south west coast of Africa. It is bordered to the north by the San Nicolai River (Angola) and to the south by the Olifants River (South Africa) (Walter 1986). Its plant life constitutes an important component of the Karoo-Namib flora, which is

unusually diverse and distinctive with several endemic species (e.g. Archibold 1995). In addition, the Namib desert may be one of the oldest deserts in the world (Ward et al. 1983). Consequently, its plant life may have had longer to evolve to arid conditions and to specialize to various microhabitat niches than those species found in deserts elsewhere (Günster 1994). This in turn means that of all desert plant communities around the world, it is those in the Namib which might be most likely to give rise to easily definable and distinct sub-communities. This makes the Namib flora a particularly appropriate focus for the current study.

Previous classifications of Namibian flora have been attempted, although primarily at the macroecological level. Geiss (1971) provided the first classification and vegetation map of Namibia, which is still widely used today (e.g. van der Merwe 1983, Müller 1984, Moyo et al 1993). According to this classification, the present study is conducted in the semi-desert and savanna transition (escarpment zone) region of the Namib desert. More recently, Jürgens (1991) has revised existing classifications of the larger Karoo-Namib region, which places the current study area in the Namaland subdomain of the Nama Karoo phytochorological unit. At a more detailed level, Walter (1986) identifies nine different biotopes within the Namib desert. These are classed in Outer and Inner Namib groups and are based primarily on geomorphological features. The present study appears to span three of these biotopes; the oases of the large "alien" riviere, the monadnocks (i.e. inselbergs, or koppes) and riviere of the inner Namib, and finally the pre-Namib. The current study follows Sullivan (1993) in attempting to develop a classification of different plant communities in the Pro-Namib desert using quantitative numerical techniques. The approach adopted is that of complementary analysis, using both classification and ordination procedures (see Kent & Ballard 1988).

Methods

Study site

The study was conducted at Tsaobis Leopard Park, a reserve on the edge of the Namib Desert

in the Karibib region of Namibia, Southern Africa (22°23'S 15°45'W). The reserve is dominated by mountains and ravines fringed by steep foothills and rolling plains, bordered to the north by the ephemeral Swakop River. The reserve encompasses a total area of 45 000 ha and a topographical range of 683-1445m altitude. Geologically, the area is composed primarily of metamorphosed Nosib and Damara sediments, intruded by post-Damara granites and pegmatite bodies (Bothe 1980). The climate is arid and unpredictable. Annual rainfall since 1900 in this region has a mean of 202mm and a coefficient of variation of 52% (data from Karibib, 40km north of Tsaobis: Figure 1). Mean annual rainfall at Tsaobis itself is lower still (85mm: N=5 years) and typically occurs only between January and April (Figure 2; note that only an annual total is available for 1989). During the study year (1991), rainfall was low at 56mm and the Swakop River failed to flow here. Monthly variation in shade temperature is plotted in Figure 3 (Karibib means, calculated from 1967-1983). Temperatures at Tsaobis were somewhat warmer and have not been known to drop below 0°C (N=5 years). With the exception of some limited goat grazing along the Swakop riverbed, there is no recent history of human subsistence activities in this area.

Data collection

Two surveys were conducted, using (1) stratified sampling and (2) grid-based sampling methods. In the first survey, four distinctive habitat types were identified in the study area. These were the Namib Hills, Namib Plains, Swakop (River) Forest and Swakop (River) Bed. Their identification was made on the basis of geomorphological and plant physiognomic features (Table 1). In each of these habitats, eight 50m x 50m quadrats were randomly placed (a total of 32 quadrats) and specimens of all *tree* species (>150cm in height) recorded. Consequently, a total area of two hectares of each habitat was sampled. This survey was conducted towards the end of the austral winter (October).

In the second survey, a sampling grid was developed to record plant species in the Namib Hills and Plains area. In this case, the vegetation was split into two basic categories:

herbs (forbs only; <50cm height) and *shrubs* (≥50cm height). Across the study site, five transects of 2.4km were marked out in parallel, each separated by a distance of 2km. The grid therefore covered an area of about 19km^2 and an altitudinal range of 750m-950m. Along each transect, sampling points were located at 600m intervals (a total of 25 points). The minimum quadrat size necessary for sampling each vegetation type was determined using the nested quadrats method (e.g. Goldsmith et al. 1986). Hence, for each vegetation category, six different quadrat sizes were tested at ten different sampling points (randomly chosen across the grid, but occurring on all five transects), and the number of species in each quadrat recorded. Species-area curves were then drawn and the quadrat size determined from the area at which species richness reached an asymptote (Figure 4). For herbs, this was 2m x 4m; for shrubs 20m x 20m. This resulted in a total survey area of 200m^2 for herbs and one hectare for shrubs.

Note that height was used as a convenient criterion for separating and subsequently sampling small and large plants. Although arbitrary, for current purposes it was preferred over divisions such as woody versus non-woody species, since size was an important determinant of sampling area and woody desert species vary tremendously in height (dwarf plants are abundant). In good rain years, this criterion may not be appropriate, since grasses and ephemeral species may grow above 50cm. However, prior to this survey, the rains were poor and no ephemerals grew above this height; indeed, only six ephemeral species were recorded of a total of 52 in the grid-based survey as a whole. Consequently, in this study, all species over 50mm were woody and the vast majority of species below this threshold also possessed woody stems.

In order to ensure that the survey was representative, a species-area curve was also plotted for the entire survey (Figure 5). This confirmed that species richness reached an asymptote within the survey area for both vegetation categories. This survey was conducted at the height of the wet season (April) to ensure that ephemerals were recorded together with the perennial species (although since the rains were poor during the study few were present:

see above). The presence and identity of all specimens of all species was recorded, through the use of keys in the field and consultation with Herta Kohlberg of the National Herbarium, Windhoek. Following the survey, it was also possible to allocate each of the grid quadrats to either Plains or Hills habitats using the criteria adopted in the stratified survey (see Table 1). This revealed that eight of the Namib grid survey quadrats fell in Plains habitats and 15 fell in Hills areas (the two remaining were intermediate and so discounted from either category).

Data Analysis

Identification of plant communities was carried out using Two-Way Indicator Species Analysis (TWINSPAN: Hill 1979a, Gauch & Whittaker 1981). This is a method of plant community classification which hierarchically divides a set of either species or quadrats into a series of several related sub-groups. These divisions are made on the basis of the abundance and co-existence of plant species in different quadrats. The sub-groups indicate either (1) those species which tend to occur together or (2) those quadrats that are most similar by virtue of the species they contain. The hierarchical division can then be displayed in the form of a dendrogram. In the case of quadrat analysis, each division of one group into two is accompanied with the identification of *indicator species*, which are those species that occur preferentially in one of the subgroups. Eigenvalues are analogous to relative measures of explained variance and are produced at each division. The TWINSPAN method is succinctly explained in Kent & Coker (1992). In the present analyses, the stopping criterion for the hierarchical division of species or quadrats was set at a minimum requirement of five items per group with no more than five divisions on any one branch.

In order to aid the interpretation of the TWINSPAN results, and in particular to ensure that this method had not produced an arbitrary classification (imposing discrete groups on a continuous distribution), the data were also analyzed using ordination. Using the technique of Detrended Correspondance Analysis (DECORANA: Hill 1979b, Hill & Gauch 1980), a set

of numerical scores for each species and quadrat was calculated. These scores, which are based on species abundance per quadrat, can be plotted against one another to reveal the ecological similarities between the species (or quadrats) through their proximity on the diagram. This method is also fully explained in Kent & Coker (1992).

Four TWINSPAN analyses are discussed here. These are the classifications of the trees in the stratified survey, and the herbs, shrubs and trees of the grid survey. The analyses of quadrats are also discussed, but emphasis is given to the species classification because only limited environmental data were collected to compare with the quadrat patterns. In all TWINSPAN analyses, divisions with eigenvalues below 0.15 are discarded (together with all other divisions subsequent to that division).

Results

Plant species abundance and their TWINSPAN associations at Tsaobis are given in Tables 2 and 3 for the stratified and grid-based surveys respectively. The dendrograms of these analyses, indicating the relationships between the different classified groups, are shown in Figure 6. In two cases (the herbs and trees of the grid survey), the datasets were skewed by the presence of outlying quadrats; these were quadrats which were entirely empty except for the presence of a species which was otherwise unrecorded in that survey. In the herbs, it was two quadrats, possessing a *Protasparagus* sp and a seedling *C. apiculatum* respectively; in the trees, it was a single quadrat with several specimens of *A. senegal*. The analyses presented here are those in which these outliers were removed from the dataset; however, the same analyses were also run with these quadrats and results of a similar nature were obtained, although the TWINSPAN groups were less well resolved. The TWINSPAN analyses were also run twice, where (1) equal weighting was given to all species (the standard run; outliers removed as just described) and (2) rare species were downweighted (in which case the outliers were included).

Stratified survey: all Habitats trees

The first division in this TWINSPAN analysis is extremely strong with an eigenvalue of 0.99 (Figure 6a). Two further divisions produce a total of four different groups in the stratified tree sample. The ordination of this dataset (Figure 7) broadly corroborates the classification. Group D (common Swakop habitats species) is clearly discrete from the Group A-C cluster (common Namib habitats species). TWINSPAN and DECORANA analysis of the quadrats (which produces an identical pattern) reveals that this second division (along Axis 2) reflects a distinction between the Namib Hills and Namib Plains habitat types: five of the six quadrats in the quadrat group which is analogous to the A+B cluster are sited in the Plains and seven of the eight quadrats in the analogous group C cluster are sited in the Hills (Fisher's exact test: $P<0.05$ two-tailed). The indicator species identified in this TWINSPAN analysis are (1) *Prosopis glandulosa* and *Salvadora persica* for the Swakop habitats and *Acacia reficiens*, *Commiphora glaucescans* and *Commiphora virgata* for the Namib habitats (at the first division); (2) *Phaeoptilum spinosum* for the Namib Plains habitat (at the second division). Note that in this case the final TWINSPAN division (between groups A and B) is not verified in the ordination. Finally, a second ordination of the tree species with downweighting applied to rare species produced a similar pattern, but in this case the Swakop and Namib groups were distantly separated and the division within the Namib group was lost. The implications of this result for the community classification are considered in the Discussion.

Grid survey: Namib herbs

The TWINSPAN analysis of the Namib herbs grid survey also exhibited a strong first division and produced seven well-defined groups (Figure 6b). The DECORANA ordination (Figure 8) supported this classification, but only to a limited degree. The first division of the species groups (E-H vs I-K) produced discrete clusters, but their spatial separation was minimal (less than that seen within groups). Ordination of the quadrats produced a similar pattern. Investigation of whether this first division reflected a discrimination between habitat types

(through the *post hoc* designation of these quadrats into Hills and Plains categories) revealed that there was a pattern of weak statistical significance (Fisher's exact test: P=0.07 two-tailed). Downweighting of rare species had little effect on this ordination; the division was unchanged although the two clusters of species at opposite ends of the first axis (on the left *Calicorema capitata*, *Crotalaria argyrea* and *Tephrosia dregeana*; on the right *Blepharis obmitrata*, *Gossypium anomalium* and a *Talinum* sp) became more clearly separated from the remaining species.

Grid survey: Namib shrubs

The TWINSPAN analysis of the Namib shrubs grid survey data produced five different groups (Figure 6c), although the eigenvalues for all divisions were low (<0.30). The ordination of these data did not confirm the discrete existence of any of these groups (Figure 9). Indeed, there was considerable overlap of the TWINSPAN groups across the graph, despite eigenvalues of reasonable value along each axis. Ordination of the quadrats was equally ambiguous; once again, there was no difference in the relative contribution of Hills and Plains samples to the two main quadrat groups (Fisher's exact test: P>0.10). The only notable feature of the species ordination is the presence of two clusters at opposite ends of the first axis (on the left *Acacia mellifera*, *G. anomalium* and *Indigofera* sp 1; on the right *A. senegal*, *Adenolobus garipensis* and a *Rhynchosia* sp). Downweighting of rare species emphasized these clusters.

Grid survey: Namib trees

Given the distinct division within the stratified trees sample between Namib Hills and Namib Plains areas, it is perhaps surprising that the grid survey of Namib shrubs did not produce clearer results. In order to investigate this further, the Namib shrubs grid survey data were re-analyzed following the removal of all plant specimens below 1.5m in height. This procedure rendered the Namib grid survey now directly comparable to the stratified all-

habitats survey; i.e. only trees were under consideration. The TWINSPAN analysis of the edited dataset produced four groups as opposed to five, with one strong division which separated the first group (comprising *A. reficiens, C. glaucescans* and *Curroria decidua*) from the remaining groups (Figure 6d). While DECORANA ordination confirmed this separation it did not support any of the subsequent TWINSPAN divisions of this dataset (Figure 10). The two species of Group T (which also occurred in the stratified survey analysis) were comparable to those of Group C, but the remaining groups (Q, R and S) did not show any consistent pattern in comparison to groups A, B and C of the Stratified survey analysis. However, consistent associations were seen between (1) *C. glaucescans* and *A. reficiens*; (2) *Acacia erubescens* and *P. spinosum*; and (3) *Euphorbia virosa* and *Acacia mellifera* (see Tables 2 and 3) across the two analyses. Downweighting of rare species did not alter these findings.

Discussion

The preceding results indicate a relatively homogeneous habitat with few distinct associations. Before discussing the patterns of species assemblages which emerged from this analysis, it is first necessary to consider briefly the effects of species rarity in these classifications.

The role of rarity

The rarity of species within the grid survey of the Namib habitats was marked (see Table 3). A total of 31 herb species and 39 shrub species were identified (including 17 species which appeared in both of these classes), but of these approximately 25% were recorded on the basis of one specimen only in their respective surveys (seven and nine species, respectively). It is a similar fraction which occur in more than five quadrats (i.e. 20% of the survey area) (six and ten species, respectively). In addition, several species were extremely patchy in their distribution. In the herb survey, *T. dregeana* occurred in only three quadrats but in one of these 31 individuals were recorded (the next most locally abundant herb only achieved a

density of 11 individuals). In the shrub survey, both *A. senegal* and *Catophractes alexandrii* were recorded in only one quadrat, but at individual densities of 12 and 28, respectively. It may be for these reasons that downweighting of rare species tended to have minimal effect on the patterns of species associations obtained in either the herb or shrub datasets; i.e. most species were patchy and rare anyway.

However, in the stratified sample, the change in pattern following downweighting did suggest two facts. First, common tree species occurred in either the Swakop or the Namib, but rarer species were not so easily grouped; and second, the division between the Hills and Plains vegetation communities was primarily the result of rarer species. These results indicate that the rarer tree species of the Namib desert may be more discriminating in their habitat requirements, revealing subtle ecological gradients within and between those already shown by the more common species. This means that rare species are providing information which may be particularly useful for the purposes of classifying these communities and perhaps also understanding the ecological processes which underlie them (see below; see also Gaston 1994).

Community Interpretation

The clearest associations emerged from the stratified survey, among tree species in distinct habitat types. A preliminary attempt may be made at interpreting these patterns, although inevitably any conclusions must remain tentative given both the paucity of autecological data for many of these species and the absence of quantitative data describing environmental conditions in the survey areas.

The first division in this group, between Namib and Swakop habitats, is a reliable one (high eigenvalues in both TWINSPAN and DECORANA analyses) which presumably reflects the well-established presence of ground water stores beneath the Swakop river (e.g. Walter 1986). Support for this inference is provided by the observation that, within the Swakop species, the drought-tolerant *Acacia erioloba* (species 11) spatially adjoins the Namib arid-

adapted species clusters, while the drought-sensitive *Acacia* (*Faidherbia*) *albida* (species 10) sits at the opposite (and presumably wetter) end of the Swakop cluster (see Ward & Breen 1983). Interestingly, the strongly halophytic habit of *Tamarix* does not appear to make it an outlier in relation to the other, non-halophilous, species in the Swakop. This is probably because this species is growing on surface salt crusts and not utilizing the deeper fresher groundwater which is exploited by other Swakop trees (see Walter 1986).

The ecological factor/s responsible for the subsequent division between Namib Hills and Plains areas in the same sample are less easy to identify. Altitude is unlikely, given the limited topographical variation at the site. However, a fine sandy substrate, as opposed to a coarser base, might be the key factor. Indeed, four of the eight Plains quadrats were located in the immediate floodplain of the Swakop River and/or its tributaries, and these were predominantly sandy. In contrast, none of the Hills quadrats contained sand. The findings of previous studies indicate that soil moisture can strongly influence spatial distribution patterns of desert plant species since sand has greater water-retention properties than gravel or other rocky substrates (e.g. Olsvig-Whittaker et al. 1983; see also Louw & Seely 1982, Walter 1986). The observation that the sandy Plains species assemblage (as defined by ordination) shares greater proximity to the Swakop cluster than the Hills assemblage is consistent with this observation. However, whether or not substratum is the determining factor, and if so whether it is water retention which is the key feature, remains an area for future investigation.

A similar classification of plains, hills and riverine communities was also obtained by Sullivan (1993) in a recent TWINSPAN and DECORANA analysis of the vegetation of the Pro-Namib Khowarib River catchment. This similarity in results, despite markedly different survey methodologies and species composition in the study regions, suggests that this classification is a robust one. This result also lends support to Walter's (1986) assertion that desert habitats may be efficiently classified in terms of geomorphological features (see also Louw & Seely 1982, Olsvig-Whittaker et al. 1983).

In light of this, the failure to identify comparable discrete groups in the ordinations of the grid survey of Namib herbs, shrubs and trees is surprising. However, there was a discrete division of groups in the ordination of Namib herbs (TWINSPAN groups E-H vs I-K) which was suggestive of such a relationship. Two alternative ecological explanations can also be considered in addition to the soil moisture hypothesis. First, since many of the herbs are ephemerals and rainfall was patchy within the survey area, the two groups may represent areas where rain did or did not fall (or has collected and has not collected: Walter 1986), respectively. Yet a comparison of the frequency of ephemerals in the two groups does not support this; ephemeral species were about equally common in both (two of 11 species in groups E-H and four of 18 in groups I-K). Second, grazing pressure from wild herbivores may have been unequally distributed in the survey area, creating distinct graze-tolerant and graze-sensitive communities (see Skarpe 1990, Dasti & Agnew 1994). However, an investigation of the distribution of species which showed evidence of grazing (collected from a phenological study undertaken on the basis of this survey system: Davies & Cowlishaw, unpublished) revealed approximately equal distribution between the two groups (three of 11 species in groups E-H and four of 18 in groups I-K). The failure of either of these explanations to account for the observed pattern suggests that the division in the Namib herbs communities may reliably reflect the two communities associated with the Hills and Plains. However, further research is required to verify this.

In the case of the Namib shrubs, both the absence of any clear division in the ordination of this dataset and the relatively low eigenvalues suggest that the TWINSPAN classification is probably falsely imposed on what is otherwise a single community. Nevertheless, the consistent positioning of *A. senegal* and *A. mellifera* at opposite extremes of axis 1 in both the stratified survey and the shrubs subset of the grid-based survey ordinations (Figures 7 and 9 respectively) suggests that a gradient from dry to wet conditions may nevertheless be present in the shrubs community (assuming that moisture is the gradient which axis 1 reflects in the ordination of the stratified survey; see above). Similarly, the

Namib trees subset of the grid survey failed to show any pattern which related to habitat type, although a division was present which showed limited similarity to that found in the stratified trees survey.

Why should the stratified survey so clearly identify distinct Hill and Plains communities when the grid surveys do not? The most probable reason is the size of sampling area. The stratified survey covered a total of 4ha of the Namib region, while the grid survey spanned only 1ha. This is why the number of tree species in the former is far greater than in the latter (compare Tables 2 and 3). Yet interestingly, a tree species-area curve for the grid-based survey (not shown here) does level off. This suggests that although a good representation of the area's species richness is being obtained, an even more comprehensive species coverage, and/or a larger survey area, is required to reliably identify sub-communities in this region (cf. Campbell 1994). This question of sampling area is further complicated by the sensitivity of the species-area curve to different spatial scales (Palmer & White 1994). The findings of this study hence raise the general issue of understanding the role of spatial scale in ecological processes (May 1994). Unfortunately, there are no simple answers, but on the basis of these results we suggest that future studies of desert communities might find it useful to contemplate the issue of scale particularly carefully, and perhaps consider an area of survey coverage in excess of that suggested by the plateau of the species-area curve alone.

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Legends to Figures

Figure 1. Mean annual rainfall at Karibib between 1900-1991. The horizontal line shows the mean value.

Figure 2. Mean monthly rainfall at Tsaobis between 1987-1991. Monthly data are not available for 1989. Note that rainfall years are calculated from July to June rather than January to December.

Figure 3. Shade temperature variation (Karibib). Minima and maxima mean average (filled circles) and maximum value (open circles) are shown. Data from 1969-1983.

Figure 4. Species-area curves for determining minimum quadrat size for the grid survey of (a) Namib herbs and (b) Namib shrubs. Species richness values plotted are the total number of species occurring in the ten quadrats at that size category. Asymptotes were judged to occur at $8m^2$ and $400m^2$ respectively.

Figure 5. Species-area curves for the grid survey of Namib herbs (open circles) and Namib shrubs (filled circles).

Figure 6. TWINSPAN dendrograms of the hierarchical division of (a) stratified trees, (b) Namib herbs, (c) Namib shrubs and (d) Namib trees. Eigenvalues are shown at each division, and the letters A-T are used to denote the identity of the different groups obtained (see Tables 2 and 3). Numbers in brackets show the number of species in each group.

Figure 7. DECORANA ordination of the stratified tree survey. Each species is numbered (Table 2) and the symbols represent the different TWINSPAN groups (Figure 6a): group A

(filled square), group B (filled circle), group C (filled diamonds) and Group D (open triangles). Note that the distinction between filled and open symbols reflects those species separated at the first division.

Figure 8. DECORANA ordination of the herbs of the grid-based survey. Each species is numbered (Table 3) and the symbols represent the different TWINSPAN groups (Figure 6b): group E (open triangles), group F (open squares), group G (open circles), group H (inverted triangles), group I (filled squares), group J (filled triangles) and group K (filled circles). Note that the distinction between filled and open symbols reflects those species separated at the first division.

Figure 9. DECORANA ordination of the shrubs of the grid-based survey. Each species is numbered (Table 3) and the symbols represent the different TWINSPAN groups (Figure 6c): group L (filled circles), group M (filled diamonds), group N (open triangles), group O (open square) and group P (filled squares). Note that the distinction between filled and open symbols reflects those species separated at the first division.

Figure 10. DECORANA ordination of the trees of the grid-based survey. Each species is numbered (Table 3) and the symbols represent the different TWINSPAN groups (Figure 6d): group Q (filled circles), group R (filled triangles), group S (filled inverted triangles) and group T (open circles). Note that the distinction between filled and open symbols reflects those species separated at the first division.

Table 1. Physiognomic features of the four habitat types.

Habitat	Predominant vegetation	Predominant substrate	Ground slope
Swakop Bed	None	loose sand	0° -
Swakop Forest	Riparian forest	loose sand	0° (0°-10°)
Namib Plains	Desert scrub	sand/gravel/rock	0° (0°-30°)
Namib Hills	Desert scrub	sand/gravel/rock	45° (30°-70°)

N = 8 for ground slope measure; median and range (in brackets) listed.

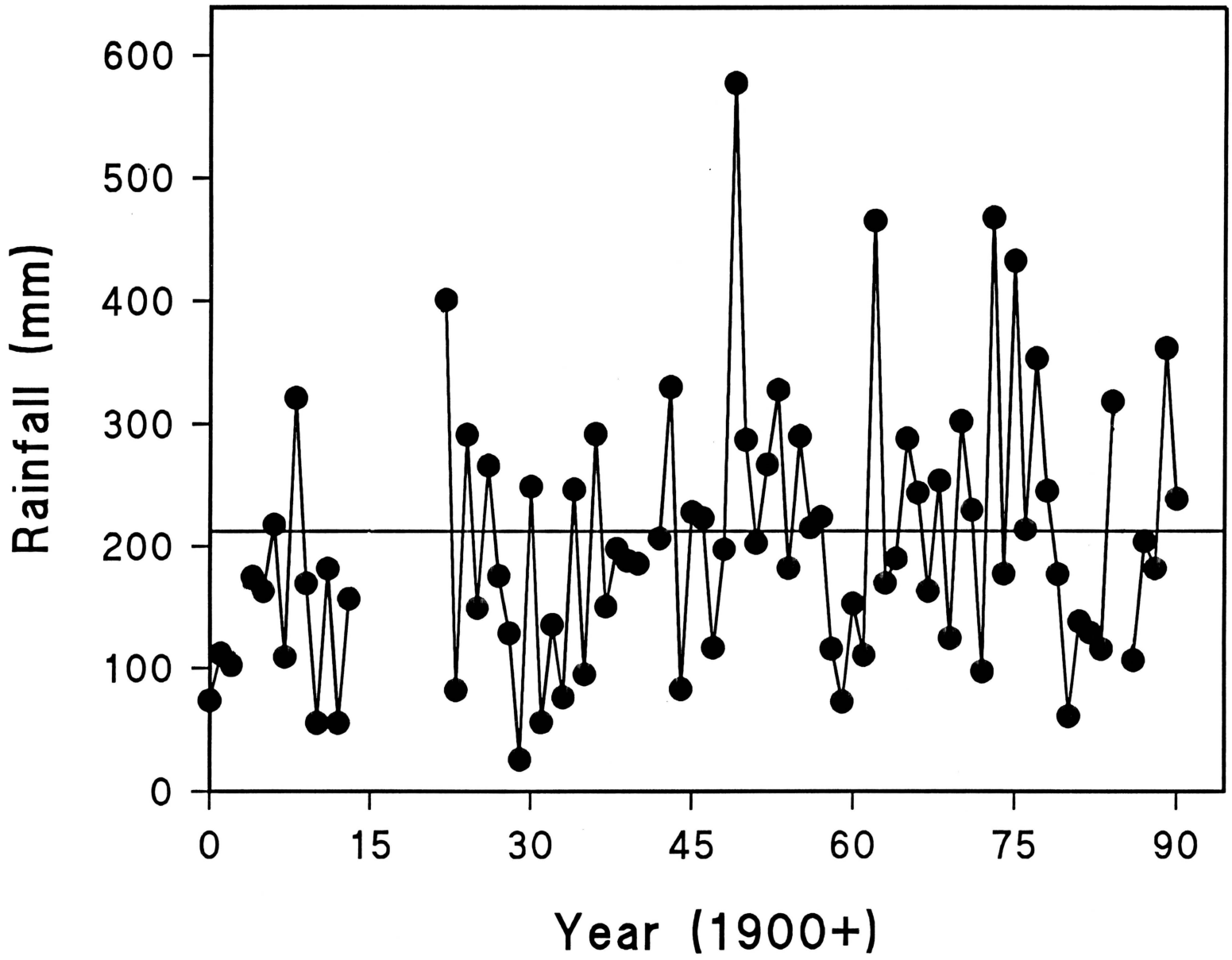
Table 2. Plant species of the stratified tree survey[1].

No	TWINSPAN Group (a)	Family	Species	Swakop: Bed N2ha^{-1}	Swakop: Forest N2ha^{-1}	Namib: Plains N2ha^{-1}	Namib: Hills N2ha^{-1}
1	B	BIGNONIACEAE	*Catophractes alexandrii*	-	-	6	1
2	C	BURSERACEAE	*Commiphora glaucescans*	-	-	3	23
3	C	BURSERACEAE	*Commiphora saxicola*	-	-	3	10
4	B	BURSERACEAE	*Commiphora virgata*	-	-	5	3
5	B	CAPPARACEAE	*Boscia albitrunca*	-	-	1	-
6	A	CAPPARACEAE	*Boscia foetida*	1	-	3	3
7	C	COMBRETACEAE	*Combretum apiculatum*	-	-	1	1
8	D	EBENACEAE	*Euclea pseudebenus*	-	7	-	-
9	C	EUPHORBIACEAE	*Euphorbia virosa*	-	-	1	1
10	D	FABACEAE	*Acacia (Faidherbia) albida*	1	8	-	-
11	D	FABACEAE	*Acacia erioloba*	-	2	1	-
12	B	FABACEAE	*Acacia erubescens*	-	-	12	6
13	C	FABACEAE	*Acacia mellifera*	-	-	2	-
14	C	FABACEAE	*Acacia reficiens*	1	-	4	9
15	C	FABACEAE	*Acacia senegal*	-	-	-	1
16	D	FABACEAE	*Acacia tortilis*	1	1	-	-
17	D	FABACEAE	*Prosopis glandulosa*	6	49	1	-
18	*	LORANTHACEAE	*Tapinanthus oleifolius*	1	15	-	-
19	B	NYCTAGINACEAE	*Phaeoptilum spinosum*	-	-	12	1
20	D	SALVADORACEAE	*Salvadora persica*	2	22%	2	-
21	C	STERCULIACEAE	*Sterculia africana*	-	-	-	2
22	D	TAMARICACEAE	*Tamarix usneoides*	-	9%	-	-
23	B	Unknown	Unidentified 1	3	0	0	0
24	D	Unknown	Unidentified 2	6	7	0	0

[1]Where individual plants are not discernable, % ground cover is listed.
*Epiphyte on *P. glandulosa* and infrequently *S. persica*

Table 3. Plant species of the systematic Namib survey (herbs and shrubs). Columns show (1) individual code, (2) TWINSPAN group identity, (3) family and species name and (4) the frequency (number of herb-shrub quadrats in which it occurs) and abundance (number of specimens in the herb survey and shrub survey). Asterisks show outliers removed from the analyses (see Results).

No	TWINSPAN Group (Fig 6) (b)	(c)	(d)	Family	Species	Freq. Shrubs -Herbs N	Abundance: Shrub survey $N400m^{-2}$	Herb survey Nha^{-1}
1	-	L	-	ACANTHACEAE	*Barleria damarensis*	02-00	2	0
2	K	M	-	ACANTHACEAE	*Barleria priomitoides*	02-01	4	1
3	K	L	-	ACANTHACEAE	*Blepharis obmitrata*	01-01	1	5
4	E	N	-	ACANTHACEAE	*Monechma arenicola*	02-02	2	3
5	G	N	-	ACANTHACEAE	*Petalidium variable*	08-02	19	2
6	-	L	-	ACANTHACEAE	*Ruellia diversifolia*	02-00	2	0
7	H	-	-	AIZOACEAE	*Corbichonia* sp.	00-02	0	2
8	I	-	-	AIZOACEAE	*Gisekia africana*	00-07	0	18
9	K	-	-	AIZOACEAE	*Mollugo cerviana*	00-01	0	2
10	-	N	-	AMARANTHACEAE	*Amaranthaceae* sp.	05-00	7	0
11	F	P	-	AMARANTHACEAE	*Calicorema capitata*	11-01	32	1
12	-	L	-	AMARANTHACEAE	*Marcelliopsis denudata*	01-00	1	0
13	-	L	-	ANACARDIACEAE	*Rhus marlottii*	01-00	1	0
14	-	L	-	ASCELPIADACEAE	*Orthantera albida*	02-00	2	0
15	K	-	-	ASTERACEAE	*Dicoma* sp.	00-02	0	3
16	K	-	-	ASTERACEAE	*Geigeria* sp.	00-01	0	7
17	-	N	Q	FABACEAE	*Acacia erubescens*	04-00	8	0
18	G	L	Q	FABACEAE	*Acacia mellifera*	02-01	3	1
19	-	P	T	FABACEAE	*Acacia reficiens*	02-00	6	0
20	-	N	*	FABACEAE	*Acacia senegal*	01-00	12	0
21	-	N	-	FABACEAE	*Adenolobus garipensis*	01-00	2	0
22	F	-	-	FABACEAE	*Crotalaria argyrea*	00-03	0	11
23	J	L	-	FABACEAE	*Indigofera* sp 1.	05-07	35	18
24	I	-	-	FABACEAE	*Indigofera* sp 2.	00-06	0	7
25	I	L	-	FABACEAE	*Ptycholobium biflorum*	01-03	1	10
26	-	N	-	FABACEAE	*Rynchosia* sp.	01-00	1	0
27	F	-	-	FABACEAE	*Tephrosia dregeana*	00-03	0	39
28	G	N	-	BIGNONIACEAE	*Catophractes alexandrii*	01-01	29	2
29	-	N	T	BURSERACEAE	*Commiphora glaucescans*	10-00	18	0
30	-	N	S	BURSERACEAE	*Commiphora saxicola*	07-00	7	0
31	K	M	S	BURSERACEAE	*Commiphora virgata*	21-02	95	3
32	-	M	R	CAPPARACEAE	*Boscia foetida*	12-00	18	0
33	-	N	-	CAPPARACEAE	*Boscia* sp.	01-00	1	0
34	G	P	-	CAPPARACEAE	*Cleome suffruticosa*	03-05	8	11
35	*	-	-	COMBRETACEAE	*Combretum apiculatum*	00-01	0	2
36	F	L	-	EUPHORBIACEAE	*Euphorbia gladuligera*	01-11	1	27
37	-	L	Q	EUPHORBIACEAE	*Euphorbia virosa*	02-00	2	0
38	*	L	-	LILIACEAE	*Protasparagus* sp.	02-01	3	1
39	K	L	-	MALVACEAE	*Gossypium anomalium*	03-01	5	1
40	K	L	-	MALVACEAE	*Hibiscus elliotiae*	05-01	11	1
41	-	N	Q	NYCTAGINACEAE	*Phaeoptilum spinosum*	02-00	4	0
42	-	O	T	PERIPLOCACEAE	*Curroria decidua*	12-00	23	0
43	-	N	-	POLYGALACEAE	*Polygala guerichiana*	01-00	1	0
44	E	-	-	PORTULACACEAE	*Portulaca* sp.	00-03	0	5
45	K	-	-	PORTULACACEAE	*Talinum* sp.	00-01	0	2
46	K	L	-	RUBIACEAE	*Amphiasma divaricatum*	02-01	4	7
47	-	L	-	RUTACEAE	*Thamnosma africana*	01-00	1	0
48	K	-	-	STERCULIACEAE	*Hermannia modesta*	00-04	0	19
49	-	L	-	VERBENACEAE	*Plexipus garipensis*	01-00	2	0
50	E	-	-	ZYGOPHYLLACEAE	*Tribulus zeyheri*	00-04	0	15
51	K	-	-	UNKNOWN	unidentified 3	01-05	3	16
52	K	-	-	UNKNOWN	unidentified 4	00-01	0	1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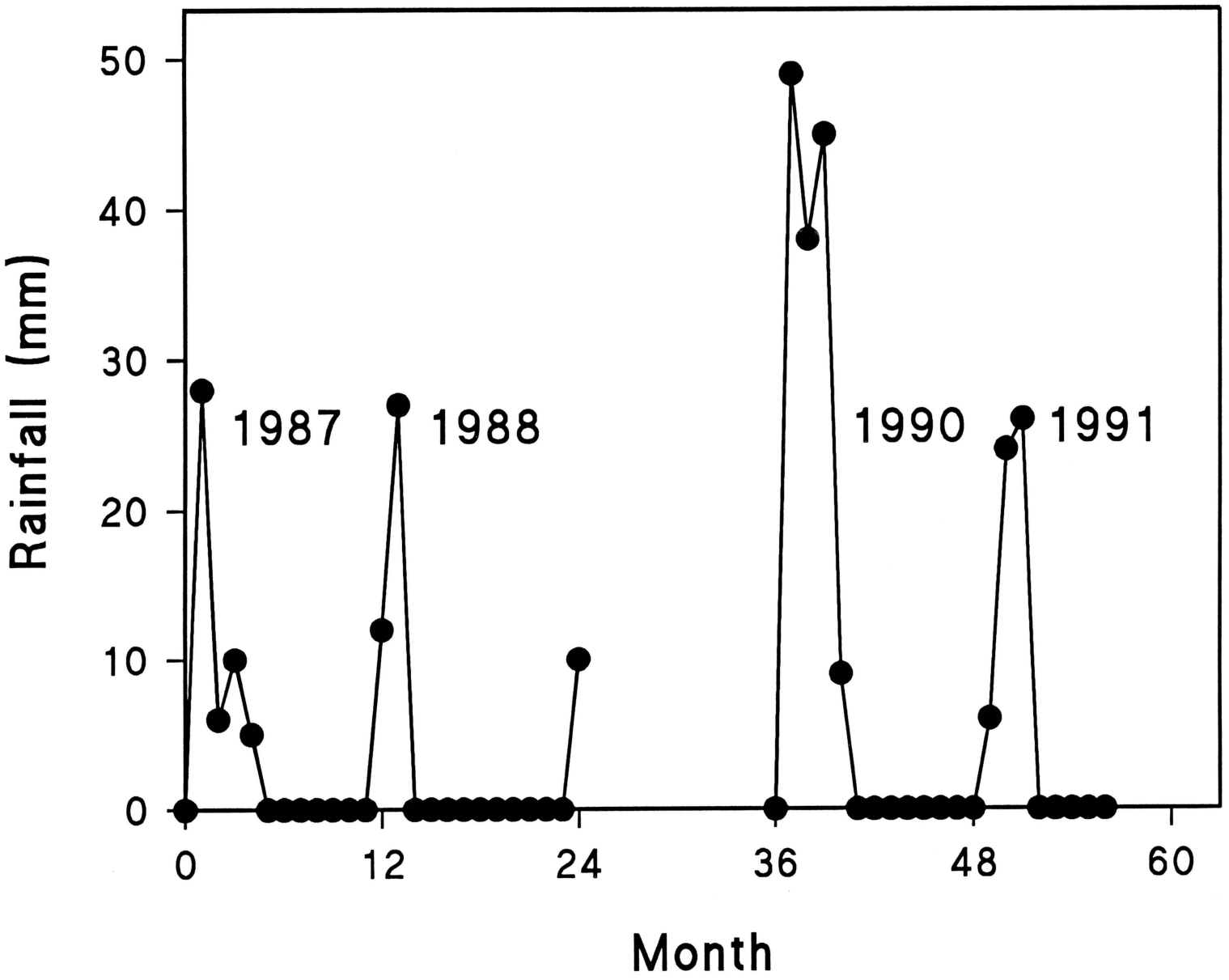
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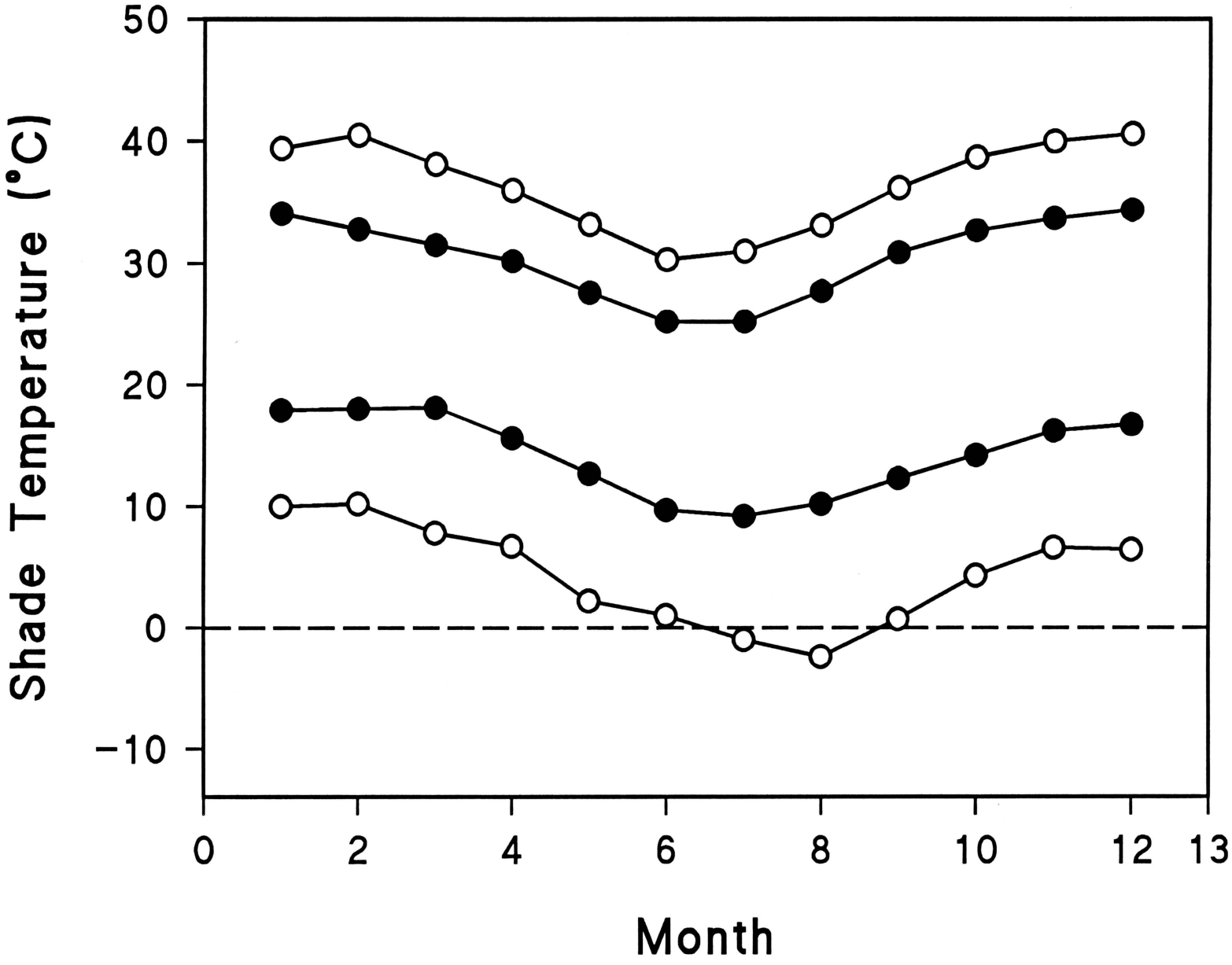
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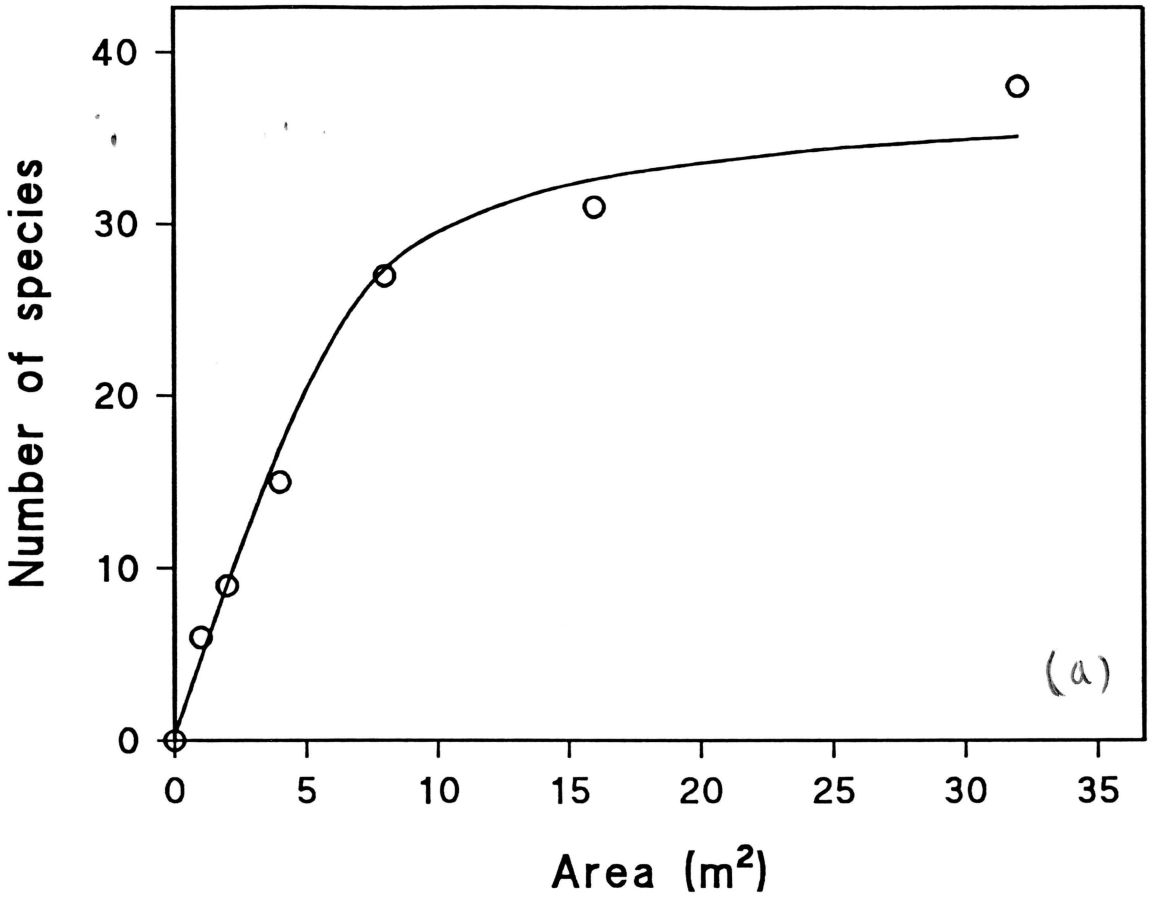
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Area (m²)
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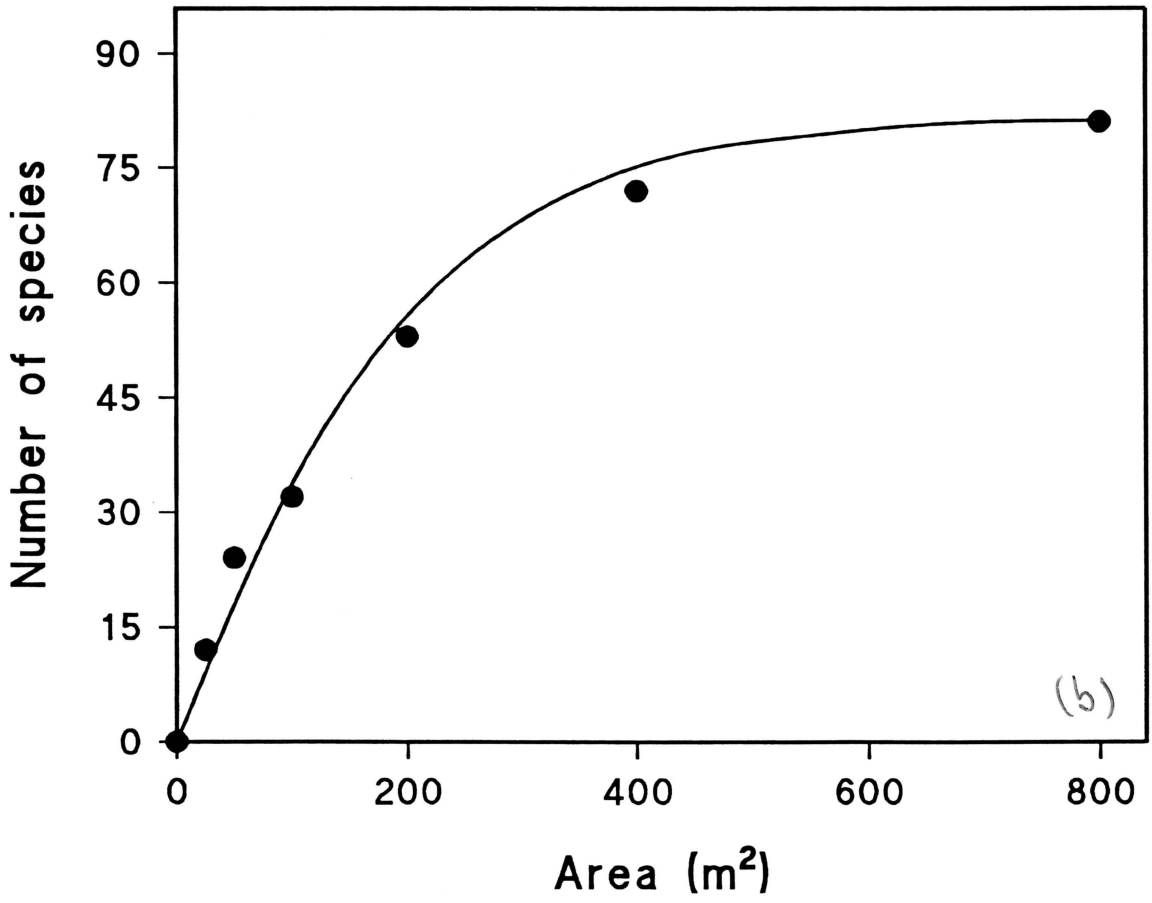
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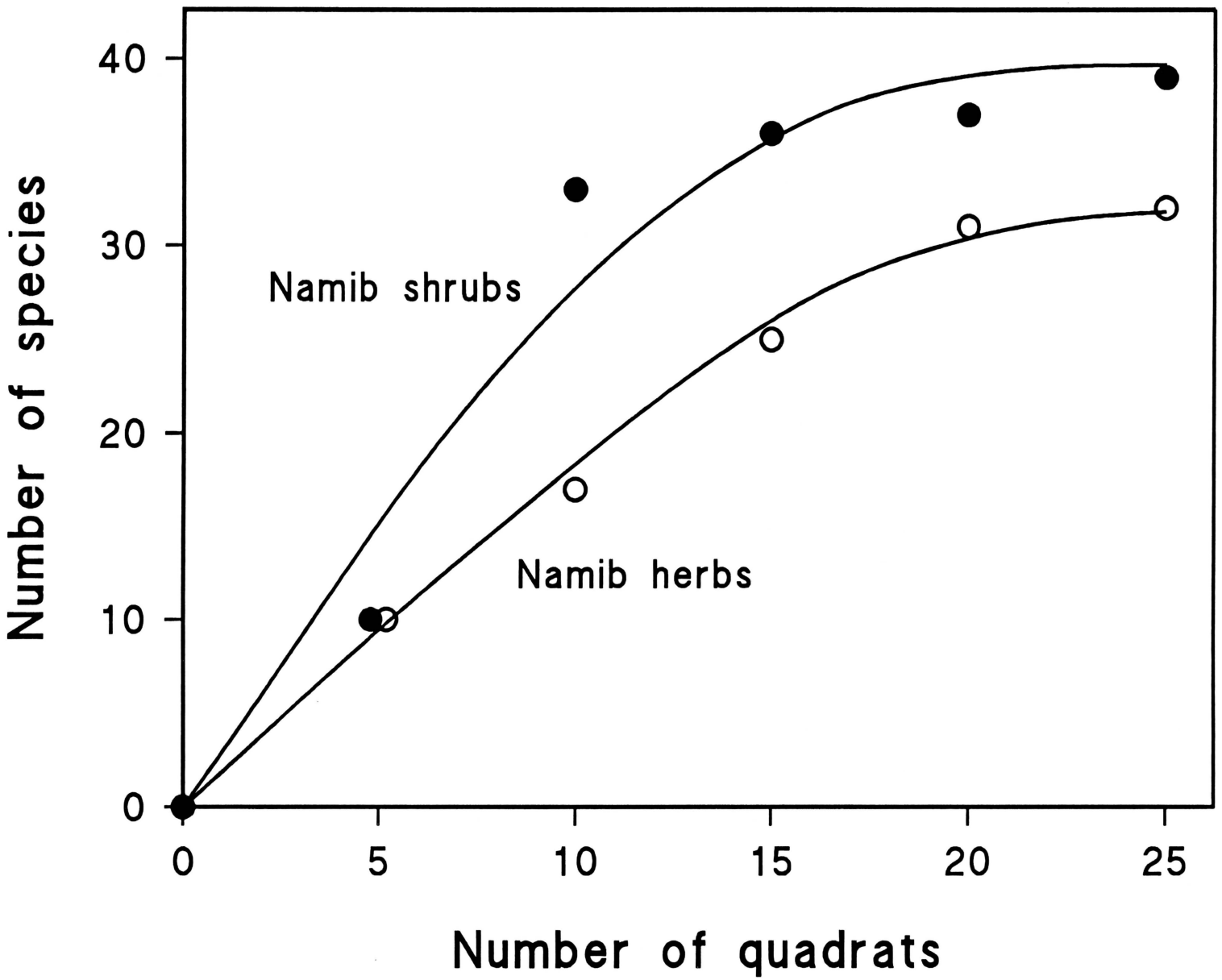
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Namib herbs
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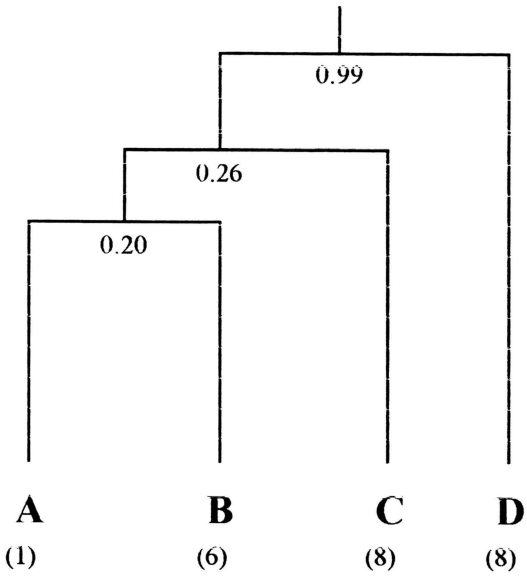
15
20
25
Number of quadrats

(a)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C
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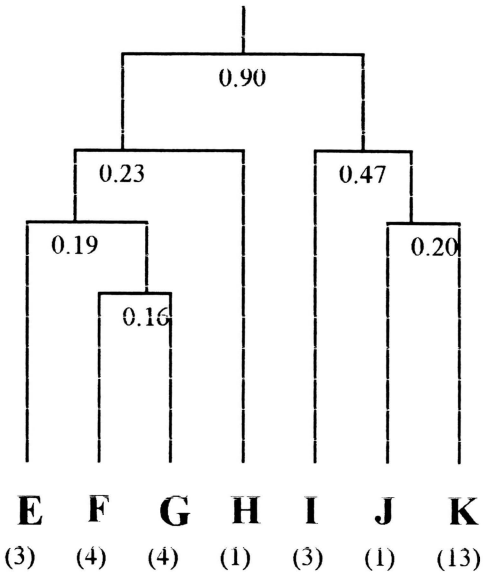
D
(8)

(b)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K
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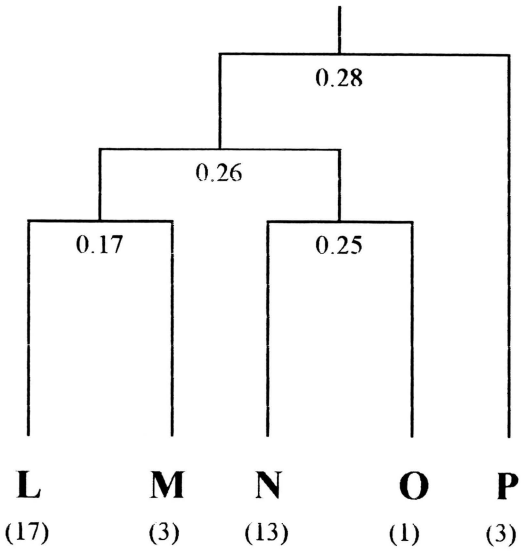
(c)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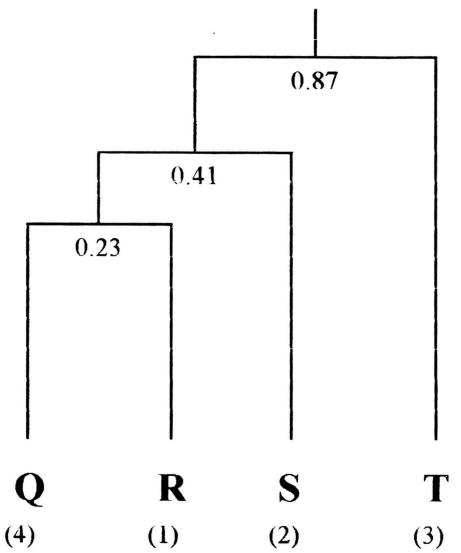
(3)

(d)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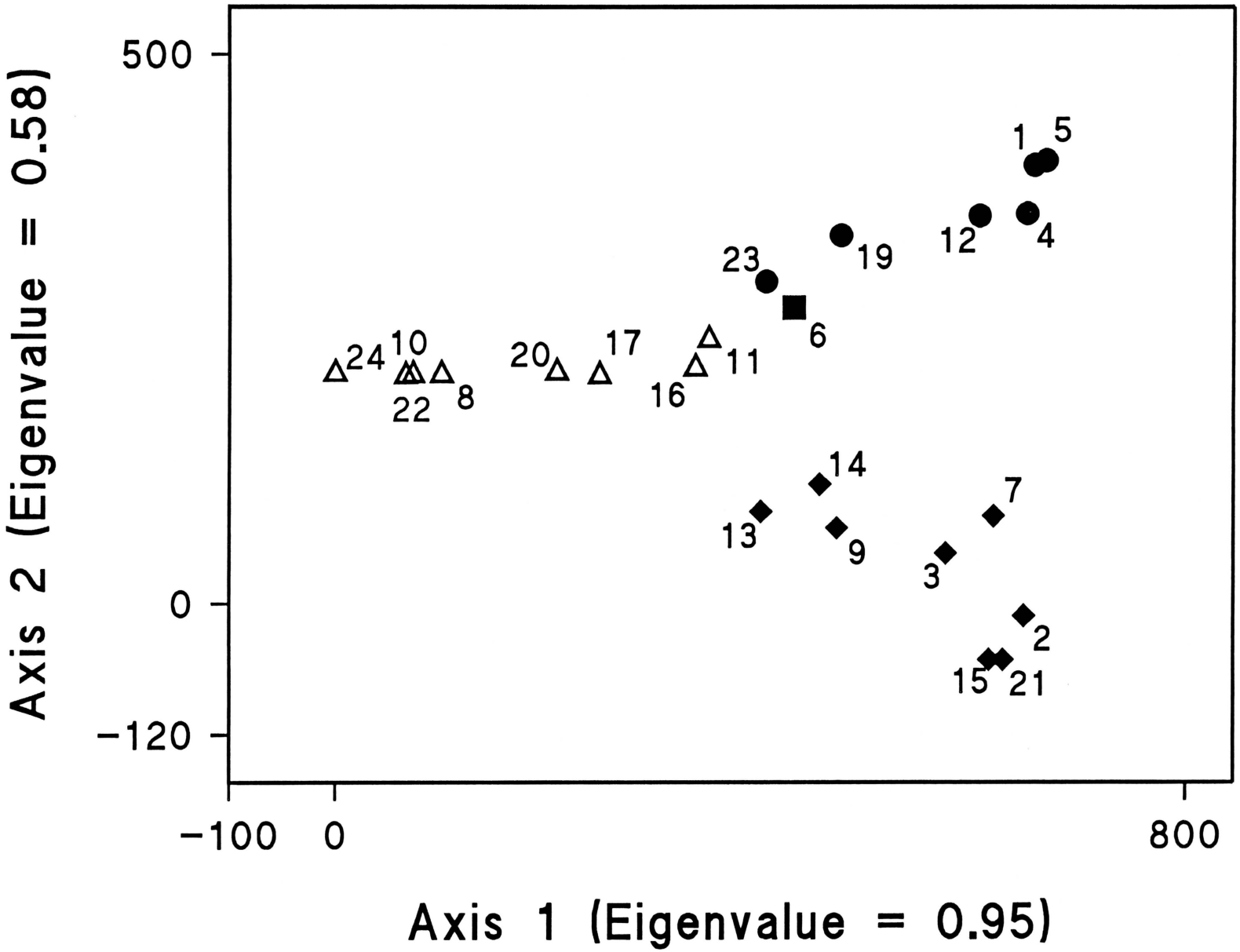
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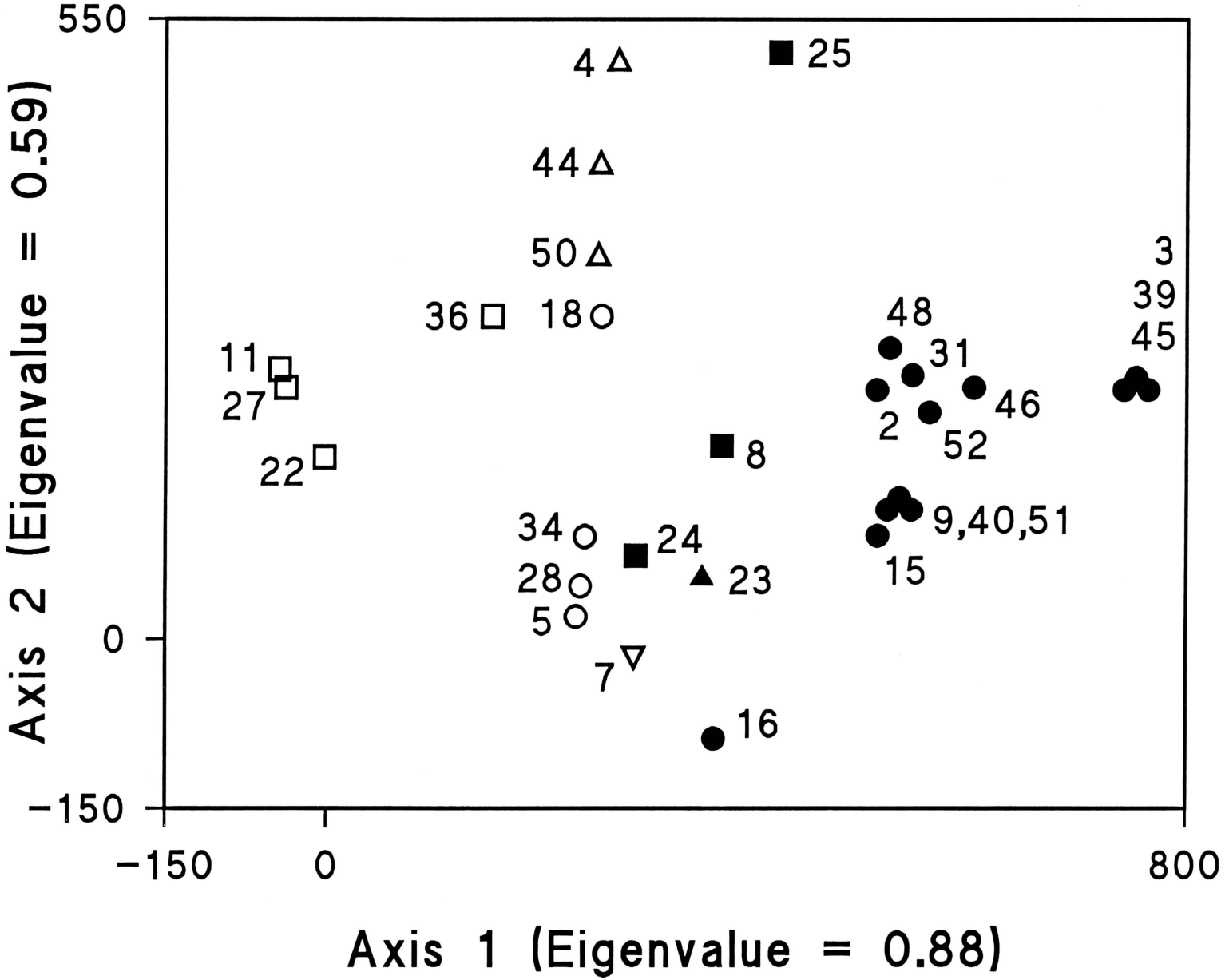
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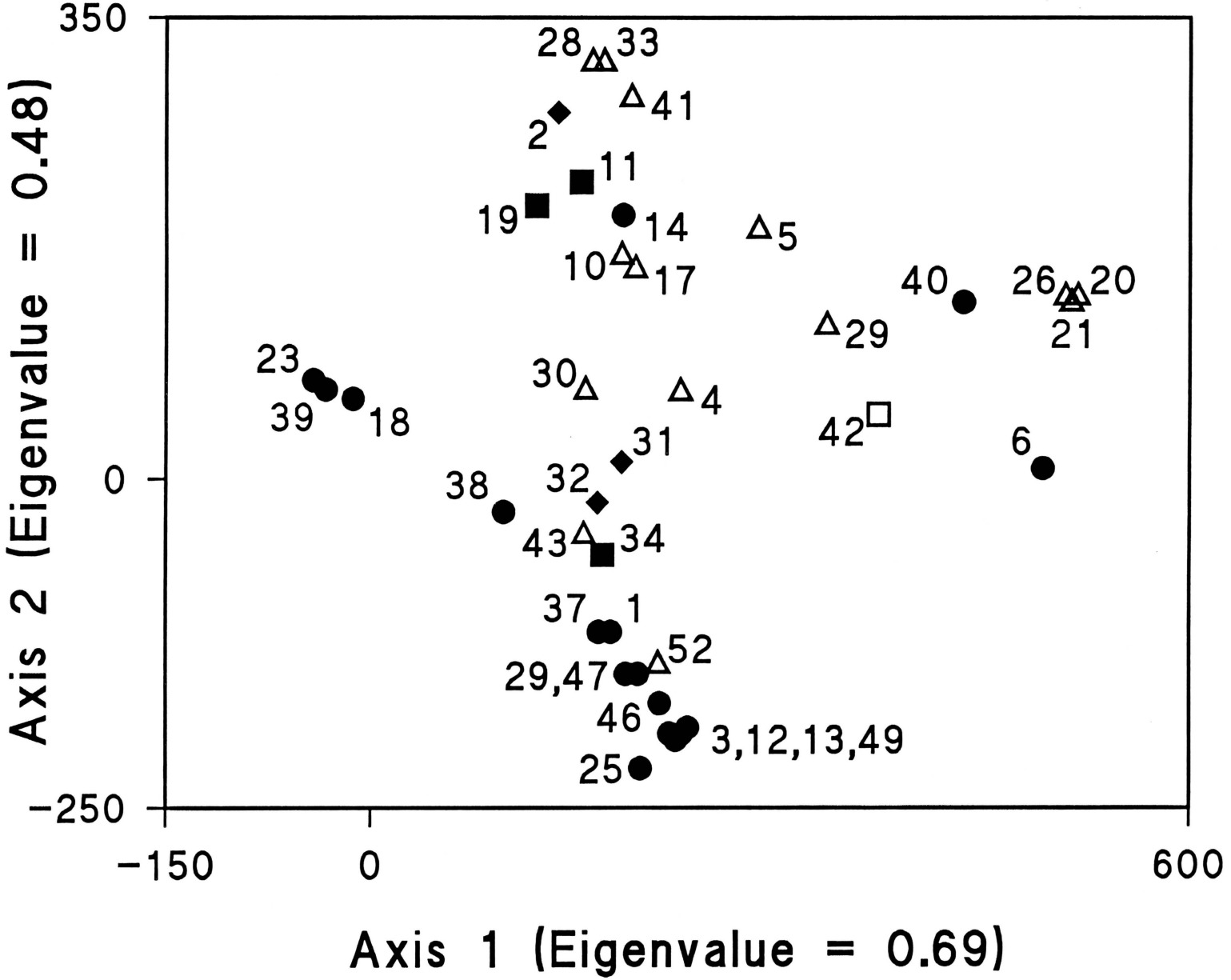
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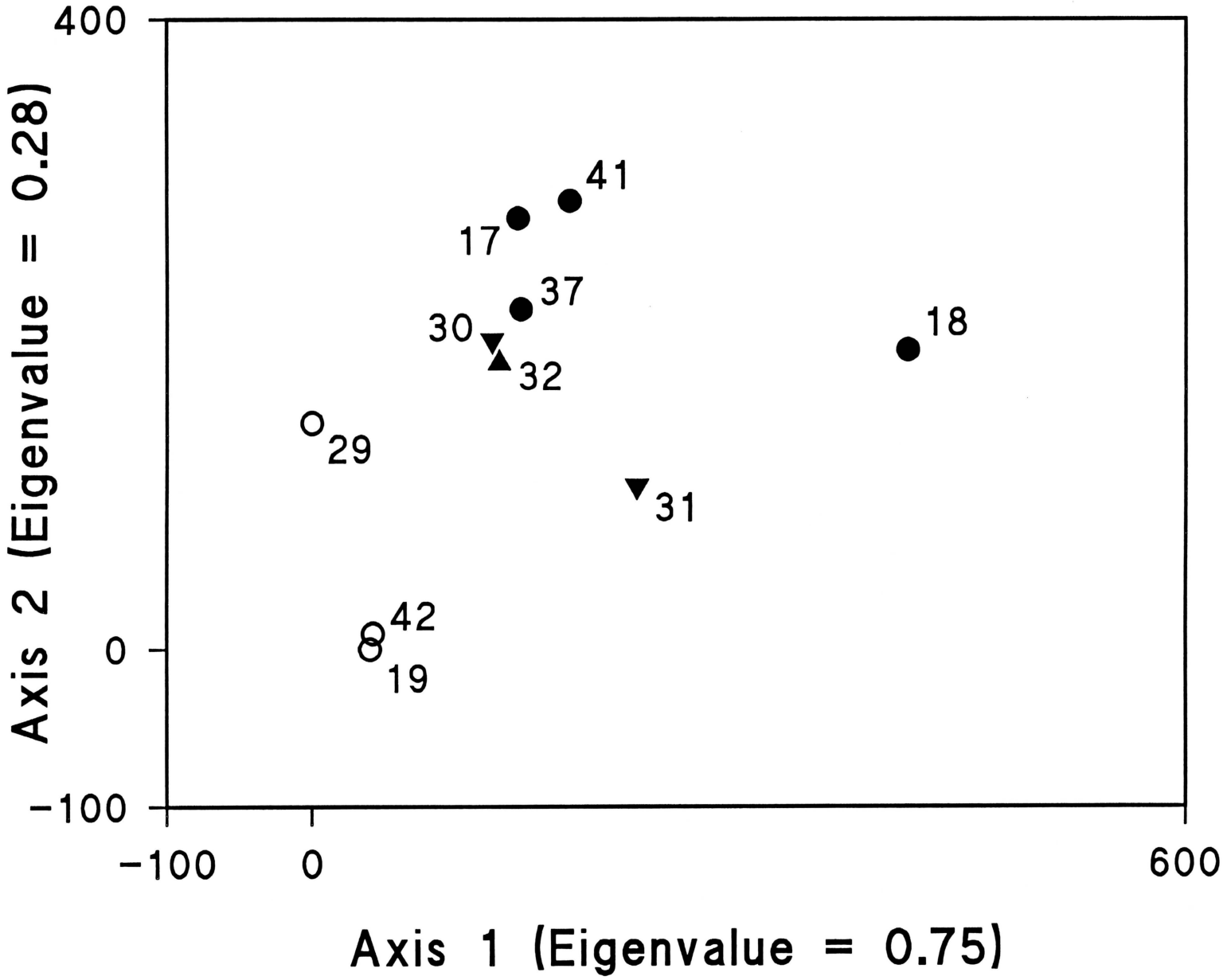
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