Scaling hierarchy of factors controlling riparian vegetation patterns of the Fynbos Biome at the Western Cape, South Africa

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Introduction

The study of ecosystems has always been highly influenced by the scale at which research is conducted. Depending on the aim of the study, one can either look at an open space around an anthill, a forest stand or an entire mountain range as the ecosystem under study. Vegetation patterns result from environmental factors operating on different levels that can be ordered in a hierarchical system from small to large (O’Neill et al. 1986; Allen & Hoekstra 1992). When studying riparian vegetation, i.e. the vegetation that is influenced by the fluctuating water levels of a river, it is necessary to consider the hierarchical scaling of environmental factors.

Davies & Day (1998) described riverine ecosystems as having four dimensions: the longitudinal axis of the river, the profile of the riverbed, the elevation of the water level, and the time scale. The dynamic character of the riparian zones creates a heterogeneous environment, offering a wide variety of ecological niches (Gregory et al. 1991). The disturbances that occur at different scales within the riparian ecosystem and the catchment make riparian ecosystems a good showcase for the hierarchical patch dynamics theory of Wu & Loucks (1996), which aims at describing patterns that result from disturbances and process rates at different organizational levels.

We document the importance of the species-diversity patterns on different organizational levels by looking at riparian systems embedded within the diverse vegetation of the Fynbos Biome in the Western Cape of South Africa. The Fynbos Biome is a region of extraordinary species and vegetation diversity (Kruger & Taylor 1979; Cowling et al. 1992). The complex vegetation patterns that are a result of the superimposed ecosystems of fynbos and riparian vegetation will be revealed by an approach that conceptually resembles the hierarchical scaling used by Van Colleter al. (2000), by recognizing different scales beforehand and collecting data on each of them, and methodologically makes use of variation partitioning (Borcard et al. 1992; Økland & Elertsen 1994; Økland 2004).
Mountain streams show a high habitat diversity; pools and riffles, cascades, waterfalls, large boulders and fallen logs together create a complicated mosaic of micro-habitats. In general, the channels in the upper reaches are much narrower than in the lower reaches, so the variation in the lateral direction (from the water’s edge up the bank) can be described in a relatively simple way. In the longitudinal direction (from the source to the foothills) the variation may seem more dramatic as the river finds its way through gorges, waterfalls and rapids. Vegetation in the riparian zones of the Western Cape mountains is subject to very complex environmental patterns resulting from a plethora of ecological and historic-biogeographical gradients. To unravel these patterns we take a closer look at each of these gradients and the levels on which they are presumed to operate. At each of these levels a direct gradient analysis can be conducted (Whittaker 1967).

1. At the first hierarchical level we assume a climatic gradient across the mountain ranges to control the patterns. The Western Cape contains very sharp climatic gradients spanning mesic climates of the Atlantic coast to arid climates in the interior (Campbell 1983; Deacon et al. 1992). The amount and seasonality of precipitation often change sharply across a single mountain range. As a result, species turnover across mountain ranges is extremely high (Kruger & Taylor 1979; Cowling et al. 1992). Adjacent river catchments may experience completely different climatic regimes. This gradient is referred to as the geographical gradient and has been described in detail for the Fynbos Biome by Campbell (1983), Deacon et al. (1992) and Rebelo et al. (2006).

2. At the second hierarchical level we investigate the influence of the gradient along the longitudinal axis of the rivers. Along this axis, the change in altitude is accompanied by changes in habitat composition at a particular river reach. Altitude has a major impact on several climatic characteristics and the resulting zonal vegetation (Campbell 1983). In general, precipitation will be higher and temperatures lower at higher altitudes. Because the steepness of the river decreases downstream, the river reaches at lower altitudes will have less erosive power than the higher river reaches. This gradient is referred to as the longitudinal gradient and has been described by Minshall et al. (1983) and Davies & Day (1998).

3. At the third hierarchical level one can detect a clear gradient (especially in the floodplains) across the riverbed, represented by zones of different inundation frequency. Close to the river, inundation frequency is high, erosive power is large, and stream power is low. Further away from the river, inundation is less frequent, deposition is more common, and stream power can be very high. The gradient described here is referred to as the lateral gradient and has been described by Kopecký (1969), Menges & Waller (1983), Gregory et al. (1991) and Bendix (1999).

These gradients are partially nested environmental gradients. Vegetation has been described in five different catchments, which are subject to a climatic gradient. Within each catchment there is an altitudinal gradient and at every site along the river there is a gradient in inundation frequency (see Fig. 1).

The aim of this study is to test the validity of the conceptual model involving three nested environmental gradients as described above. In particular we attempt to provide answers to the following question: How does each of these gradients contribute to the variation in vegetation found in the riparian zones in the study area?

Material & Methods

Study area

The study was carried out in the Hottentots Holland Mountains (HHM), situated east of Cape Town (Western Cape Province of South Africa) between 33°53' and 34°12' S and 18°52' and 19°11' E (Fig. 1). Phytogeographically this area is part of the Cape Floristic Region and is classified as the Fynbos Biome (Rebelo et al. 2006), mostly consisting of mediterranean-type evergreen shrublands. The HHM forms, together with the neighbouring Kogelberg the core area of the Fynbos Biome (Cowling et al. 1992). The species and habitat diversity in the area are very high (Campbell 1983; Deacon et al. 1992) which makes this area attractive for gradient analysis.

The HHM enjoy a mediterranean-type climate characterized by hot/dry summers and mild/wet winters. There are considerable climatic differences between the high altitudes and the low-reach river valleys, with high altitudes much richer in precipitation. Precipitation patterns in the mountains are very complex; most precipitation consists of rainfall (Wicht et al. 1969). Most mountains in the Western Cape have an annual precipitation between 1000 and 2000 mm, but on the highest peaks it can exceed 3000 mm. Temperatures in the valleys range from freezing point up to 39°C. Temperatures at higher altitudes are lower but only few records are available (Fuggle & Ashton 1979).

The geology of the HHM is dominated by strongly quartzitic sandstones of the Table Mountain Group (Ordovician). Within the sandstone, there are shale bands imbedded (De Villiers et al. 1964). On the western slopes of the mountain range much older (Archaean) Cape Granite Suite igneous rocks cover the valley bottoms.
Shales of the Malmesbury Group (about 700 Myr old) are found in a small area on the southwestern slopes of the Stellenbosch Mountain in the Eerste River catchment (Anon. 1980).

Most soils developing on sandstone and quartzite are very shallow, sandy and nutrient-poor. Those over shales and granite are nutrient richer and show higher content of fine particles. Podzolization is the most important soil-forming process (Fry 1987; Deacon et al. 1992). The substrates in riparian habitats mainly consist of assorted rocky skeleton showing a broad spectrum of particle sizes. Most of the fine (loamy and clay) particles are washed away along upper and middle reaches of the rivers (Anon. 1991).

Five major rivers (Berg, Riviersonderend, Palmiet, Eerste, Lourens) originate here and possess catchments in this region. The geomorphology of the terrain is quite variable, with particularly steep gorges in the Berg river and Lourens river catchment and more gently sloping terrain in the Palmiet river catchment.

Methods of data collection

In the study area 137 vegetation samples or relevés were collected during the spring and summer seasons of 1998 and 1999 according to the Braun-Blanquet field sampling protocol (Westhoff & van der Maarel 1978). These relevés were collected in transects laid out on the riverbanks across the rivers within the area. In total 73 transects were laid out in 19 tributaries of the five catchments. Transects were 10 m wide and stretched across the width of the respective riparian zone. They consisted of several homogenous plots, each representing a single riparian zone. Many transects only contained a single relevé or they had only a single relevé after data-deficient relevés (for example rocky wetlands without soil) were removed. The plot sizes of individual relevés were not always similar, because riparian zones can have different widths at different locations.

For each transect the environmental variables slope, aspect and geology were recorded. Soil variables and rockiness were recorded in every relevé within a transect. For every soil sample, electrical resistance and pH were recorded; organic matter content was determined using the Walkley-Black method (Walkley 1935). Particle size distribution was determined by sieving (sieve sizes 2 mm, 250 µm, 106 µm and 63 µm) to separate Coarse sand, Medium sand, Fine sand and Silt, respectively. Soil types were determined by extrapolation from the available data on the character of the topsoil layer and according to Fry (1987). Distance and elevation from the water edge and their product were recorded for every riparian zone. These variables can be considered as a proxy for inundation frequency and stream power, since the direct measurements of flood regime are very costly and labour-intensive (Bendix 1999; Sieben 2003).

Other environmental data, such as altitude and the steepness of the river reach, were obtained from orthophotographic maps (scale 1:10 000). Precipitation data were obtained from several weather stations located near and/or in the within the study area (Wicht et al. 1969; Computing Centre for Water Research, Pietermaritzburg, now part of the School of Bioresources, Engineering and Environmental Hydrology of the University of KwaZulu-Natal, unpubl. data). Table 1 features the list of the environmental variables scored for every relevé.

Data transformation

All of the precipitation data were transformed into a grid using the model of Dent et al. (1984). The precipitation values in each grid cell represent the estimated values in the centre of the cell. This is why there is always a potential error towards the margins of a cell, because
precipitation gradients are quite steep within the grid cells (which are about one square minute). Two climatic indices were calculated: the ratio between precipitation in July and precipitation in January (Pjan_jul), and the inverse of the fraction of precipitation that falls in the four driest months, from January to March (indicated as Psummer). When these indices are plotted in a grid they show a gradient that is less steep than the original precipitation values (see Fig. 2).

Compositional variables (a group of variables that together make 100%) like particle size distribution and rock cover were log-transformed prior to numerical analysis (ter Braak & Šmilauer 1998). In addition to CCA, Partial Canonical Correspondence Analysis (pCCA) was used and is useful to determine the fractions of variation that can be explained by specific sets of variables (ter Braak 1988). In order to test the conceptual model of three hierarchical levels, the variation was partitioned according to the algorithm of Økland (2003).

The fraction of the Total Variation Explained (TVE) that is explained by each of the variable sets A, B and C has been calculated in order to test the validity of the conceptual model of three hierarchical levels. The conceptual model is valid if the variation explained exclusively by a single variable set is large in comparison to the overlap with other sets. In this way, it is also possible to determine the relative importance of each environmental gradient.

### Table 1. Environmental variables investigated in each vegetation sample. Gradients indicated: (1) Geographical gradient, (2) Longitudinal gradient and (3) Lateral gradient. Ratio-scale variables indicated by (R), Nominal Variables by (N). Compositional data consists of several Ratio-scale variables that together make 100%. These are the various fractions of soil particle sizes and the cover estimates for rock classes. The abbreviations of the nominal data classes are underlined and these abbreviations have also been used later on in the ordination analyses. CCWR = Computing Centre for Water Research.

<table>
<thead>
<tr>
<th>Level</th>
<th>Variable</th>
<th>Type</th>
<th>Measurement</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Psummer</td>
<td>R</td>
<td>Inverse of the fraction of the annual precipitation that falls in the four driest months: December, January, February and March (Source: CCWR)</td>
</tr>
<tr>
<td>1</td>
<td>Pjan_jul</td>
<td>R</td>
<td>Ratio between the July precipitation and the January precipitation in (Source: CCWR)</td>
</tr>
<tr>
<td>1</td>
<td>Slope</td>
<td>R</td>
<td>Angle measured with slope meter in degrees</td>
</tr>
<tr>
<td>1</td>
<td>Geology</td>
<td>N</td>
<td>Geological Map (South African Committee for Stratigraphy, 1:250 000) and field observation. Classes: Sandstone (San), Tillite (Til), Shale (Sha), Granite (Gra) and Alluvial (All)</td>
</tr>
<tr>
<td>1</td>
<td>Soil type</td>
<td>N</td>
<td>Determined from literature (Fry 1987; Anon. 1991) and observations on top soil layer and soil depth. Classes: Mispah, Maqua, Oakleaf, Fernwood and Glenrosa</td>
</tr>
<tr>
<td>2</td>
<td>Altitude</td>
<td>R</td>
<td>Read from orthophotographic maps (scale 1:10 000)</td>
</tr>
<tr>
<td>2</td>
<td>MAP</td>
<td>R</td>
<td>Mean Annual Precipitation (Source: CCWR)</td>
</tr>
<tr>
<td>2</td>
<td>Pjan</td>
<td>R</td>
<td>Precipitation in January (Source: CCWR)</td>
</tr>
<tr>
<td>2</td>
<td>Pjuly</td>
<td>R</td>
<td>Precipitation in July (Source: CCWR)</td>
</tr>
<tr>
<td>2</td>
<td>GRAD1</td>
<td>R</td>
<td>Estimate of the height difference within 10 m of river stretch</td>
</tr>
<tr>
<td>2</td>
<td>GRAD2</td>
<td>R</td>
<td>Tangent of the gradient of a longer river stretch read from an orthophotographic map (1:10 000)</td>
</tr>
<tr>
<td>3</td>
<td>Distance</td>
<td>R</td>
<td>Distance of the upper edge of the vegetation zone from the river</td>
</tr>
<tr>
<td>3</td>
<td>Elev</td>
<td>R</td>
<td>Elevation of the upper edge of the vegetation above the water level</td>
</tr>
<tr>
<td>3</td>
<td>Distelev</td>
<td>R</td>
<td>Distance and Elevation multiplied</td>
</tr>
<tr>
<td>3</td>
<td>Resis</td>
<td>R</td>
<td>Resistance to an electrical current measured with YSI model 3200 in Ohms</td>
</tr>
<tr>
<td>3</td>
<td>PH</td>
<td>R</td>
<td>pH-meter: ORION 420A, measured in H₂O</td>
</tr>
<tr>
<td>3</td>
<td>Organic</td>
<td>R</td>
<td>Percentage calculated by titration of Walkley-Black method</td>
</tr>
<tr>
<td>3</td>
<td>Gravel</td>
<td>R</td>
<td>Percentage of coarse material in soil sample (from 2 mm to 2 cm)</td>
</tr>
<tr>
<td>3</td>
<td>Soildept</td>
<td>R</td>
<td>Depth of soil estimated in cm</td>
</tr>
<tr>
<td>3</td>
<td>CSAND</td>
<td>R</td>
<td>Fraction of soil particles in the category Coarse Sand (250 μm - 2 mm)</td>
</tr>
<tr>
<td>3</td>
<td>MSAND</td>
<td>R</td>
<td>Fraction of soil particles in the category Medium Sand (106 μm - 250 μm)</td>
</tr>
<tr>
<td>3</td>
<td>FSAND</td>
<td>R</td>
<td>Fraction of soil particles in the category Fine Sand (63 μm - 106 μm)</td>
</tr>
<tr>
<td>3</td>
<td>SILT</td>
<td>R</td>
<td>Fraction of soil particles in the category Silt (&lt; 63 μm)</td>
</tr>
<tr>
<td>3</td>
<td>Bedrock</td>
<td>R</td>
<td>Estimate of cover by bedrock</td>
</tr>
<tr>
<td>3</td>
<td>Boulders</td>
<td>R</td>
<td>Estimate of cover by boulders (&gt; 24 cm)</td>
</tr>
<tr>
<td>3</td>
<td>LG_COBB</td>
<td>R</td>
<td>Estimate of cover by large cobbles (10 - 24 cm)</td>
</tr>
<tr>
<td>3</td>
<td>SM_COBB</td>
<td>R</td>
<td>Estimate of cover by small cobbles (5 - 10 cm)</td>
</tr>
<tr>
<td>3</td>
<td>PEBB</td>
<td>R</td>
<td>Estimate of cover by pebbles (2 - 5 cm)</td>
</tr>
<tr>
<td>3</td>
<td>Slope2</td>
<td>R</td>
<td>Slope derived from the width and elevation difference for every vegetation zone</td>
</tr>
</tbody>
</table>

### Data analysis

Canonical Correspondence Analysis (CCA) was used to analyze the vegetation data. This is a multivariate technique that is very suitable to relate vegetation data to the environment (ter Braak 1987; Legendre & Legendre 1998). In addition to CCA, Partial Canonical Correspondence Analysis (pCCA) was used and is useful to determine the fractions of variation that can be explained by specific sets of variables (ter Braak 1988). In order to test the conceptual model of three hierarchical levels, the variation was partitioned according to the algorithm of Økland (2003).
by comparing the fractions of VTE explained by each variable set. The variation explained by one of the variable sets will be depicted as $V(A)$, $V(B)$ and $V(C)$. Variation that is shared by two sets cannot be calculated directly by CCA or pCCA, but it is easily calculated from the other components because eigenvalues are additive. The outcome of a pCCA using $A$ as explanatory variables and both $B$ and $C$ as covariables will determine the value of $V(A \mid B \cap C)$, which is the variation explained by the geographical gradient, not included in the variation explained by the two other gradients. Shared variation can be calculated easily by the formula that is supplied by Økland (2003):

$$V(X_1 \mid X_2) = V(X_1) - V(X_1 \cap X_2) = V(X_2) - V(X_2 \cap X_1)$$

$$= V(X_1) + V(X_2) - V(X_1 \cup X_2) \quad (1)$$

In the case of three sets of variables, pCCA has to be conducted six times to calculate $V(A \cap B \cup C)$, $V(B \cap A \cup C)$, $V(C \cap A \cup B)$, $V(A \cap B \cap C)$, $V(A \cap C)$ and $V(B \cap C)$ respectively. With three sets of variables, there are $2^3 - 1 = 7$ components of variation, namely $V(A \cap B \cup C)$, $V(B \cap A \cup C)$, $V(C \cap A \cup B)$, $V(A \cap B \cap C)$, $V(A \cap B)$, $V(A \cap C)$, $V(B \cap C)$ and $V(A \cap B \cap C)$. All these components of variation can be calculated easily by adding and subtracting using the formula above. All ordinations have been carried out using Canoco 4.5 (ter Braak & Šmilauer 2002).

CCA without data partitioning was carried out for each hierarchical level to show importance of explanatory variables on that level.

For the purpose of illustration in ordination diagrams ten broad clusters of vegetation types were identified, based on a subjective vegetation classification. The cluster with the tallest vegetation is Afrotemperate Forest, followed by Riparian Scrub. There are three clusters of typical fynbos, namely ‘ericaceous fynbos’, ‘transitional fynbos’ and ‘asteraceous fynbos’ (following the definitions of Campbell 1986 plus an extra intermediate category). The Shale Fynbos is actually a special form of Asteraceous Fynbos on a very distinct substrate. At last, there is Wetbank vegetation comprising sparse vegetation types directly bordering the river and dominated by sedges and rushes. The Pioneer Wetbank vegetation is limited to rocky, shaded habitats. The Erosion Wetbank vegetation is found in rocky and sunny habitats. The Deposition Wetbank vegetation is found on alluvial sands downstream. A short description of vegetation growing in the different communities is given in Table 2. In this table, the range of sample sizes (resulting from the varying widths of riparian zones) for each vegetation type is indicated.

Fig. 2. Derivation of the climatic indices for rainfall seasonality. Note that the gradients in the graphs below are less sharp than those of Rjuly.
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Results

The results of the CCA ordinations without partitioning of data are displayed in Figs. 3, 4 and 5 for the geographical, longitudinal and lateral gradients, respectively. Each of them displays the variation on the first two canonical axes and the variation for the respective explanatory variable set only. The entire data set (137 relevés sharing 157 species) was used for all hierarchical levels.

Variation along the geographical gradient

The results of the CCA with variables of the first hierarchical level are shown in Fig. 4. The variation on the first axis is mainly explained by the nominal variables, especially geology. It is obvious that there is also a correlation with the climatic gradient from south to north, expressed in the variables Pjan_jul and Psummer. The topographic distribution of seasonal precipitation is shown in Fig. 2. The northern part of the study area has a more pronounced winter rainfall aspect than the southern part. This means that water stress in summer is more likely in the northern areas. The community that stands out mostly in this diagram is the Shale Fynbos, which is only found in the extreme western part of the study area. There is not really a clear distinction between the different types of Wetbanks in the diagram, but the different types of Fynbos, Forest and Riparian Scrub can be well differentiated within the diagram.

Variation along the longitudinal gradient

The variation within the catchment is determined strongly by altitude. The ordination diagram for this level is shown in Fig. 4. The river gradient and altitude combined can explain the distribution of Wetbank vegetation with Deposition Wetbanks occurring at low altitudes and with less steep gradients and Pioneer Wetbanks mostly at the lower altitudes under Forest. It is also clear that Forests, Riparian Scrub and Asteraceous Fynbos tend to occur at lower altitudes and at steeper gradients. Altitude explains a higher fraction of the variation on the first axis and this is probably because the precipitation data were not very precise and because altitude also has an impact on other environmental factors, like temperature, hours of sunshine and the occurrence of mist. There is, however, no direct data of these factors available.

Table 2. Broad vegetation clusters in this study, including the average plot sizes used in this study.

<table>
<thead>
<tr>
<th>Vegetation type</th>
<th>Dominant species</th>
<th>Average plot size and range (in m$^2$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1a Pioneer Wetbanks</td>
<td>mosses, ferns</td>
<td>21.2 (10 - 40) ($n = 8$)</td>
</tr>
<tr>
<td>1b Erosion Wetbanks</td>
<td>$Prionium$ serratum, Drosera spp.</td>
<td>21.4 (5 - 70) ($n = 20$)</td>
</tr>
<tr>
<td>1c Deposition Wetbanks</td>
<td>Juncus spp., Isolepis prolifera</td>
<td>30.4 (10 - 60) ($n = 5$)</td>
</tr>
<tr>
<td>2 Ericaceous Fynbos</td>
<td>Restio spp., Erica spp.</td>
<td>26.7 (10 - 80) ($n = 22$)</td>
</tr>
<tr>
<td>3 Transitional Fynbos</td>
<td>Erica spp., Cannomois, Brabejum</td>
<td>27.5 (10 - 45) ($n = 11$)</td>
</tr>
<tr>
<td>4 Asteraceous Fynbos</td>
<td>Myrsine africana, Helichrysum spp.</td>
<td>39.5 (10 - 90) ($n = 18$)</td>
</tr>
<tr>
<td>5 Shale Shrublands</td>
<td>Cliffordia odorata, Persium aquilinum</td>
<td>33.1 (15 - 100) ($n = 10$)</td>
</tr>
<tr>
<td>6 Afromontane Forest</td>
<td>Cenonia capensis, Maytenus acuminate</td>
<td>51.9 (15 - 100) ($n = 29$)</td>
</tr>
<tr>
<td>7 Riparian Scrub</td>
<td>Brachylaena, Metrosideros</td>
<td>23.4 (13 - 60) ($n = 14$)</td>
</tr>
</tbody>
</table>

Fig. 3. CCA ordination diagram of the relevés on the first hierarchical scale (137 relevés, 157 species). The nominal variables are illustrated floating in the diagram in which the cluster centroid of each class is shown.
Variation along the lateral gradient

The variation on the third hierarchical gradient is illustrated in Fig. 5. Explanatory variables at this level have the same effect on vegetation throughout the entire area, although the vegetation types furthest from the river can differ greatly from catchment to catchment. Forest and Riparian Scrub is less common in the Riviersonderend/Palmiet River catchment and well-developed Wetbank vegetation types are less common in the Eerste/Berg River catchment. The most important explanatory variables on the first axis are ELEV and DISTELEV, which provide an estimate of a measure of inundation frequency. The pH and Organic matter are also strongly explanatory on the first axis, with higher organic matter contents further away from the river. The water in the river is quite acidic, and this explains why Wetanks have mostly a low pH. In this diagram, the distinction between Wetbanks and other vegetation becomes much more clear. Other vegetation types found in the left part of the diagram are Ericaceous Fynbos (which tends to grow closer to the river at higher altitudes) and Riparian Scrub, which often replaces Wetbank vegetation in very turbulent boulder-strewn river reaches. The most important explanatory variable on the second axis is Boulders. Places with many boulders often have Forest or Riparian Scrub and the Wetbank is often a Pioneer Wetbank. The combination of inundation frequency and stream power would be the best measure to describe the lateral gradient.

Variation partitioning

The total inertia for the complete data-set is 9.728. The sum of all canonical eigenvalues in a CCA including all environmental and spatial variables is 4.193. This means that 43.1% of the total variance is explained by the explanatory variables that are available. The rest is unexplained variation.

Of the variation explained by the environmental variables, 51.7% is explained by the first hierarchical level (most important variables: Psummer, Pjan_jul, Slope, Geology), 31.1% by the second hierarchical level (most important variables: Altitude, Pjan) and 47.9% is explained by the third hierarchical level (most important variables: ELEV and DISTELEV).
variables: Distielv, Boulders, Silt, Organic, Csand). The sum of these fractions is higher than 100% which suggests that there is considerable overlap between the different hierarchical levels. The fraction of the variation that is explained by all three hierarchical levels is 8.4%, so the conceptual model of splitting the variation into three hierarchical levels applies to 91.6% of the variation.

Discussion

Variation partitioning is facilitating the gathering of information about the components of variation within vegetation patterns, even though the major part of the variation is stochastic and cannot be explained. Økland (1996) suggests that the terms explained and unexplained variation should rather be abandoned and focus should be directed on the proportions of the explained variation by different sets of environmental variables. Borcard et al. (1992) applied variation partitioning mainly to separate the spatial component from the rest of the variation, but it can also be useful when looking at influences operating at different levels (Økland & Eilertsen 1994). Both of these cases are relatively simple because they both used only two sets of variables whereas Qian et al. (2003) used data partitioning for a higher number of variable sets.

The geographical gradient operating at the first hierarchical level explains most variation and is the most important gradient in this study. This is probably because of the extremely high species turnover in the Fynbos Biome. There have been several studies that attempted to quantify the beta and gamma diversity in the zonal vegetation of the Fynbos Biome and found both to be very high (Cowling 1990; Simmons & Cowling 1996; Kruger & Taylor 1979). The results of this study show that species turnover is equally high for azonal vegetation like riparian vegetation. It is likely that the importance of the geographical gradient is correlated to the overall species turnover across landscapes and within the Fynbos Biome this is high in general but particularly in the southwestern Cape (Cowling & Holmes 1992).

The lateral gradient is the next most important gradient. This gradient accounts for a high proportion of the variation because the environmental stresses next to a river are very specific (Gregory et al. 1991; Bendix 1999). It seems, however, that this variation is more obvious in the lower reaches of the rivers, where riparian zonation is more distinct. In the highest reaches the riparian zones are often so much intertwined that they cannot be distinguished from each other. Also, discharges during floods are often not very high in these reaches, so that different flood levels do not result in broad vegetation zones. Mountain streams return to base levels more rapidly after a flood than rivers in the lowlands, hence inundation periods are less determinative on the vegetation.

The longitudinal gradient, operating at the second hierarchical level, is the least important and shows a large overlap with the geographical gradient, because, within a catchment, the variation in climate can still be quite large. The other variables operating on the longitudinal gradient have a small influence. The differences within the mountain reaches do not have a direct influence on the vegetation. The only aspect that is important about the reach is the degree of erosion and deposition and this influence is best visible in the vegetation zones closest to the river (Gregory et al. 1991). In this study, only the higher stretches of river were studied. If the lower reaches would be included in a study of composite gradients, the role of the longitudinal gradient would be more important. This is especially true in the Western Cape, where the geology often changes from sandstone and granite to shales and calcareous sands in the lower reaches of the rivers (Campbell 1983).

The fact that there is relatively little overlap in the explained variation by each of the three gradients, shows that the hierarchical scaling approach is valid and that variation partitioning is a good method to describe it. The weakness of the method is that the different variables operating at the different levels have to be defined prior to the analysis. In general this is easy, but for some variables the relation to the spatial level is unclear or some variables operate at different levels (Slope, Organic matter, pH, Resistance). The results of this study however show that these variables in general do not explain a large part of the variation, with the notable exceptions of organic matter and pH. This will also reflect in the overlap between different levels as illustrated in Fig. 6.

The approach used in this study is in sharp contrast with the approach of riparian vegetation by Van Coller et al. (2000), who defined more nominal ‘patchy’ variables and set up a hierarchy for these nominal variables. This main difference lies in the simple fact that Van Coller et al. (2000) studied the lower reaches of the Sabie River while this study aims at describing the mountain stream habitat. The morphological units as they are defined by Van Coller et al. (2000) are present in mountain streams but on a much smaller scale and are mostly not vegetated at all, because of the poor substrate.

A combination of hierarchical scaling and variation partitioning according to these scales is a suitable method to describe a complex ecosystem with nested gradients (Qian et al. 2003). Riverine ecosystems fall into this category especially in the mountain reaches where there are steep ecological gradients (Davies & Day 1998). In the lower reaches the geographical and longitudinal gradients are in general less steep, except in the case of very large stretches of river, but lateral gradients can be more complex.
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