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INDIRECT ORDINATION OF FOREST STANDS OF THE NORTHWEST HIGHLAND RIM

Richard J. Jensen

Wright State University
Dayton, Ohio 45435

Abstract

Twenty-eight forest stands in Montgomery and Stewart Counties, Tennessee were sampled using a modified random-pairs method. The data were arranged in a matrix of values representing the density of each species in each stand. Forty tree species, those that a) occurred in at least four stands and/or b) had a density of .10 or higher in at least two stands, are represented in the matrix. Ordination was performed using reciprocal averaging, an eigenvector method analagous to principal components analysis. Interpretation of the first two axes suggests that axis 1 reflects a moisture gradient very similar to that determined earlier by subjective methods. There is no evident gradient on axis 2, but possible trends involving soil conditions are noted.

Introduction

The descriptor, "Northwest Highland Rim", does not represent a physiographically or floristically distinct region. Rather, it represents the general area; specifically, Montgomery and Stewart Counties, Tennessee in which the data utilized in this study were collected. These counties are situated near the western-most boundary of what Braun (1950) has termed the Western Mesophytic Forest; a region described as transitional between the Mixed Mesophytic Forest Region to the east and the Oak-Hickory Forest Region to the west. More recently, Küchler (1964) has described this region as a mosaic of Oak-Hickory Forest and Bluestem Prairie.

There have been few previous studies of forest composition in this area. Frick (1939) studied slope vegetation at the boundary of the Highland Rim and the Nashville Basin at a site approximately 40 kilometers southeast of the present study area. The slopes Frick (1939) studied are mostly of southern exposure, are parts of the dissected Highland Rim, and vegetationally, are very similar to the south-facing slopes described by Jensen et al. (in press; see below). Duncan and Ellis (1969) described the forest communities of Montgomery county, Tennessee after taking samples located randomly from a grid established throughout the county. Their data were summarized for the entire county and community descriptions were basically the result of qualitative observations. In a more recent study, Jensen et al. (in press) described seven forest communities of the Northwest Highland Rim based on sampling in predetermined habitat types. The habitat types were based on a subjectively derived gradient reflecting apparent differences in soil moisture. Each of the seven communities was then described by summarizing data from four stands representing that habitat type (e.g., four stands representing south-facing slopes). The purpose of the present study is to reassess the community descriptions of Jensen et al. (in press) in terms of the relationships between the 28 stands sampled and 40 taxa included.

The results presented in Jensen et al. (in press) may be viewed as a form of direct gradient analysis, i.e., an ordinations of communities based on an evident physical gradient (Whittaker, 1967). The physical gradient, in this case moisture, was not actually measured but was subjectively determined. Therefore, a more meaningful approach to these data may be found in what Whittaker (1967) termed indirect gradient analysis, i.e., the ordination is based on floristic differences between the stands. Whittaker (1967) prefers direct analysis because, obviously, there is no confusion concerning the type or direction of the gradient. With indirect analysis, however, it is often difficult to interpret the resulting ordination. Nevertheless, there are often cases in which the gradient is too complex to be obvious or information concerning a gradient is unavailable. In such cases, indirect analysis is the only means for producing an ordination.

Hill (1973) discussed the diffierences in these kinds of ordinations and also discussed methods of preparing such analyses, particularly principal components analysis (PCA) and reciprocal averaging (RA). According to Hill, the latter technique is superior because it allows simultaneous ordination of both stands and species. Gauch et al. (1977) compared several ordination techniques including PCA, RA and polar ordination (PO). Gauch et al. recognized, as did Beals (1973), that PCA is not suitable for analyzing nonlinear ecological data and suggested that RA is more tolerant of such data structure. Their results indicate that RA is superior to both PCA and PO in respect to its simultaneous stand and species ordinations and that RA is somewhat less subject to problems resulting from sample clusters, sample error, and outliers than is PCA. While PO is probably superior to RA in terms of distortions resulting from nonlinearity, Gauch et al. (1977) point out that PO is limited by its requirement that the end points of the ordination must be chosen *a priori,* although there are methods for automatic end point selection based upon the largest distance between pairs of species or samples (Bray and Curtis, 1957; Gauch, 1977; Swan, 1970). RA remains a viable method for an indirect analysis of the type suggested here.

Methods

Data were collected (Jensen et al., in press) in 28 stands using 25 tree pairs on a transect across each stand. For this study, the only data needed are the species of each tree sampled as well as the *relative* density of each species in each stand. The density is expressed simply as per cent occurrence, e.g., if a stand has 8 individuals of *Quercus alba* (nomenclature follows that of Fernald, 1950), then the density of this species in that stand is 0.16.

In this study only those species that a) occurred in at least four stands and/or b) had densities of 0.10 or higher in at least two stands are included. These restrictions resulted in a data matrix (see Appendix) consisting of 28 columns (= stands) and 40 rows (= species). Analyses were prepared by using ORDIFLEX (Gauch, 1977), a computer package containing programs for PCA, PO, and RA.

Results and Discussion

Figures 1 and 2 present, respectively, the distribution of stand and species positions on the first two axes. These two axes account for 14.8% and 13.7% of the total variation in the data matrix. Stand placement along axis 1 of Fig. 1 suggests that this axis reflects a moisture gradient. The stands in the lower left of Fig. 1 are streambank (SB) and ravine (R) stands while those in the lower right are stands described (Jensen et al., in press) as xeric ridges (X). Between these endpoints are found two remaining ravine stands, stands representing upland flats (U), north facing slopes (N), south facing slopes (SS), and one other xeric ridge.

The positioning of the other four stands, representing limestone bluffs (L), is at odds with earlier placement along the moisture gradient and requires some explanation. Jensen et al. (in press) felt that these stands, due primarily to their thin, porous soils, belonged at the dry end of the gradient. According to Fig. 1, these stands are near the midpoint of the presumed moisture gradient (axis 1), but are well separated (axis 2) from all other stands. In attempting to interpret the factor causing stands L1-L4 to segregate on axis 2, pH soil was suspected. However, according to the soil survey of Montgomery County, Tennessee (Lampley, et al., 1975) the soils in these stands are strongly to very strongly acid with medium water capacity; no different in this respect from the soils of stands SS1, SS2, N1, N2, and R2. However, their shallow nature means higher pH at relatively shallow subsoil depth; this factor may be operating here.

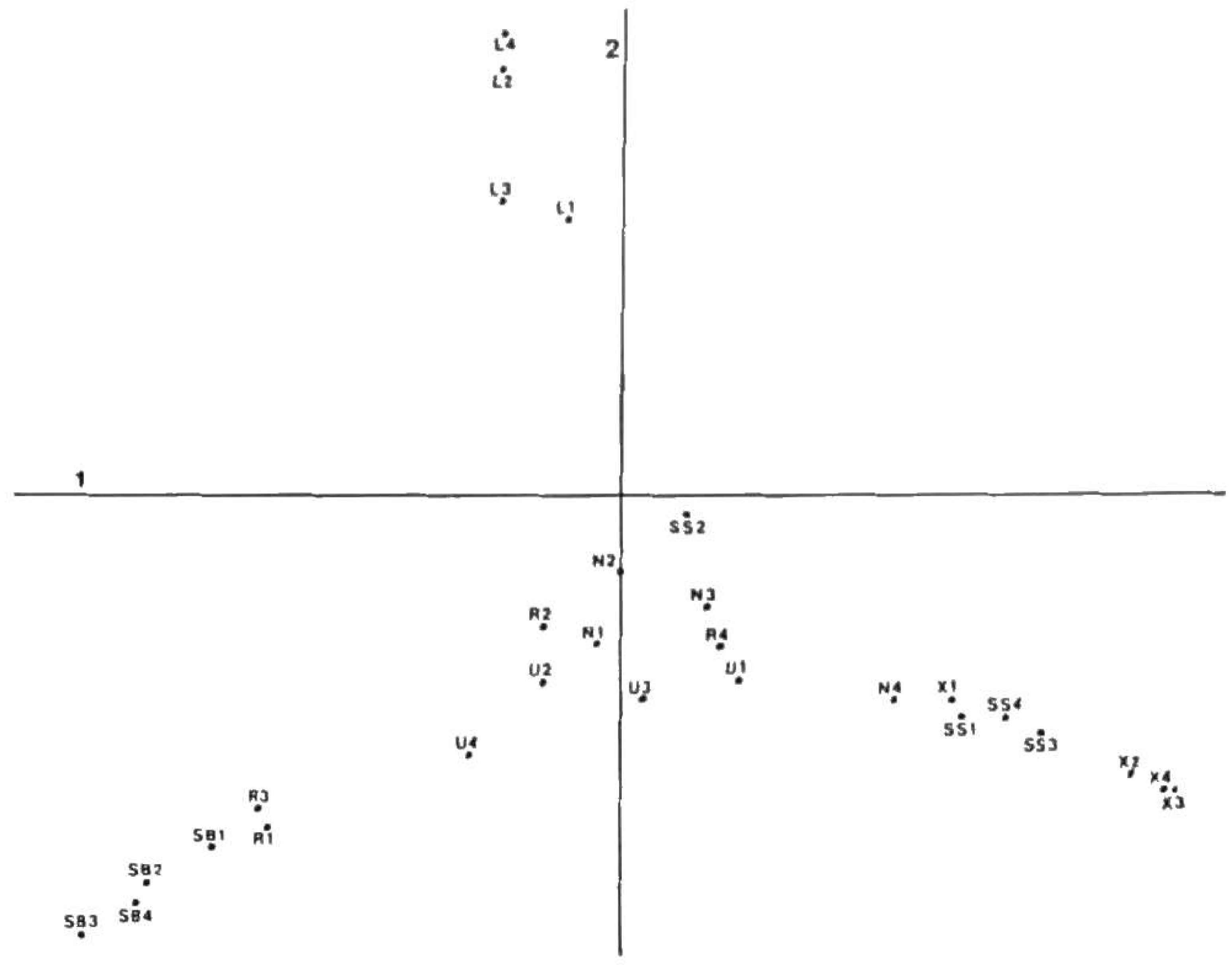

FIGURE 1: *Stand relationships as Indicated by Axis 1 and Axis 2 of a Reciprocal Averaging Analysis. Per cent total variation: axis v = 14.8%; axis 2 = 13.7% (see Appendix for explanation of symbols).*

The pattern shown in Fig. 1 suggests a comment made by Gauch et al. (1977). These authors noted that with RA, species that they termed "characteristic" i.e., with narrow distributions, ordinate above the arching distribution of points along axis one. Conversely, those species that have wide distributions, termed "companion" species, ordinate centrally. Inspection of Fig. 2 illustrates that species occurring primarily in the limestone bluff stands, which may be described as narrowly distributed, are found above the arching of points along axis one. These species include *Juniperus virginiana,* found exclusively in the limestone bluff stands, and *Fraxinus americana, Maclura pomifera, Quercus muehlenbergii,* and *Ulmus alata,* species that are very common in these stands and of limited occurence in other stands.

However, the interpretation that the placement of the four limestone bluff stands is a function of their narrowly distributed species, in the sense noted by Gauch et al. (1977), may not be correct. For example, if Fig. 1 is rotated 90° clockwise, then the "arch" has its end points in stands X2-X4 on the left and L1-L4 on the right. This results in stands SB2-SB4, R1 and R3 being above the arch. Inspection of Fig. 2 and the Appendix reveals that the species dominating the latter stands, e.g. *Acer negundo, A. saccharinum, Platanus occidentalis, Populus deltoides,* may be termed characteristic; they are found almost exclusively in these stands. The same pattern is seen if Fig. 1 is rotated 90° counterclockwise. In this case, stands X2-X4 are above the arch and these stands also have characteristic species. The implication is that axis 2 does reflect a gradient of sorts.

Again, rotate Fig. 1 90° clockwise, as above. When viewed from this perspective, a soil gradient of sorts extending from X2-X4 on the left to L1-L4 on the right can be envisioned. The soils in stands X2-X4, SS3, and SS4 are described (Lampley et al., 1975) as strongly to extremely acid with low to medium water capacity. The soils in stands SS1, SS2, N1, N2, R2, and L1-L4 are less acid with somewhat higher water capacity. Additionally, there is an increase in the limestone content of the soils from X2-X4 to L1-L4. These soil differences have not been quantified, but do suggest a trend that might account for the observed relationships. The soils that are least acid and have the highest water capacity are found in stands R1 (medium acid, medium water) and SB1-SB3 (low acid, high water). This suggests that axis two may be a pH or soil fertility gradient.

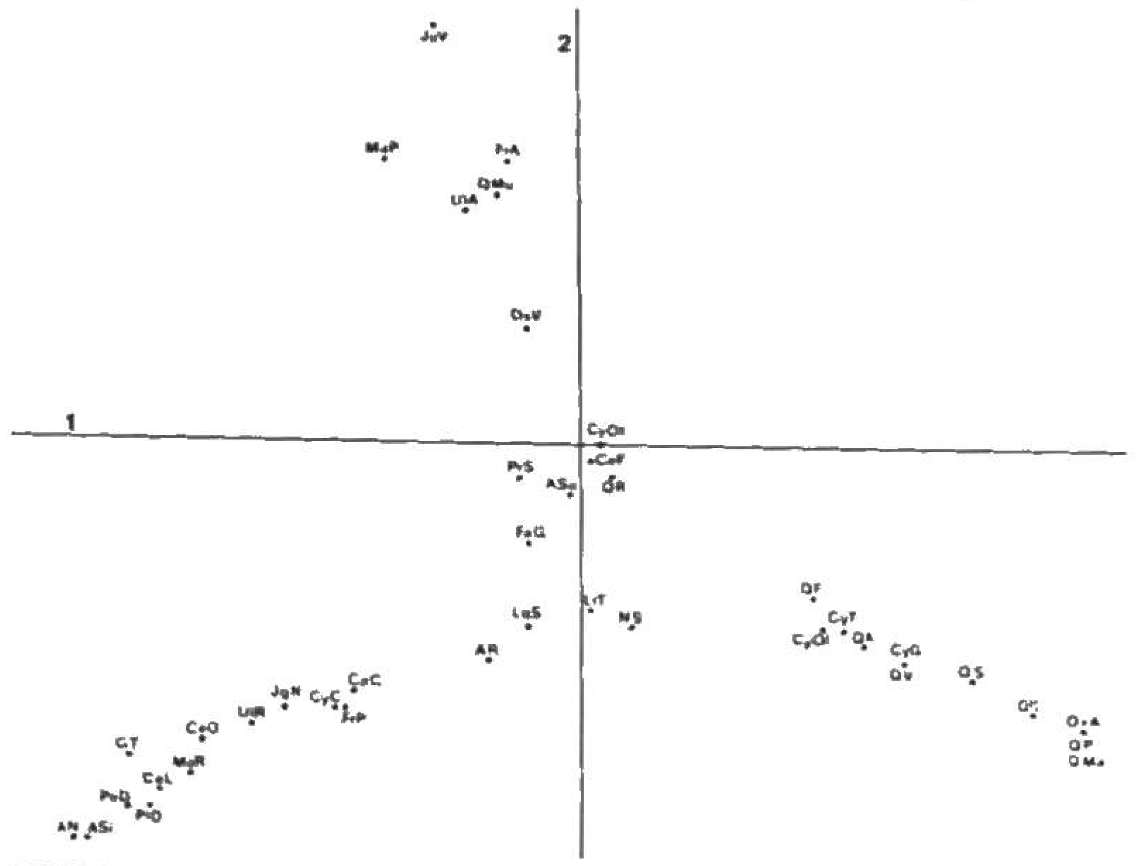

FIGURE 2: *Species Relationships as Indicated by Axis 1 and Axis 2 of a Reciprocal Averaging Analysis. Per cent total variation: axis 1 = 14.8%; axis 2 = 13.7% (see Appendix for explanation of symbols).*

As noted by Whittaker (1967) and Hill (1973), the interpretation of such indirect ordinations as presented here is often difficult. The gradients that determine the species distributions (which in turn dictate stand relationships) are not obvious for the data analyzed here except that axis 1 suggests a definite moisture gradient.

Other environmental factors are interacing in complex fashion to produce secondary gradients that are not as obvious. Although Hill (1973) indicates that higher order axes may be instructive, they were not attempted here in view of the difficulty of interpretation of axis two. It is gratifying, though, that these analyses support the subjectively derived gradient postulated by Jensen et al. (in press) as well as they do. Along axis 1, the gradient can be interpreted as streambanks, ravines, upland flats, north slopes, south slopes, xeric ridges. The only alteration from Jensen et al. is found in ravines and upland flats being reversed and the limestone bluffs not being the dry end of the gradient.

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APPENDIX

RELATIVE DENSITIES OF TREE SPECIES IN 28 FOREST STANDS

Species	L1[1]	L2	L3	L4	X1	X2	X3	X4	SS1	SS2
Acer negundo (AN)[2]	0	0	0	0	0	0	0	0	0	0
A. rubrum (AR)	0	0	0	0	0	0	0	0	0	0
A. saccharinum ASi)	0	0	0	0	0	0	0	0	0	0
A. saccharum (ASu)	.10	0	.02	0	.06	0	0	0	0	.40
Carpinus caroliniana (CpC)	0	0	0	0	0	0	0	0	0	0
Carya cordiformis (CyC)	0	0	0	0	0	0	0	0	0	0
C. glabra (CyG)	0	0	0	0	.10	.20	.08	.10	.08	.06
C. ovalis (CyOl)	0	0	0	0	0	0	0	0	0	.02
C. ovata (CyOt)	.10	0	0	0	.02	0	0	0	0	.12
C. tomentosa (CyT)	0	0	0	0	.16	0	0	0	.22	.02
Celtis laevigata (CeL)	0	0	0	0	0	0	0	0	0	0
C. occidentalis (CeO)	0	.02	0	0	0	0	0	0	0	0
Cornus florida (CoF)	0	.06	.02	0	.02	0	0	0	.02	.02
Fagus grandifolia (FaG)	0	0	0	0	0	0	0	0	0	.02
Fraxinus americana (FrA)	.38	0	.06	.08	0	0	0	0	0	.02
F. pennsylvanica (FrP)	0	0	0	0	0	0	0	0	0	0
Gleditsia triacanthos (GT)	0	0	.02	0	0	0	0	0	0	0
Juglans nigra (JgN)	0	0	0	0	0	0	0	0	0	.02
Juniperus virginiana (JuV)	.12	.62	.38	.68	0	0	0	0	0	0
Liquidambar styraciflua (LqS)	0	.02	0	0	0	0	0	0	0	0
Liriodendron tulipifera (LrT)	0	0	0	0	0	0	0	0	0	0
Maclura pomifera (MaP)	0	.02	.06	.04	0	0	0	0	0	0
Morus rubra (MoR)	0	0	0	0	0	0	0	0	0	0
Nyssa sylvatica (NS)	0	0	0	0	.12	0	.02	.02	.10	.02
Ostrya virginiana (OsV)	.06	0	.02	.04	0	0	0	0	0	.04
Oxydendrum arboreum (OxA)	0	0	0	0	0	.04	.14	.04	0	0
Platanus occidentalis (PlO)	0	0	0	0	0	0	0	0	0	0
Populus deltoides (PoD)	0	0	0	0	0	0	0	0	0	0
Prunus serotina (PrS)	0	0	.12	0	0	0	0	0	0	0
Quercus alba (QA)	0	0	.02	0	.28	.10	.06	.20	.28	.08
Q. coccinea (QC)	0	0	0	0	.04	.14	0	.06	0	0
Q. falcata v. falcata (QF)	0	.02	0	0	0	0	0	0	0	0
Q. marilandica (QMa)	0	0	0	0	0	.08	.18	.02	0	0
Q. muehlenbergii (QMu)	.14	0	.10	.12	0	0	0	0	0	.08
Q. prinus (QP)	0	0	0	0	0	.14	.38	.36	0	0
Q. rubra (QR)	.08	0	0	.04	0	0	.02	0	0	.02
Q. stellata (QS)	0	0	0	0	.20	.22	0	.16	.02	0
Q. velutina (QV)	0	0	0	0	0	.02	.08	.02	.24	0
Ulmus alata (UlA)	0	.20	.12	0	0	0	0	0	0	0
Ulmus rubra (UlR)	0	0	.06	0	0	0	0	0	0	0

SS3	SS4	N1	N2	N3	N4	R1	R2	R3	R4	U1	U2	U3	U4	SB1	SB2	SB3	SB4
0	0	0	0	0	0	0	0	.18	0	0	0	0	0	.04	.16	.52	.24
0	0	0	0	.02	0	0	0	0	.06	.02	.04	.14	.34	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	.20	.18	.16	0
0	0	.06	.16	.08	0	0	.06	.10	0	.06	0	0	0	0	0	0	0
0	0	.02	0	0	0	.12	.04	0	0	0	.06	0	.04	0	0	0	0
0	0	.06	0	.02	0	.04	0	.02	.08	0	0	0	0	.18	0	0	.02
.02	.02	.02	.04	.02	0	0	0	0	0	.12	0	0	0	0	0	0	0
0	.20	0	0	0	.32	0	0	0	.14	0	0	0	0	0	0	0	0
0	0	0	0	.04	0	0	.06	0	.02	.04	0	0	0	0	0	0	0
.04	.04	0	0	.08	0	0	.02	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	.02	.02	.06	0	0	0	0	0	.02	0	.06	.02
0	0	0	0	0	0	0	0	.02	0	0	.02	.02	.02	.12	.08	0	.06
0	0	.12	0	0	0	0	0	0	.02	.04	0	.02	0	0	0	0	0
0	0	.12	.46	0	0	0	.30	0	0	.02	0	0	0	0	0	0	0
0	0	0	0	.02	0	0	0	0	.02	0	0	0	0	0	0	0	0
0	0	.02	.02	0	0	0	0	0	0	0	0	.02	.06	0	.04	.02	0
0	0	0	0	0	0	.02	0	0	0	0	0	0	0	0	.02	.02	.10
0	0	0	.02	.02	0	.04	.06	.02	0	0	0	0	0	0	.06	.02	.04
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	.04	0	0	0	.04	0	.26	.24	.06	.18	0	0	0	0
0	0	.16	.02	.02	.18	.06	.24	0	.14	0	0	.04	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	.02	0	0
0	0	0	0	0	0	.02	0	0	0	0	.02	0	0	0	.04	0	.02
0	0	.10	.04	.12	0	0	0	0	.06	.24	.32	.68	.04	0	0	0	0
0	0	0	.12	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	.16	.02	.10	0	0	0	0	.06	0	.08	.06	.34
0	0	0	0	0	0	.04	0	.02	0	0	0	0	0	.04	.12	0	0
0	0	0	0	.16	0	0	.02	.04	.08	0	0	0	0	0	0	0	.02

SS3	SS4	N1	N2	N3	N4	R1	R2	R3	R4	U1	U2	U3	U4	SB1	SB2	SB3	SB4
.22	.28	.02	.04	.10	.20	0	0	0	.22	.04	0	0	0	0	0	0	0
.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
.08	.04	0	0	.02	.02	0	0	0	0	0	0	0	.02	0	0	0	0
.02	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	.02	0	0	0	0	.04	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	.02	.02	.02	.06	.06	0	0	0	.08	0	0	0	0	.04	0	0	0
.22	.18	0	0	.02	0	0	0	0	0	0	0	0	0	0	0	0	0
.36	.20	.02	0	0	.22	0	0	0	0	.12	0	0	0	0	0	0	0
0	0	0	0	.02	0	0	0	0	.04	0	.08	0	0	0	0	0	0
0	0	.08	.02	0	0	.36	.06	.22	.02	0	.10	0	.12	.20	.12	.04	.12

[1] stand abbreviations refer to the following habitat types: L = limestone bluffs; X = xeric ridges; SS = south facing slopes; N = north facing slopes; R = ravines; U = upland flats; SB = streambanks.

[2] The species abbreviation in parentheses correspond to those used in Fig. 2.