DERIVING CONSERVATION TARGETS FOR RIVERS

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by

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EXECUTIVE SUMMARY

Introduction

Conservation planning and rivers

Freshwater ecosystems are the most threatened ecosystems globally experiencing the fastest loss of biodiversity and the greatest number of species extinctions. The last national appraisal of South African freshwater ecosystems estimates that over 80% of South African river ecosystems are threatened. The intimacy between catchment condition and river health is one reason why freshwater systems are amongst the most threatened systems globally.

One tool available to conservationists to staunch the current rate of loss to freshwater biodiversity and ecosystems is systematic conservation planning, which provides a structured approach in identifying biologically significant areas for conservation action. A necessary component of conservation planning is to set targets for how much of each biodiversity feature (i.e. element of biodiversity which can be quantified and spatially represented) needs to be protected, and additionally for rivers, to maintain connection between different biodiversity patches.

Target-setting follows either participatory or empirical approaches. Participatory approaches are typically based on expert opinion, and done on a case-by-case basis. Empirical approaches use statistical relationships, and can be applied nationally using more automated approaches. This means that the latter approach is more appropriate for national conservation planning initiatives. Because rivers are characterized by length and not by area, and because species persistence at one site is very often a function of upstream and downstream ecological processes, current statistical methods for setting river targets are not suitable. The current South African approach in freshwater planning makes use of a 20% target value, while a target value of 17% for inland water areas was recently proposed at the 10th meeting of the Conference of the Parties to the Convention on Biological Diversity. This approach is inadequate because it assumes that all rivers have similar diversity patterns down their lengths and between systems, which is not the case.

Setting river targets

The focus of conservation is moving from single-species conservation to communities of species and how these change in space. Consequently, targets should be based on established measures of species diversity and river ecology theory: The river continuum concept, which makes predictions of species diversity patterns with downstream distance based on ecosystem processes; and the hierarchical understanding of river systems. Much is already known about species diversity and rivers too: at the habitat scale, aquatic macroinvertebrates show strong associations with different hydraulic biotopes and geomorphological types. At a larger scale, there have been a number of studies which show that aquatic fauna correlate strongly with different longitudinal river zones and between river basins based on changes in geology. Interpreting patterns of species diversity can, however, be confounded by the effects of organic pollution and changes in flow.

In this conceptual framework, these measures provide a powerful approach for setting species targets, because a combination of these indices incorporates scale issues, which are critical to understanding river systems. The location of highest alpha-diversity, as related to the river continuum concept, and species turnover along a river's longitudinal axis (beta-diversity), determine where and how much of a river should be targeted to conserve maximum species diversity. Between-river diversity (gamma-diversity) determines how many river systems should be conserved in each ecoregion, and this relies on a suitable river classification system. Within this approach, hypotheses of drivers of species diversity are implicitly provided (for example, disturbance and degree of connectivity between habitat components). Such an approach encompasses spatio-temporal variability and incorporates ecological processes operating at different scales along environmental gradients. At the spatial scale of this study, this approach means that:

- Species targets are set based on good biological data along a species axis.
- For alpha diversity to be maintained, upstream and downstream processes that conserve the diversity (or pattern) within a segment need to be conserved.
- Low beta diversity (i.e. low disparity between sites) implies that a relatively short section of river needs to be conserved. However, if beta diversity is large, then more of the river needs conservation measures.
- The more variable the system, the higher the beta diversity, and the longer the length needed to protect diversity, i.e. segment length depends on predictability. Conversely, more stable predictable systems are more resilient, beta diversity is lower, and the length of river requiring protection is relatively shorter.
- River systems in similar ecoregions should have lower gamma-diversity than rivers in different ecoregions.

This study proposes a new direction for setting river targets, based on established measures of species diversity. The **aim** of this research was to develop a scientific methodology, equivalent to the species-area curve used for terrestrial systems, to set conservation targets for river lengths. Achieving this provides a transparent, objective approach for setting river conservation targets, such that the target represents a value based on biodiversity patterns and processes rather than a 20% "societal agreement" value. While recognising that the 20% value has served a useful function in entrenching the concept of river targets, it was also recognised by the aquatic scientists in South Africa that this target should be revised over time, as suggested by the cross-sector policy objectives for conserving South Africa's freshwater biodiversity. This research successfully achieved this aim.

Methods

Aquatic macroinvertebrates and fish species data were assessed from nine rivers in South Africa (Western, Eastern Cape and KwaZulu-Natal provinces), using longitudinally located sites from surveyed and historical data. Data from previous studies (Great Fish, Berg, Thukela, Sabie-Sand, Mzimkhulu, Mkuze and Mvoti Rivers) were used together with data collected between November 2009 and June 2010 for the Mvoti, Mzimkhulu, Mkuze and Keurbooms Rivers. Species diversity patterns and rates of turnover were calculated and interpreted using river profiles and site characteristics (flows, water temperatures and geomorphology). Statistical analyses and a probability model were developed to predict specific sites where river conservation should focus, and river lengths upstream and downstream of these focal sites which should be conserved. Initial estimates of gamma diversity between rivers were estimated based on total numbers of species per river excluding common species.

Summary of results

Alpha diversity

Numbers of fish species showed no pattern with downstream distance for the Mkuze, Mvoti and Mzimkhulu Rivers, while a weak increase in numbers of species with downstream distance occurred in the Sabie River. Conversely, for aquatic macroinvertebrates, observed and expected alpha diversities were highest in the upper third and in the mid-order reaches of rivers sampled.

Beta diversity

Fish community patterns changed on an annual basis, with some sites changing more than others. Species turnover of aquatic macroinvertebrates was greater between different geomorphological zones, while being more similar within the same geomorphological zones. This turnover followed a sequential downstream pattern with a number of interesting trends. Firstly, the Berg River (Western Cape Province) had no species in common with the rivers in KwaZulu-Natal. Secondly, while the Berg River showed a constant rate of turnover with downstream distance, the KwaZulu-Natal Rivers showed a low turnover between the three river systems (i.e. common set of core species). Lastly, there was relatively little turnover in the upper-mid river reaches, and then more rapid turnover for the lowland sites in the case of all three rivers.

Beta diversity for aquatic macroinvertebrates generally showed exponential decay, with half-turnovers (50% change) being achieved at 20-50% downstream distance from source. Median rates of decay were *ca*. $x^{-0.3}$, although each river system exhibited its own decay function. Successive removal of rare species (“very” rare as single site, single abundance species, and rare as single site species) had the effect of decreasing the rate of turnover, while retaining the shape of the turnover signature for each river system. Beta diversities for fish showed no significant trends with downstream distance, and fish were not included in further analyses.

Average species turnover model

The three rivers showing the best statistical relationships of turnover with downstream distance (Berg, Mkuze and Mzimkhulu Rivers) were used to develop a model to estimate the probability of a downstream site not being representative (i.e. site pair similarity ≤50%) of an upstream source site as a function of downstream distance. This model predicts that on average, there is complete turnover 20% of a river's length away from a source zone.

Drivers of turnover

Environmental gradients

Analyses based on physical, water temperature and flow metrics revealed that each river assessed was unique. Based on physical habitat and water quality, sites separated out into clear, high altitude rivers versus turbid, low altitude rivers with a secondary contribution of narrow, shallow, sandy-bottomed rivers to wider, deeper and rockier rivers. Sites followed a progressive downstream trend when characterised by water temperatures, with site groups defined warm versus cool temperatures, range of seasonal temperatures, water temperature predictability and timing of maximum water temperatures (early vs. later summer). Finally, flow predictability and how often rivers dried up were key variables when classifying sites by flow regimes.

River profiles

River profiles for four rivers in KwaZulu-Natal and the Berg River all showed clear inflection points, separating the rivers into upper and lowland zones. When profiles were plotted in conjunction with measures of alpha diversity and community similarity (from uppermost site and downstream paired sites), the sites of highest diversity and zones of highest turnover coincide with the profile inflection points.

Gamma diversity

Total river species similarities between paired river systems were 40-50% for rivers in KwaZulu-Natal, and 5% on average between the Berg River in the Western Cape and the KwaZulu-Natal rivers. Gamma diversity was highest for the Mzimkhulu-Berg and Mkuze-Mzimkhulu Rivers, and lowest between the adjacent Mkuze-Mvoti Rivers.

Discussion

Alpha diversities – selection of focal river reaches

Highest species diversity occurred in mid-order streams and at an intermediate distance down a river's longitudinal axis. Within this diversity gradient, community structure is complicated by the relative contributions of rare, abundant, and very abundant species. Site-specific alpha diversity is typically made up of few very common or very rare species, with many "middling" common ("abundant") ones. Common species provide a better approximation of overall species patterns as opposed to rare ones. However, what should guide the selection of target river zones are the conservation planning goals: are the goals for rarity or maximum species number (pattern), or process (which would target the more common species which are driving system energy dynamics).

Beta diversity – how much river should be conserved?

In this study, fish were not a useful measure of determining river conservation targets, while aquatic macroinvertebrate species patterns exhibited predictable patterns of turnover with downstream distance, and are valuable in setting conservation targets. Average species turnover happened at predictable rates, and these rates could be decomposed into turnover of common ("core") species, which are further accelerated by rare species (single occurrences) and narrow range species (single site occurrences). Moreover what drives this turnover with downstream distance are break-points and river geomorphology. Sharp environmental change occurs as a result of geomorphology and topography, while gradual environmental change is driven by geography and climate. Understanding turnover patterns thus requires a spatially hierarchical understanding of river systems before targets should be set.

To understand the sharper ecotones requires knowledge of geological history and how this translates into different river profiles. The clear differences in turnover patterns between the Berg and Mzimkhulu Rivers, for example, can be partially explained through their different geological histories. The more subtle environmental changes driven by geography and climate were a combination of physical habitat, water temperature (magnitude and timing) and flows (predictability, magnitude of high flow events and perenniality).

Disruptions to the river continuum impact on the rate of turnover. The amount of natural vegetation at the catchment scale is a good predictor of river habitat integrity. The turnover pattern may thus be clouded by both catchment and river disturbance, where taxa sensitive to pollution and disturbance decline and generalist, opportunistic species increase.

Consistent with other research on South African rivers, aquatic macroinvertebrate communities in this study could be grouped into upland versus lowland assemblages, and also defined by geomorphological zones. The rate of species turnover in the rivers assessed was related to environmental gradients and breakpoints, where the more variable upper sites have more rapid turnover than reaches further downstream, i.e. upper reaches require more representative conservation zones than the reaches further downstream. Using a blanket 20% target per river type is thus probably a simplistic approach to setting targets, particularly for the upper river zones with higher species turnover.

Gamma diversity – how many basins should be targeted?

As only four rivers were assessed in this study, it was difficult to draw definite conclusions on gamma diversity. The basic gamma diversity estimates showed that to achieve riverscape-level conservation of aquatic biodiversity, it is necessary to explicitly target as many different primary catchments as possible. Under resource-limited conditions, it is more pragmatic to choose primary catchments further apart than closer together within the conservation planning region.

Key Conclusions

- A blanket 20% target for river types is not adequate;
- Upper river zones are the key sections of river length driving species patterns, and consequently upper river zones should be weighted more heavily in conservation planning than lowland zones;
- River types assume boundaries and ecotones, and the obvious ecotonal boundary to advocate more than a single generalized target value per river type is the clear distinction in turnovers between the steeper upper river zone and the less steep lowland zone;
- The 20% target should be adjusted to cater for upland and lowland targets as an initial refinement to the existing 20% targets, with at least a 20% target in lowland zones and a 40% target in the upper zones;
- Secure upper catchments in identified river systems, to maintain natural rates of species turnover in river sections where species richness is highest, and secure ecosystem services for downstream users;
- Link ecosystem services to level of river health, where catchment stakeholders decide on the level of services they would require or like (a desired state), which is then related back to ecosystem integrity by freshwater ecologists.

Recommendations for future research

- Refine differential targets for different geomorphological zones, using as a basis the hydraulic biotope heterogeneity per zone as the dialectic, as these are one of the key drivers in species turnover.
- Quantify the effects of seasonality on alpha diversity; the contributions of alpha and beta diversity to gamma diversity, and patterns of common and rare species as a function of downstream distance and biotope types.
- Refine river type classifications for upper river zones (upstream of profile inflections), and focus on selected whole systems rather than a percentage target of types.
- Refinement of a river classification of river types for South Africa. This should be hierarchical, beginning at the level of a river system (defined here as the mainstem in a secondary catchment), and sub-quaternary, focussing on biotope heterogeneity, geomorphology, and intra-annual flow patterns.
- Automating the process of setting river targets in a spatial conservation planning system.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

Conservation planning and rivers

Freshwater ecosystems are the most threatened ecosystems globally, experiencing the fastest loss of biodiversity and the greatest number of species extinctions. The last national appraisal of South African freshwater ecosystems estimates that in excess of 50% of the rivers are critically endangered, while 82% of river ecosystems are threatened (Driver et al., 2005; Nel et al., 2007). This proportion is much higher than those reported for the country's terrestrial ecosystems (Driver et al., 2005). The intimacy between catchment condition and river health is one reason why freshwater systems are amongst the most threatened systems globally (World Conservation Union, 2000; Abell, 2002; Groves, 2003; Jenkins, 2003).

One of the tools in beginning to staunch the current rate of loss to freshwater biodiversity and ecosystems is to identify areas of biodiversity importance through the use of systematic conservation planning. Systematic conservation planning has been applied to numerous regions in many different countries, and provides a structured approach in identifying biologically significant areas which require conservation action (see, for example Groves, 2003; Higgins et al., 2005). Using this approach, conservation planners aim to protect biodiversity (which includes patterns and processes at a range of temporal and spatial scales) by planning for representivity and persistence (Margules and Pressey 2000). Surrogates for biodiversity are typically used to predict areas of unique biodiversity (Margules and Pressey, 2000), particularly in the absence of comprehensive biological spatial data. Surrogates have been used for regional conservation planning in a number of studies (see, for example, Roux et al., 2002; Higgins et al., 2005; Groves, 2003; Rivers-Moore and Goodman, 2010; Rivers-Moore et al., 2011).

Owing to their complexity as fluid, longitudinal systems which show continuous gradients and relatively high variability, conservation planning for freshwater systems is conceptually at least a decade behind the application of this process to terrestrial systems (Groves, 2003). In spite of this lag, a growing recognition of the threatened status of many freshwater and wetland systems and species (Abell, 2002; Jenkins, 2003; Millennium Ecosystem Assessment, 2005) has added new impetus to this endeavour.

With the focus of conservation moving from single-species conservation to regional communities, an alternative approach of considering community turnover and associated spatial scales over which biodiversity patterns differ versus species-centric conservation is emerging (Clarke et al., 2010). While such an approach requires an understanding of how diversity patterns change at different spatial scales, there is no particular scale at which streams should be studied.

A necessary component of conservation planning is to determine targets (*sensu* Margules and Pressey, 2000) which provide an objective means of choosing how much of each type should be protected, and, certainly for rivers, maintaining connection between different biodiversity patches to allow gene flow and enable survival of the species during times of resource and habitat diminishment. Three types of targets should ideally be set to ensure persistence, viz. species targets (minimum viable populations); system targets (minimum land area required to conserve *x*% of the total estimated number of species within each ecoregion or vegetation type); and process targets (minimum area required to conserve ecological processes). The current South African approach in freshwater planning makes use of a 20% target value (Roux et al., 2006) which has become entrenched in the scientific literature, while a target value of 17% for inland water areas has recently been proposed by the 10th meeting of the Conference of the Parties to the Convention on Biological Diversity (COP-10).

Target-setting approaches

Target-setting approaches can be broadly classified into either empirical or participatory approaches. The approach taken should be dictated by the conservation goal, and address needs for protection of representative biodiversity patterns or ecosystem processes (persistence) (Rondinini and Chiozza, 2010). In the former case, species-area curves (for example, Desmet and Cowling, 2004) have proved to be a suitable pattern-focussed tool for terrestrial systems. This relationship assumes a logarithmic relationship between species number and land area, based on island biogeography theory (MacArthur and Wilson, 1967). This approach is popular amongst conservation planners because of its scientific dependability, but requires a large amount of species data collected using quadrats of different sizes within different vegetation zones. It is also better suited to vegetation targets rather than faunal targets because of this. Because rivers are characterized by length and not by area, and because species persistence at one site is very often a function of upstream and downstream ecological processes, the species-area method for setting targets in freshwater systems is not suitable. Rather, river zones of high alpha and beta diversity are better suited as determinants in choosing how much of a river should be conserved. One approach which has shown some promise is a modification of the species-area relationship to an equivalent species-discharge relationship.

Xenopoulos and Lodge (2006) demonstrated that this approach could be applied in modelling impacts of flow reduction on fish species diversity in large river systems in the United States. However, in smaller river systems, such as in South Africa, fish species numbers are not high enough to make any meaningful correlations between discharge and fish species numbers (Rivers-Moore, 2007, unpublished data). Additionally, this method makes no provision for setting targets in fish-free rivers, of which there are a number of examples in South Africa. An approach with a theoretical grounding similar to the species-area curve is necessary for setting meaningful targets in freshwater conservation planning.

"Ecoprofiles" are defined as an alternative, more adaptive means of setting conservation targets, where an ecoprofile is defined in the context of networks, where a set of species demand similar dimensions of ecosystem network in order to persist at a regional scale. In this process, targets are set using three-dimensional matrices in a participatory approach. The matrix axes consist of ecosystem types, ecosystem area requirements (a measure of carrying capacity per species) and species dispersal capacity (a measure of the inter-patch area that can be crossed by each species). Because the process of populating the matrix is a participatory one involving different stakeholders, two of the strengths of the ecoprofile approach highlighted by Opdam et al. (2008) are that it is a flexible yet negotiated target which is achieved, which has predictive power in that the degree of species persistence provides a measure of the target's validity. The disadvantage of this method is that it is better suited to case-by-case applications, and therefore presents difficulties for applying targets at a regional scale.

Being longitudinal segments, river length rather than vegetation area, and their location relative to biodiversity patterns, are more appropriate determinants in choosing how much of a river should be conserved. An approach with a theoretical grounding similar to the species-area curve is necessary for setting meaningful targets in freshwater conservation planning. A suitable approach is to base targets on established measures of species diversity and river ecology theory. The location of highest alpha-diversity, as related to the river continuum concept, and species turnover along a river's longitudinal axis (beta-diversity), determine where and how much of a river should be targeted to conserve maximum species diversity. Between-river diversity (gamma-diversity) determines how many river systems should be conserved within each biome, and this relies on a suitable river classification system. Such an approach encompasses spatio-temporal variability, and would incorporate ecological processes operating at different scales along environmental gradients. The aim of this research was to develop a scientific method to set conservation targets for river lengths. In this report, a new method is proposed, based on established measures of species diversity and river ecology theory, to identify suitable river segment lengths for conservation action.

Measures of biodiversity

Two of the fundamental pillars of freshwater ecology remain the river continuum concept (Vannote et al., 1980) which, *inter alia*, makes predictions of species diversity patterns with downstream distance based on ecosystem processes; and the hierarchical understanding of river systems proposed by Frissel et al. (1986). These present very useful concepts in setting river conservation targets and were used as a basis to this study.

At the habitat scale, aquatic macroinvertebrates show strong associations with different hydraulic biotopes and geomorphological types (see, for example, De Moor et al., 1999; De Moor, 2002). These differences and affinities only emerge at the species level, although where time and/or resources are limiting the use of selected taxa (Ephemeroptera, Trichoptera and Simuliidae) is acceptable (De Moor, 2002). Local-scale species diversity has been shown to change on a seasonal basis for a number of South African rivers (Harrison and Elsworth, 1958; Harrison, 1958), in response to seasonal changes in channel networks (Ward and Tockner, 2001). At a larger scale, there have been a number of studies which show that aquatic fauna correlate strongly with different longitudinal river zones (Harrison and Elsworth, 1958; Harrison, 1958a; Oliff, 1960a; Oliff and King, 1962) and between river basins based on changes in geology (Harrison and Agnew, 1962). Interpreting patterns of species diversity can, however, be confounded by the effects of organic pollution (Harrison, 1958b; Oliff, 1960b; Oliff and King, 1962) and changes in flow (Rivers-Moore et al., 2007a). Superimposed on spatial drivers of community patterns are patterns driven by levels of seasonal unpredictability, so that the diversity of aquatic insect communities depends strongly on the diversity and stability of hydraulic biotopes (Cucherousset et al., 2008).

Early measures of species diversity and turnover along a river axis provide insights into parameters which freshwater targets should include. Harrison and Elsworth (1958) adopted species categories for their river surveys, originally proposed by Tansley (1923):

- Exclusive species – those confined to one community and/or biotope;
- Characteristic species – those more common within the community than outside it; and
- Constant species – those present in every (or almost every) example along a river's axis.

These measures of diversity were formalised by Whittaker (1972) as:

- Alpha (α) diversity (which includes exclusive, characteristic and constant species) - the number of species in a sample of standard size;
- Beta (β) diversity - the extent of differentiation of communities along biotope gradients (essentially the turnover in exclusive and characteristic species, and excluding constant species); and
- Gamma (γ) diversity - the diversity of a landscape, and is the product of its alpha and beta diversity.

Species diversity measures provide an index of system processes through the environmental gradients they represent, and a basis for testing ecological hypotheses (for example, that species diversity is low in unstable environments (Whittaker, 1972)). Ward and Tockner (2001) add an additional spatial refinement to these measures of species diversity, by presenting them in a hierarchical model from biotope to basin, thereby linking these measures explicitly to the hierarchical model of Frissel et al. (1986). Inherent within these measures of diversity is the issue of scale, where beta diversities at the biotope scale become alpha diversities at the site scale, and so on up the spatial resolution scale. Within this model, hypotheses of drivers of species diversity are also provided (disturbance – see Connel, 1978; ecotone density and patch size – see Naiman et al., 1988; and degree of connectivity between habitat components), so that species patterns may be likened with abiotic drivers and measures of seasonality.

Turnover model

The model is based on measures of species diversity using the indices developed by Whittaker (1972). Measures of alpha-diversity (within-habitat and site-specific), beta-diversity (between-habitat diversity and incorporates environmental gradients and local processes) and gamma-diversity (a composite of alpha and beta diversity and large-scale processes) (Ludwig and Reynolds, 1988) provide a powerful conceptual framework for setting species targets, because a combination of these indices incorporates scale issues, which are critical to understanding river systems (Frissel et al., 1986). The location of highest alpha-diversity, as related to the river continuum concept, and species turnover along a river's longitudinal axis (beta-diversity), determine where and how long a river segment should be to conserve species diversity. Between-river diversity (gamma-diversity) determines how many river systems should be conserved within each ecoregion, and this relies on a suitable river classification system.

Here, scale becomes a critical issue. For example, different biotopes at a site might produce greater diversity than the same biotope at different sites. Thus, one scale to define these three measures of biotope could be biotopes within a single site and turnover between these biotopes, versus pooled diversity per site and turnover between sites. In this model, the scale is explicitly between site and between rivers. Thus, within a basin (or riverscape), the aim of this model is to identify the following:

- Alpha diversity - Where is diversity highest along a longitudinal axis of a single river?
- Beta diversity – How does species turnover change along the longitudinal river axis?
- Gamma diversity – How different is River *A* to River *B*?

Answers to these questions will inform conservation planners on which rivers to select, and where and how long the chosen river segments should be. At the spatial scale of this study, the model assumes the following:

- Species targets are set based on good biological data along a species axis.
- Sampling was from all available biotopes (stones-in-current; bed sediments and marginal vegetation), and data were pooled.
- For alpha diversity to be maintained, upstream and downstream processes that conserve the diversity (or pattern) within a segment need to be conserved.
- Analogous to the species-area curves (Desmet and Cowling, 2004), low beta diversity (i.e. low disparity between sites) implies that a relatively short section of river needs to be conserved. However, if beta diversity is large, then more of the river needs conservation measures.
- The more variable the system, the higher the beta diversity, and the longer the length needed to protect diversity, i.e. segment length depends on predictability. Conversely, more stable predictable systems are more resilient, beta diversity is lower, and the length of river requiring protection is relatively shorter.
- River systems in similar ecoregions should have lower gamma-diversity than rivers in different ecoregions.

Consider two paired river systems, *A* and *B* (Figure 1). In system *A*, system variability is low; site-specific (alpha diversity) is low; species turnover is low, and paired rivers are similar. System *B* is highly variable, and exhibits high site-specific diversity, high species turnover, and paired rivers are different. According to the model predictions, either one of the two paired rivers in system *A* will require protection, location of river segment to be conserved is not critical, and segment length for protection is relatively short. However, in system *B*, both river sections require protection, the river segment requiring protection must coincide with the zone of highest alpha-diversity, and be long enough to include most beta-diversity.

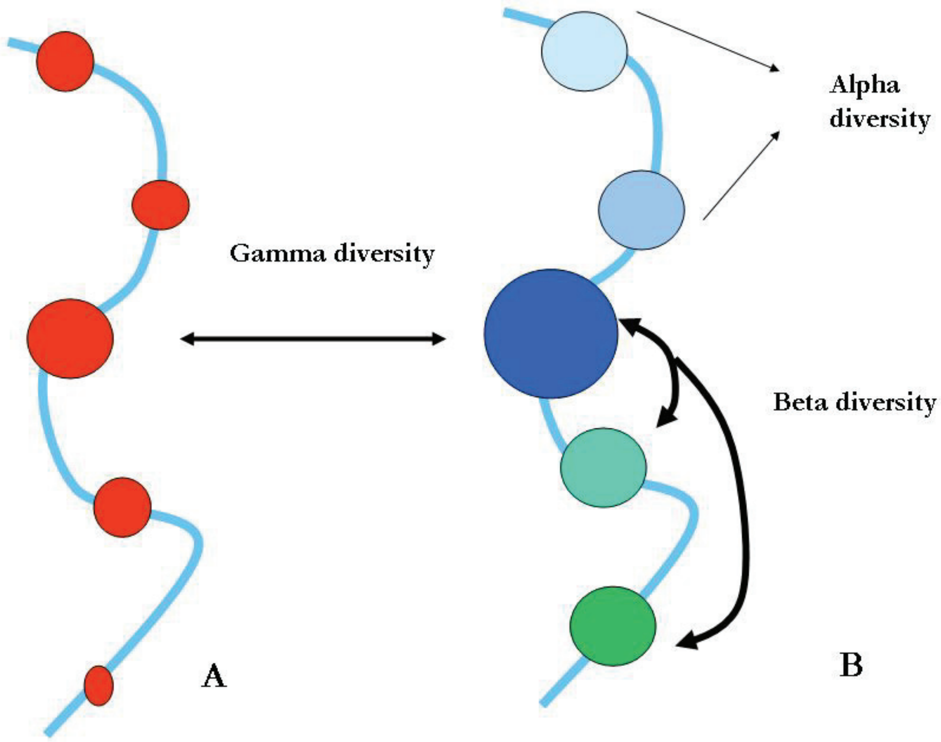

Figure 1 Conceptual model of two different river systems, where five sampling sites indicate varying levels of alpha diversity per site (as reflected by circle area). In the system on the left (A), species turnover (beta diversity) between sites is low while on the right (B) it is higher (as indicated by different circle colours). Catchment (gamma) diversity is high between the paired systems, such that irreplaceability between both systems is high.

METHODS

Historical data

Biotic and abiotic data were available for a number of studies previously undertaken in what were free-flowing (*sensu* WWF, 2006) South African rivers (Figure 2; Table 1), with the exception of the Great Fish River. Data for the Berg, Mvoti, Mkuze and Mzimkhulu Rivers were extracted from the database developed by Dallas et al. (1999). For the Thukela River (Oliff, 1960a), species presence data were available for nine different river zones, whose locations were determined based on site descriptions matched to 1:50 000 map sheets.

Table 1 South African rivers selected for testing of the species diversity index model, type of data available and data source

River (km)	Fish Data	Aquatic macroinvert. data	Data source
Sabie (240) & Sand (130)	X		Weeks et al., 1996; Rivers-Moore et al., 2004
Great Fish (720)		X	Palmer and O'Keeffe, 1990; Rivers-Moore et al., 2007
Thukela (528)		X	Oliff (1960a)
Berg (284)		X	Harrison (1958a); Harrison and Elsworth (1958)
Mvoti (236)	X	X	EKZNW (2010; fish); Brand et al. (1967), Author
Mkuze (360)	X	X	EKZNW (2010; fish); Archibald et al. (1969), Author
Mzimkhulu (378)	X	X	EKZNW (2010; fish); Kemp et al. (1976), Author
Keurbooms (87)		X	Author

Current data

Three free-flowing river systems, as defined by WWF (2006) within KwaZulu-Natal were sampled to supplement the historical data, verify the fish records from EKZNW (2010), and to provide macroinvertebrate data which could be linked to system variability (Figure 2). Free-flowing rivers were chosen to provide data as close to "reference" condition as possible. In this study, this was defined according to two of the categories of Stoddard et al. (2006), viz. “historical” (assumes pinning to an historical period) and “least disturbed”, with a focus on statistical distributions evident from random sampling in preference to the “representative reach (Ladson et al., 2006). Sites from each river were selected based on geomorphological break-points along river profiles, using the methodology developed by Dollar et al. (2006), and developed for South Africa by Moolman (2006, 2008). Where possible, sites were located near flow gauging weirs (Table 2).

Table 2 Rivers and numbers of sites surveyed, and downstream distances of sites plus geomorphological zones present within the selected river systems, sources of flow data and whether temperature data were collected

River	Site	Downstream Distance (km)	Geomorph. Zone*	Flow data	Temp. data
Mkuze	1	74	E	Simulated	X
	2	115	E	Simulated	X
	3	197	E	W3H008[1]	X
	4	257	F	W3H011[2]	
Mvoti	1	16	D	Simulated	
	2	48	E	U4H002[3]	X
Mzimkhulu	1	59	E	T5H005[3]	X
	2	78	E	Simulated	
	3	115	E	Simulated	X
	4	123	E	Simulated	
	5	308	E	Simulated	
	6	344	F	Simulated	X

[1] 43 years: 1965-2010; [2] 18 years: 1971-1988; [3] 62 years: 1949-2010

* D = Upper foothills, E = Lower foothills, F = Lowland

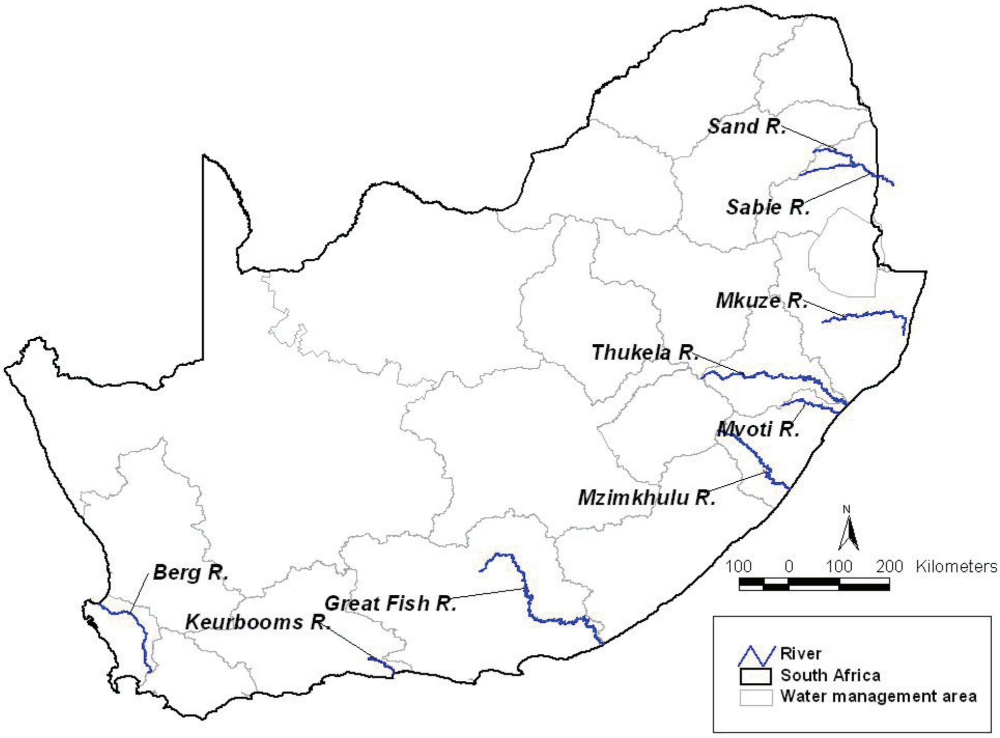

Figure 2 Location of nine South African river systems studied

Aquatic macroinvertebrate and fish community samples were taken from hydraulic biotopes using stratified random sampling along the longitudinal profiles of the selected river systems. Fish diversity (relative abundances by species) was assessed using standard electrofishing techniques. Aquatic macroinvertebrate samples were collected using a combination of box samplers and hand nets (25 cm ø net with 250 μm mesh). Sampling of aquatic macroinvertebrates broadly followed the methods used by Oliff (1960a, b) and Harrison and Elsworth (1958). Four sub-samples were taken from each site from available biotopes (stones-in-current; bed sediments and marginal vegetation), and samples were pooled. Fish were identified to species level; when possible, aquatic macroinvertebrates were identified to species level using appropriate taxonomic guides.

Water quality (conductivity, turbidity, pH) and geomorphology (substrate roughness – Statzner and Higler (1986), substrate type, river width and depth) measures were collected at all sites. Seven months of hourly recorded water temperatures (November 2009-May 2010) were collected for all three rivers for seven of 12 sites using Hobo Tidbit v2 data loggers (Onset 2008). Mean daily flow rate time series were obtained from South Africa's Department of Water Affairs (2010), and used where appropriate. Mean daily simulated flow data for 1950-1999 using the daily time-step agro-hydrological model ACRU (Schulze, 1995) were used in the absence of observed flows for appropriate quinary sub-catchments from the University of KwaZulu-Natal's School of Bioresources Engineering and Environmental Hydrology.

Statistical analyses

Datasets of fish and aquatic macroinvertebrates from previous studies in eight river systems within South Africa (Table 1), which cover a range of stream orders, were combined with data collected during this study. For each river system, site-specific alpha diversity was calculated. Species turnover (beta diversity) along river longitudinal axes was estimated using a number of techniques (see below), while gamma diversity (between river systems) was also calculated.

Alpha diversities

Whittaker (1972) recommended using direct measures of species numbers in preference to mathematically predicted species numbers. However, expected alpha diversities may exceed observed species numbers as not all species were necessarily sampled. Because of this relationship, expected numbers of species were predicted using log-normal species-abundance curves. Relative abundances were classified into octaves (2^n), and expected numbers of species calculated using lognormal distributions (Ludwig and Reynolds, 1988). For illustrative purposes of the model (i.e. where to start in the river system), alpha diversities were plotted against downstream distance and stream order, per river system. Hill's diversity indices N_1 (Equations 1a-b) and N_2 (Equation 1c-d) were plotted with downstream distance and stream order. The former index provides an indication of the number of abundant species, which will be mid-way between total species and number of *very* abundant species (N_2) (Ludwig and Reynolds, 1988). A modified Hill's ratio evenness index was calculated to provide an indication of the degree to which a single species dominated sites as a function of downstream distance (Equation 1e).

$$N_1 = e^{H'} \qquad [1a]$$

$$H' = -\sum_{i=1}^{S^*} (p_i \ln p_i) \qquad [1b]$$

$$N_2 = \frac{1}{\lambda} \qquad [1c]$$

$$\lambda = \sum_{i=1}^{S} p_i^2 \qquad [1d]$$

$$E = \frac{N_2 - 1}{N_1 - 1} \qquad [1e]$$

where H' is Shannon's Index, p_i is proportional abundance of the ith species, λ is Simpson's diversity index and *E* is the modified Hill's ratio evenness index.

Beta diversities

The purpose of this metric was to estimate rates of species turnover (using site pair similarity coefficients) along different river systems, to determine how much of a river system should be conserved. Raw alpha diversities (observed numbers of species) were used for each site in each river system assessed.

Quantitative analyses

To begin with, Bray-Curtis polar ordinations (Sørenson distance measure) using relative abundances of aquatic macroinvertebrates to examine quantitative species turnover in selected river systems were used (McCune and Mefford, 1999). Species with single site and single individual occurrences ("singletons") were removed prior to analyses, as they contribute to noise and not gradients of change. These analyses provided insights into turnover of functional groups with downstream distance.

Qualitative analyses

Next, a qualitative approach to beta diversity using presence/absence data, which permitted analyses from a wider range of datasets, was used. Sørenson's similarity coefficients between site pairs were calculated for each site (Equation 2), based on recommendations by Whittaker (1972). Similarities between all sites in nine river systems (Fish = Sabie, Sand, Mvoti, Mkuze and Mzimkhulu Rivers; Macroinvertebrates = Great Fish, Thukela, Berg, Keurbooms, Mvoti, Mkuze and Mzimkhulu Rivers) were calculated within a matrix, in a sequential downstream manner. In each successive iteration, the starting site was assigned as "source", and the downstream distance from source (actual and percentage of total river length down to most downstream site) was calculated (Figure 3). Thus, distance from source to most downstream site was 100%. Conversion to percentage values allowed for standardization of all river systems considered, although it is acknowledged that this may ignore possible differences in river size in attempting to generalize principles (i.e. 20% of a 200 km river system would be different to 20% of a 10 km river). To understand the effect of rare species (defined on two levels: "very rare" = single occurrences and "rare" = single site species) on rates of turnover, site pair similarities were again calculated with rare species filtered out.

$$\frac{2c}{S_j + S_k} \qquad [2]$$

where c is the number of species in common between site pairs, $S_{j,\,k}$ are species numbers at sites j and k respectively.

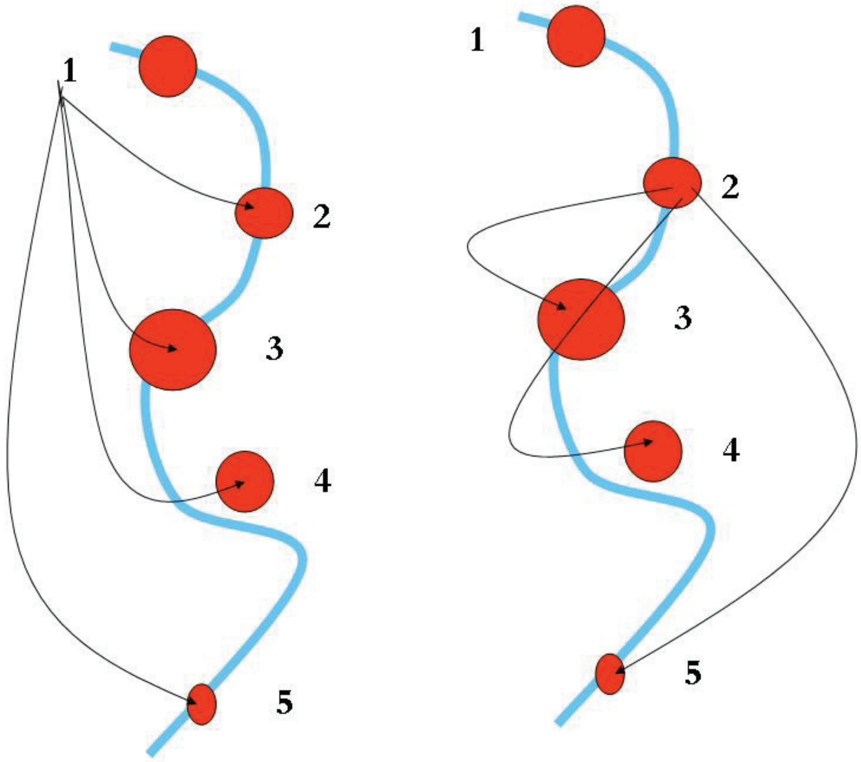

Figure 3 Site pairs for which Sørenson community similarities were calculated, indicating the moving window of using a "source" site

The fidelity of beta diversity to geomorphological zones at the 1:500 000 scale (Moolman, 2006; 2008) was determined for each site in the river systems assessed. Change in geomorphological zone between site pairs was calculated i.e. a site pair was assigned a value of one if site pairs were in the same zone, and two if zones were different. Sites for five river systems (Berg, Mvoti, Mkuze, Mzimkhulu and Thukela Rivers) were sorted by similarity (ascending), ranked from 1 to *n*, and then sorted based on 1 or 2. Similarity coefficients within *vs.* between geomorphological zones were tested using Wilcoxon-Mann-Whitney test (Siegal and Castellan, 1988).

Beta diversities (species turnover/site similarity) were plotted against downstream distance. Curves were fitted to these points for each river system, to estimate average rates of change or species turnover with downstream distance, using equation coefficients. Beta diversity half-turnovers were calculated using Equation 3, and from these the % downstream distances where the 50% turnover point was reached was calculated for each river system. Note that the logarithm of each term, as used by Whittaker (1972), provides the number of half changes in beta diversity along the environmental gradient.

$$\frac{a-z}{2} \qquad [3]$$

where *a, z* are site similarities at the start and end points of the coenocline (*sensu* Whittaker, 1972)

Average species turnover model

A threshold value of 50% similarity was chosen as being the deciding factor for site *n+1* being "representative" of site *n.* Similarity values for the Mkuze, Berg and Mzimkhulu Rivers were pooled, and assigned binary numbers where similarities >0.5 = 1 and <0.5 = 0. A logit binomial model with 95% confidence intervals was fitted in R (R Development Core Team, 2009).

To link species turnover probabilities to existing conservation planning approaches, river types as surrogates for biodiversity (*sensu* Rivers-Moore et al., 2011) and how these relate to a 20% target in river length per river type were compared with the number of river lengths required to achieve representivity by the model.

Drivers of turnover

Environmental gradients

Since aquatic macroinvertebrate communities have been shown to reflect hydraulic conditions (De Moor, 2002), species diversity measures were related to metrics based on water quality and river flow signatures, viz. predictability (coefficient of variability; Colwell's (1974) indices and seasonality). Further flow statistics were calculated using the Indicators of Hydrological Alteration software (Richter et al., 1996). The hourly water temperature time series were resolved into daily measures (mean, minimum and maximum daily temperatures), from which temperature metrics relating to temperature variability were calculated. Before multivariate analyses were done, correlation matrices were used to reduce redundancy in variables by eliminating highly correlated variables. Principal components analyses (PCA) of sites vs. physical variables, flow and water temperature metrics were undertaken using PC-Ord (McCune and Mefford, 1999) to classify sites in terms of their abiotic habitat templates. PCAs were based on centred, correlation matrices to standardize data (McGarigal et al., 2000).

River profiles

Further insights on rates of species turnovers and downstream distance were gained by plotting alpha and beta diversities on the same axes as river profiles, to determine whether profile inflexion points corresponded to changes in species turnover. River profiles were derived for 4 main-stem rivers within KwaZulu-Natal from the 1:500 000 river coverage. A 200 m Digital elevation model (DEM) was overlaid by each of these arcs, to derive a profile using Idrisi's 'Profile' function (Clark Labs, 2009). Thus, at a resolution of 4 ha, and over a distance of 600 km, altitudes were assigned for every 200 m of river length from sea to source. Because of the error between the DEM and the river arcs, these data were smoothed using a 15 pixel (or 3 km) moving average.

Gamma diversity

Whittaker (1972) defines gamma samples as "usually alpha samples combined from several communities" (p. 232), and recommends two methods for estimating this value. For the first method, gamma is completely determined by alpha and beta using Whittaker's (1972) multiplicative law (Equation 4a), as applied, for example by Jost (2007) and Clarke et al. (2010). In the second approach, gamma diversity is based on a measurement of relative similarity of samples (Equation 4b).

For this study, because of data limitations, comparisons of gamma-diversity were based on the second approach and based on the data for Mkuze, Mvoti, Mzimkhulu and Berg Rivers. While these four rivers are all from different ecoregions (level I classification developed by Kleynhans et al. (2005)), estimates of gamma diversity are seen as a demonstration only.

$$\gamma = \alpha\beta \quad [4a]$$

$$\gamma = S_1 + S_2 - c \quad [4b]$$

where S_1 and S_2 are total numbers of species recorded in the first and second communities respectively, and c is the number of species common to both communities.

RESULTS

Site data

Water quality in all three KwaZulu-Natal rivers surveyed was typical of the zone where sampling occurred, indicating that community structure as a function of water quality was largely accounted for (Appendix A1). Mean flow rates ranged from 0.99 $m^3.s^{-1}$ (Mvoti River) to 34.97 $m^3.s^{-1}$ (lowest site – Mzimkhulu River) (see Appendix A2). Water temperatures ranged from 19.22-25.38°C with a coefficient of variation ranging from 12.87-16.27°C for sites.

There was a total diversity of 125 taxa across all sites sampled on the Mkuze, Mvoti and Mzimkhulu Rivers (Appendix B). This species number was conservative, not accounting for different life history stages and because several genera had 2-3 species unidentified within them. The most diverse sites were Mz3 with 44 taxa and Mv1 with 42. The greatest number of taxa recorded on the Mkuze River was Mk1, with a total of 26 taxa. The diversity was lowest overall on the Mkuze River.

None of the taxa recorded appear on the IUCN red data lists as anything other than "least concern", although many aquatic invertebrate taxa have not been investigated for the IUCN list. All major taxonomic aquatic macroinvertebrate orders were represented, with the diptera (and particularly *Simulium* spp.) dominating the samples. The Ephemeroptera were diverse with seven different families present, most notably as baetids. The Coleoptera were not high in individual taxa numbers, but with many Elmidae larvae present. The Trichoptera were represented by three major families, but within each family there was a good diversity, even if generally low in abundance (exception within the Hydropsychidae). Odonata and Hemiptera were also low in abundance but fair in terms of their diversity.

Actual numbers of fish, and numbers of fish species sampled, were lower than expected for the Mkuze, Mvoti and Mzimkhulu Rivers, based on historical species records from the provincial conservation agency (Appendix C). Numbers of species sampled per site ranged from one to six, with the highest numbers of fish species occurring in the Mzimkhulu River, and the lowest number of species sampled in the Mkuze River.

Alpha diversity

Numbers of fish species (historical data) showed no pattern with downstream distance for the Mkuze, Mvoti and Mzimkhulu Rivers (Figure 4), while a weak increase in numbers of species with downstream distance was shown to occur in the Sabie River, which varied inter-annually (Figure 5).

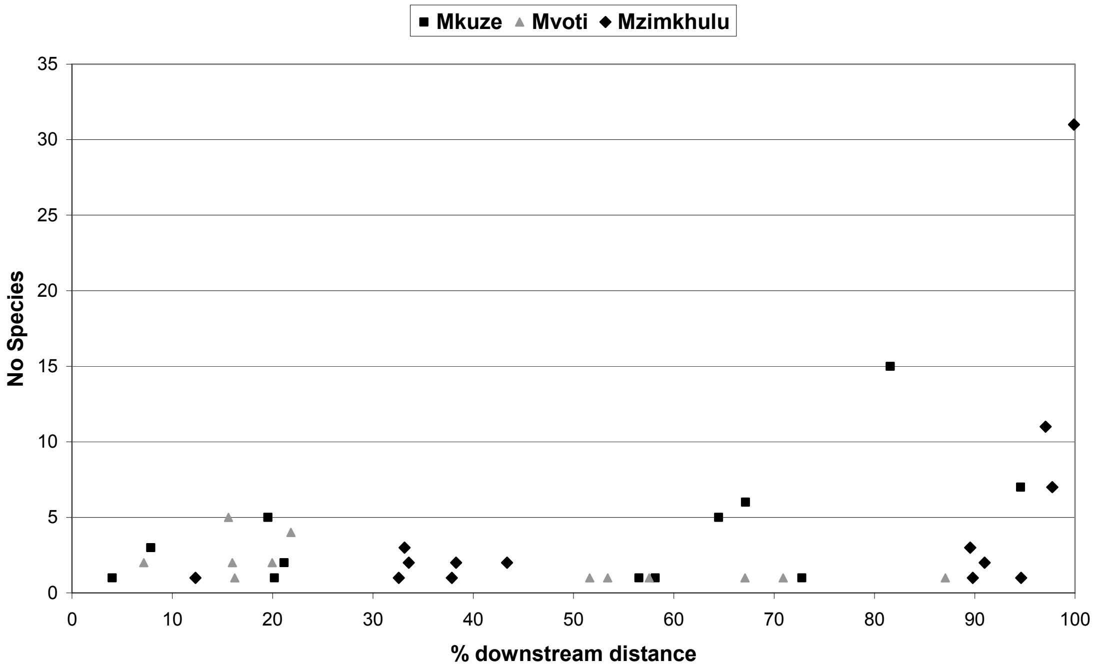

Figure 4 Fish diversity with downstream distance for the Mkuze, Mzimkhulu and Mvoti Rivers

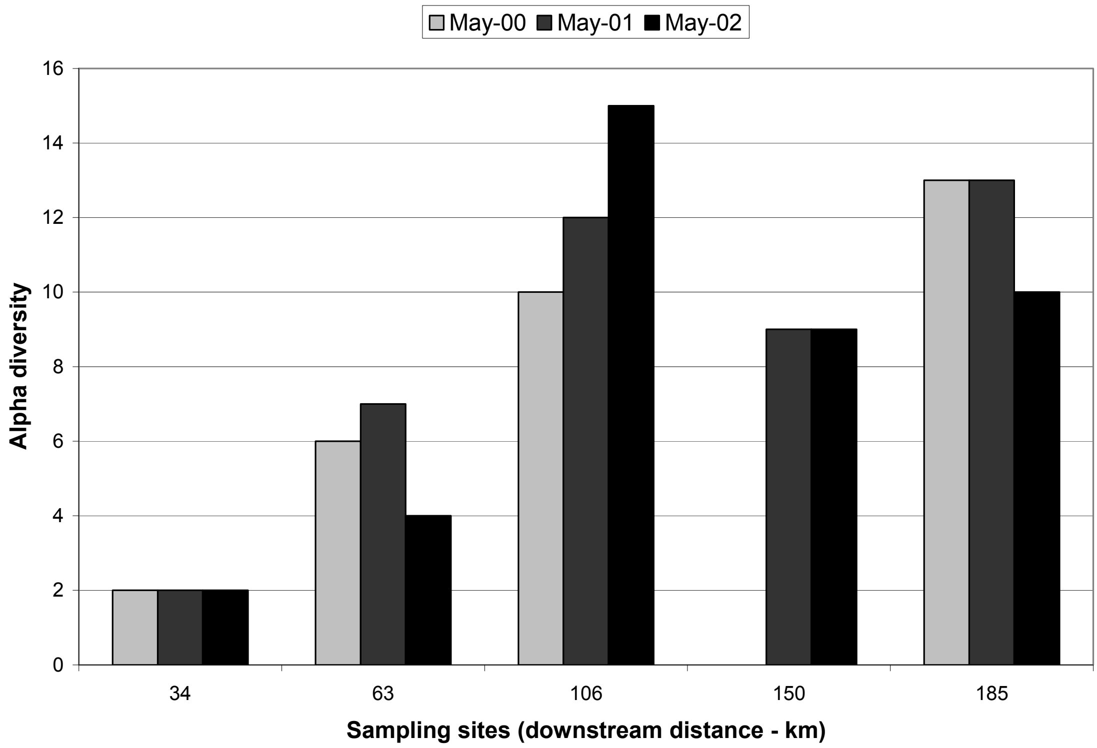

Figure 5 Alpha diversity of fish for five sites from 2000-2002 along the longitudinal axis of the Sabie River, from mountain stream zone (3) to lower foothills zone (20) (Rivers-Moore et al., 2004)

In general, observed species numbers ("raw" alpha diversities) were underestimates of potential expected alpha diversities. Based on the lognormal plots, differences between observed and expected alpha diversities ranged from 0-200% underestimates, with a mean (±SD) of 56.0±55.8%. Octaves for the Berg River predicted the best agreement between observed and expected numbers of species (5.8% difference) versus the worst undersampling for the Mkuze River (107.2%) (Appendix D).

Observed and expected alpha diversities were highest in the upper third (Figure 6) and in the mid-order reaches of rivers sampled (Figure 7). Hill's N_1 and N_2 diversities (number of abundant and very abundant species) mirrored the total number of species recorded per site (see subsequent section, Figures 22 and 24 for Mzimkhulu and Berg Rivers respectively). Interestingly, species evenness (degree to which a site is dominated by a single species) remained relatively constant on the Berg River (Figure 25), but decreased on the Mzimkhulu River (Figure 23), where the lowest site, closest to the estuary, was largely dominated by the freshwater shrimp *Caridina nilotica*. Similarly, the lowest site on the Mkuze River was dominated by the freshwater snail *Melanoides tuberculata* (Mollusca: Thiaridae)

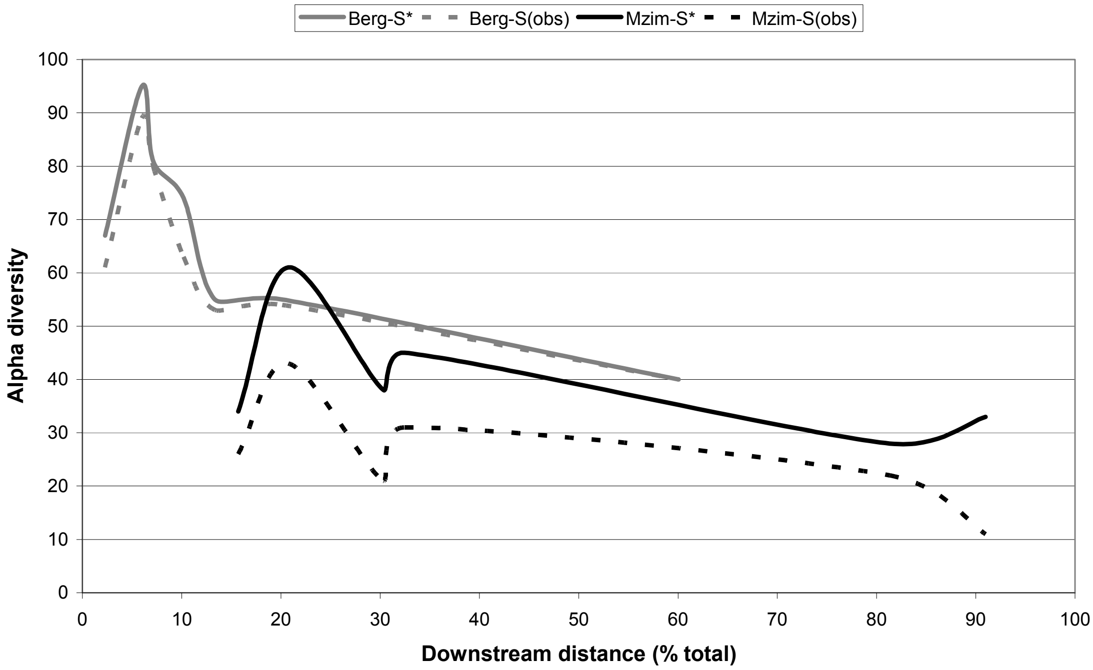

Figure 6 Expected (S^*) and observed alpha diversities of aquatic macroinvertebrates versus % downstream distance for two of the nine river systems

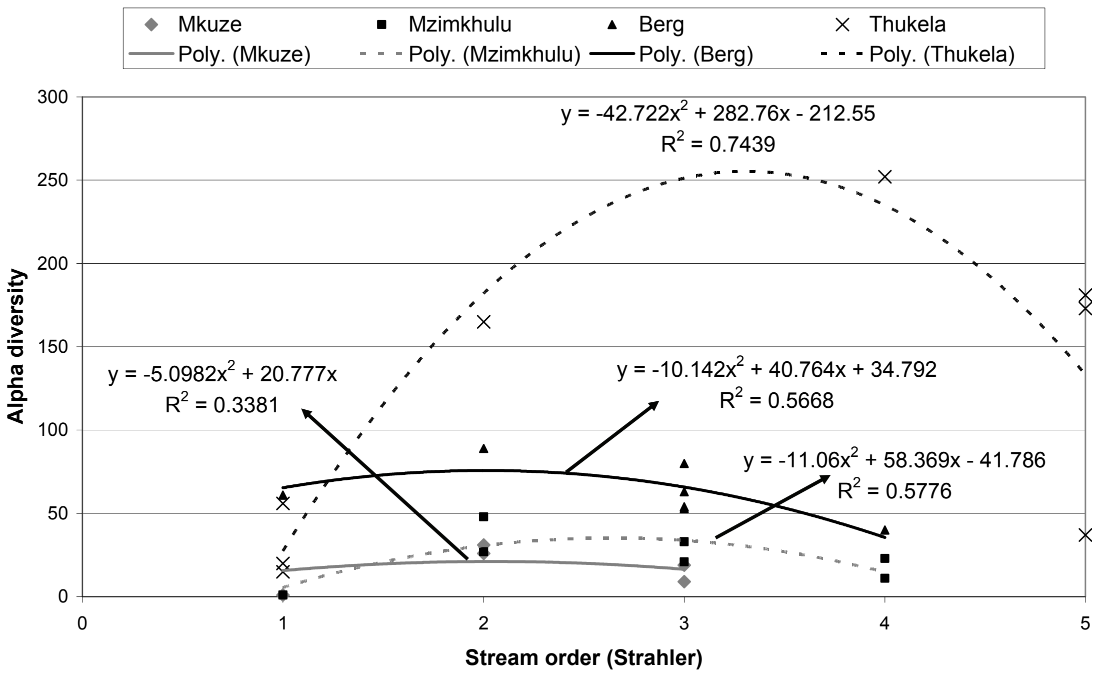

Figure 7 Observed alpha diversities of aquatic macroinvertebrates versus stream order for four river systems

Beta diversity

Quantitative analyses

Fish community patterns changed on an annual basis, with some sites changing more than others (Figure 8). Again, knowledge of the river system assists with interpretation of the diversity patterns –

floods in the Sabie River in February 2000 would have altered fish community patterns, and subsequent surveys demonstrate a change in fish communities at each site as river conditions seek a new equilibrium (see Rivers-Moore et al., 2004).

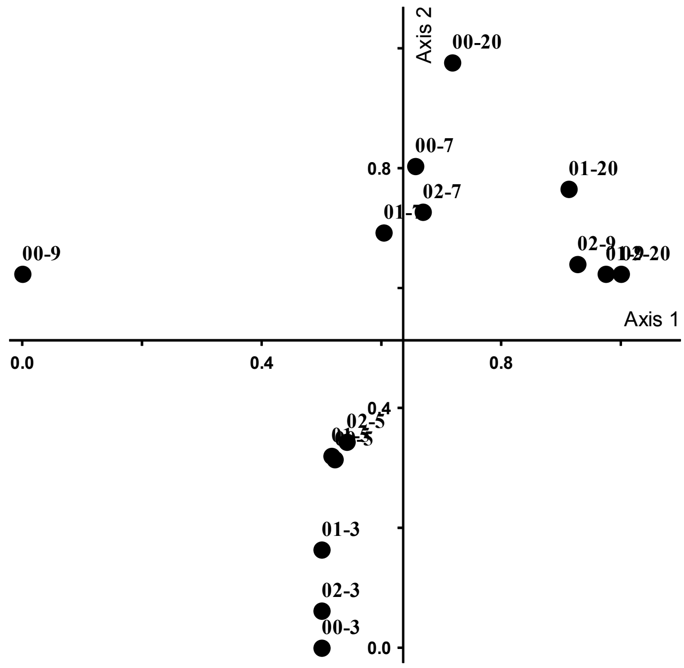

Figure 8 Approximation of beta diversity differences for fish communities on the Sabie River, based on a Bray-Curtis ordination of sites surveyed. Sites have been classified based on species relative abundance data (after Rivers-Moore et al., 2004). Data for three years (2000-2002) have been represented by the prefixes 00, 01 and 02.

Species turnover of aquatic macroinvertebrates followed a sequential downstream pattern, as demonstrated by Bray-Curtis plots. For example, for ten sites on the Great Fish River, where sites S1-S10 follow the downstream river axis, sites S1-3 were upstream of an impoundment; species turnover was disrupted between S3 and S4, this displaced sites S4 and S5 way out of the main ordination and downstream conditions only returning to pre-disturbance turnover at site S8 (Figure 9). An NMS (based on Bray-Curtis) for the Berg, Mkuze, Mvoti and Mzimkhulu Rivers showed a number of interesting trends. Firstly, species turnover occurred in a sequential, downstream manner; secondly, the Berg River (Western Cape province) had no species in common with the rivers in KwaZulu-Natal. Thirdly, while the Berg River showed a constant rate of turnover with downstream distance, the KwaZulu-Natal Rivers showed a low degree of beta diversity between the three river systems (i.e. common set of core species) (Figure 10). Lastly, there was relatively little turnover in the upper-mid river reaches, and then more rapid turnover for the lowland sites (Figures 10-11).

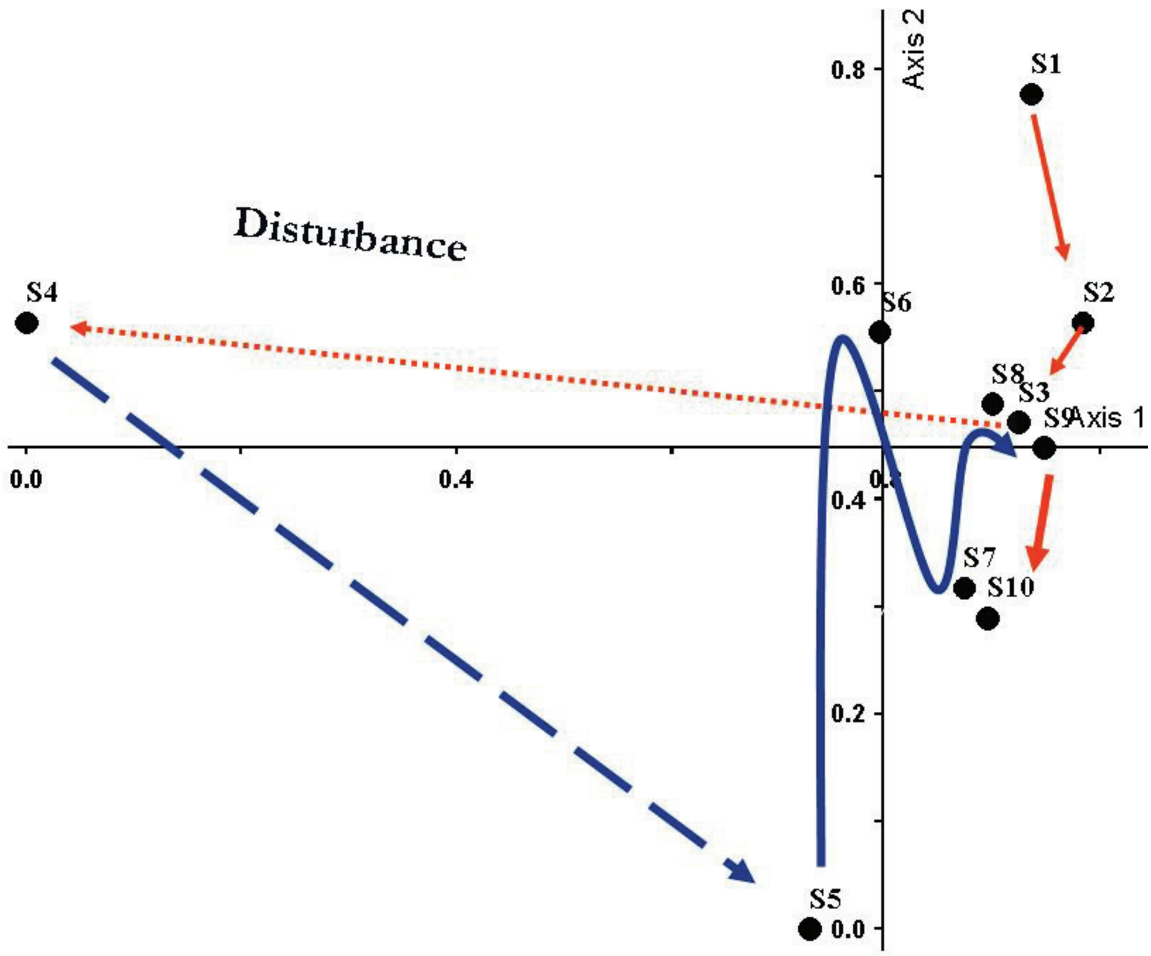

Figure 9 Bray-Curtis ordination of beta diversity differences for aquatic macroinvertebrate communities on the Great Fish River. Sites have been classified based on species relative abundance data (after Palmer and O'Keeffe, 1990)

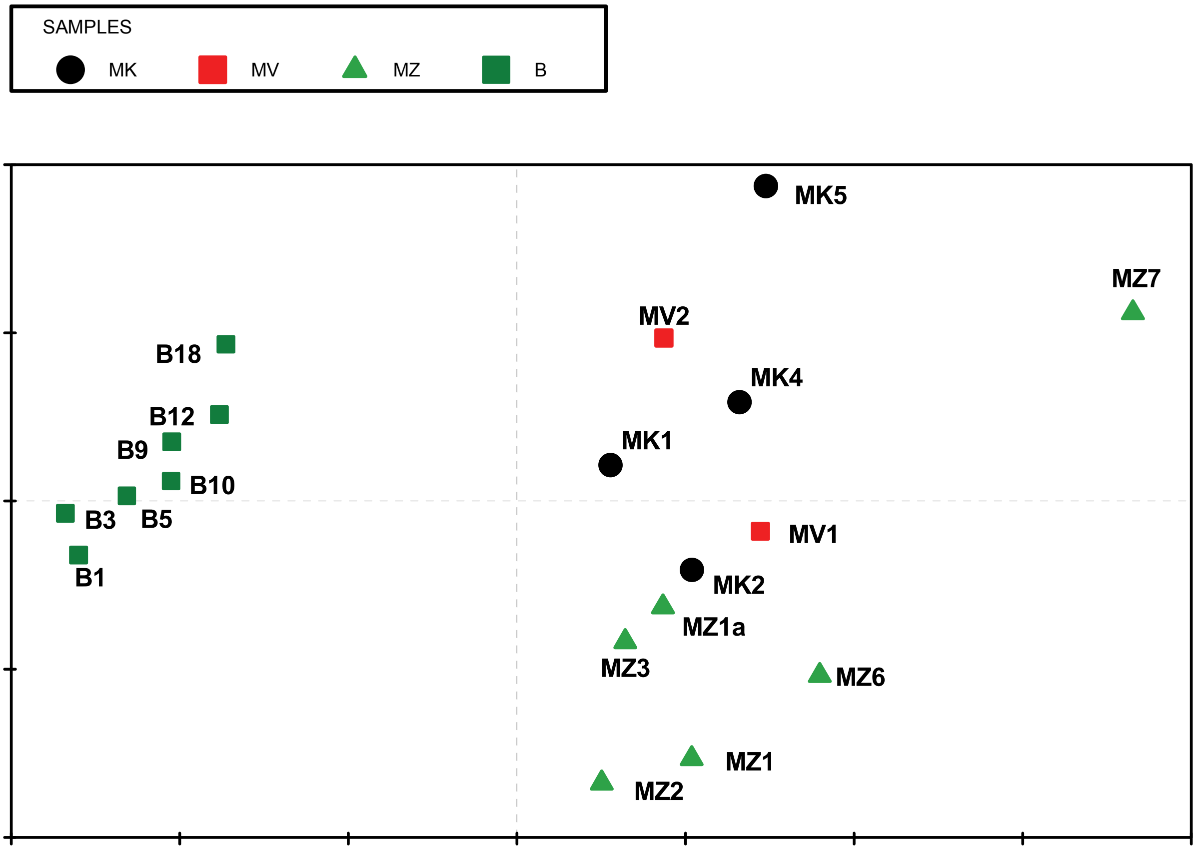

Figure 10 NMS (based on Bray-Curtis distances) of species composition from three KZN rivers and the Berg river. Singleton species excluded. Stress = 0.10415.

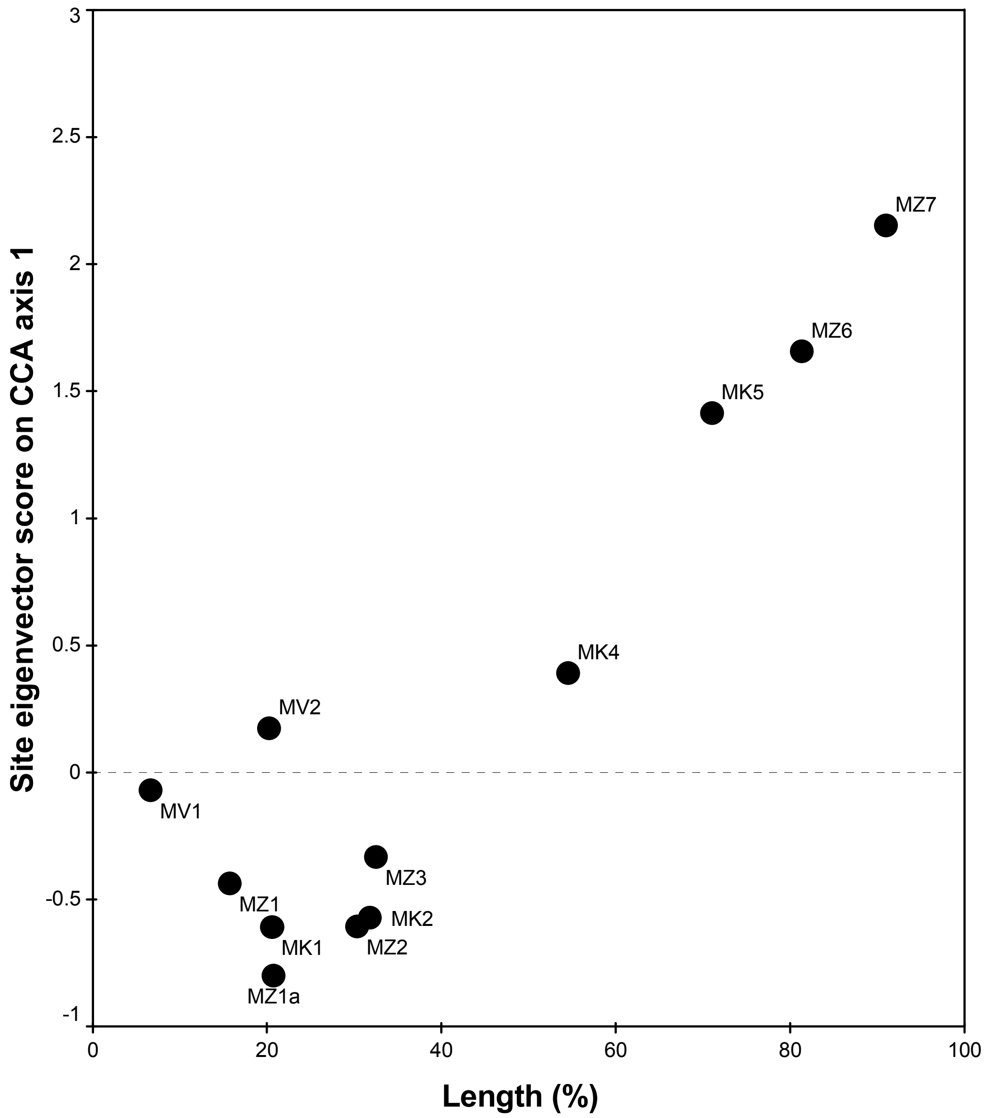

Figure 11 Site eigenvector scores (from a partial CCA constrained to fit river length) versus length of river (%), i.e. spatial position downstream. [Note: sites scores do not change appreciably for the first half of the river but diverge rapidly in composition along the lower half, i.e. little turnover in composition in the upper to mid reaches and most turnover in the lower part – see above plot for species most prevalent in each].

Qualitative analyses

The survey from the Mzimkhulu River is presented as an example of how turnover between site pairs as a function of downstream distance was calculated. Site pair similarities of aquatic fauna (aquatic macroinvertebrates and fish) were calculated and presented in a matrix (Table 3). These were combined into data columns (Table 4). Downstream distances between site pairs were calculated on the basis that the source site was distance 0, and the downstream site ("sink") site was the absolute distance between the two sites. Thus, for example, for site pair 1_2, the source site was 59.40 km from the source of the upper Mzimkhulu River, while site 2 had an absolute distance of 114.73 km from the river source. Thus, the distance between source and sink was 55.33 km (114.73-59.40 km).

The percentage downstream distance was expressed as 55.33 as a percentage of the total length from river source to most-downstream site sampled (site Mz7 = 344.09 km).

Table 3 Matrix of site pair similarities

	MZ1	MZ2	MZ3	MZ4	MZ5	MZ6
MZ1	1.00					
MZ2	0.49	1.00				
MZ3	0.60	0.38	1.00			
MZ4	0.49	0.54	0.46	1.00		
MZ5	0.38	0.28	0.37	0.34	1.00	
MZ6	0.11	0.11	0.13	0.19	0.18	1.00

Table 4 Site pair similarities and the respective absolute and % total distances between source site (distance 0) and "sink" site

Site pair	Similarity	Zone	DD	Dist. from source	% DD
1_1	1.00	1	59.40	0	0.00
1_2	0.49	1		19.06	5.54
1_3	0.60	1		55.33	16.08
1_4	0.49	1		63.4	18.43
1_5	0.38	1		248.17	72.12
1_6	0.11	2		284.69	82.74
2_2	1.00	1	78.46	0	0.00
2_3	0.38	1		36.27	10.54
2_4	0.54	1		44.34	12.89
2_5	0.28	1		229.11	66.58
2_6	0.11	2		265.63	77.20
3_3	1.00	1	114.73	0	0.00
3_4	0.46	1		8.07	2.35
3_5	0.37	1		192.84	56.04
3_6	0.13	2		229.36	66.66
4_4	1.00	1	122.80	0	0.00
4_5	0.34	1		184.77	53.70
4_6	0.19	2		221.29	64.31
5_5	1.00	1	307.57	0	0.00
5_6	0.18	2		36.52	10.61
6_6	1.00	1	344.09	0	0.00
Total			378.22		

Species turnover was shown to be greater between different geomorphological zones, while being more similar within the same geomorphological zones, independent of downstream distance (Table 5).

Table 5 Within vs. between geomorphological zone aquatic macroinvertebrate similarities, where each pair of adjacent sites were in the same geomorphological zone (1) and in different zones (2) and significance refers to greater similarities within than between zones.

River	No. site pairs	Same zone (1)	Diffnt zone (2)	z-value
Berg	26	3	23	2.488**
Mvoti (Hist.)	55	27	28	-0.918
Mzimkhulu(Hist.)	15	7	8	3.067**
Mzimkhulu	15	10	5	3.123**
Mkuze	6	3	3	1.746*
Thukela	28	5	23	4.559**

* $p<0.1$; ** $p < 0.05$

For the pairwise site similarity comparisons as a function of downstream distance, obvious outliers were excluded from the analyses, as there was a chance that other unaccounted-for drivers were affecting community structure, and the analyses were concerned with riverscape-level trends. Beta diversity for aquatic macroinvertebrates generally showed exponential decay, with half-turnovers being achieved at 20-50% downstream distance from source (Table 6; Figure 12). These values translated into numbers of half changes per river transect of, for example, 2.20 (Berg River) and 3.21 (Mzimkhulu), based on estimates of similarity between the top site on each river compared with subsequent downstream sites. Median rates of decay were *ca*. $x^{-0.3}$, although each river system exhibited its own decay function. The Thukela River was not a good reflection of actual turnover because the site points could not be explicitly identified, and were instead midpoints for different geomorphological zones.

Successive removal of rare species ("very" rare as single site, single abundance species, and rare as single site species) had the effect of decreasing the rate of turnover, while retaining the shape of the turnover signature for each river system (Figures 13-14 and Table 7). Beta diversities for fish showed no significant trends with downstream distance (Figure 15), and fish were not included in further analyses.

Table 6 Beta diversity relationships with % downstream distance (%DD), and % downstream distance where beta-half turnovers were achieved for aquatic macroinvertebrates. Only numbers of sites and numbers of site pairs assessed are provided for fish as the data did not allow for calculation of turnovers.

River	Sites/site pairs	Equation	R^2	Rate of decay	%DD at Half turnover
Berg	7/19	$y = 1.212x^{-0.312}$	0.80	-0.312	40.82
Mvoti (Hist)	8/28	$y = 0.393e^{-0.005x}$	0.14	-0.005	31.83
Mzimkhulu (Hist)	6/14	$y = 0.531x^{-0.145}$	0.30	-0.145	19.91
Thukela	9/25	$y = -0.003x + 0.279$	0.75	-0.003	N/A
Fish	12/66	$y = 0.772x^{-0.035}$	0.08	-0.035	N/A
Mzimkhulu	6/15	$y = 1.049x^{-0.354}$	0.46	-0.354	22.25
Mkuze	4/6	$y = 1.137x^{-0.308}$	0.58	-0.308	47.48
Mvoti	2/1	N/A	N/A	N/A	N/A
Keurbooms	5/10	$y = 4.070x^{-0.693}$	0.43	-0.693	34.22
Mkuze	12/66	N/A	N/A	N/A	N/A
Mvoti	12/66	N/A	N/A	N/A	N/A
Mzimkhulu	14/92	N/A	N/A	N/A	N/A
Sabie/Sand	9/36 & 6/15	N/A	N/A	N/A	N/A

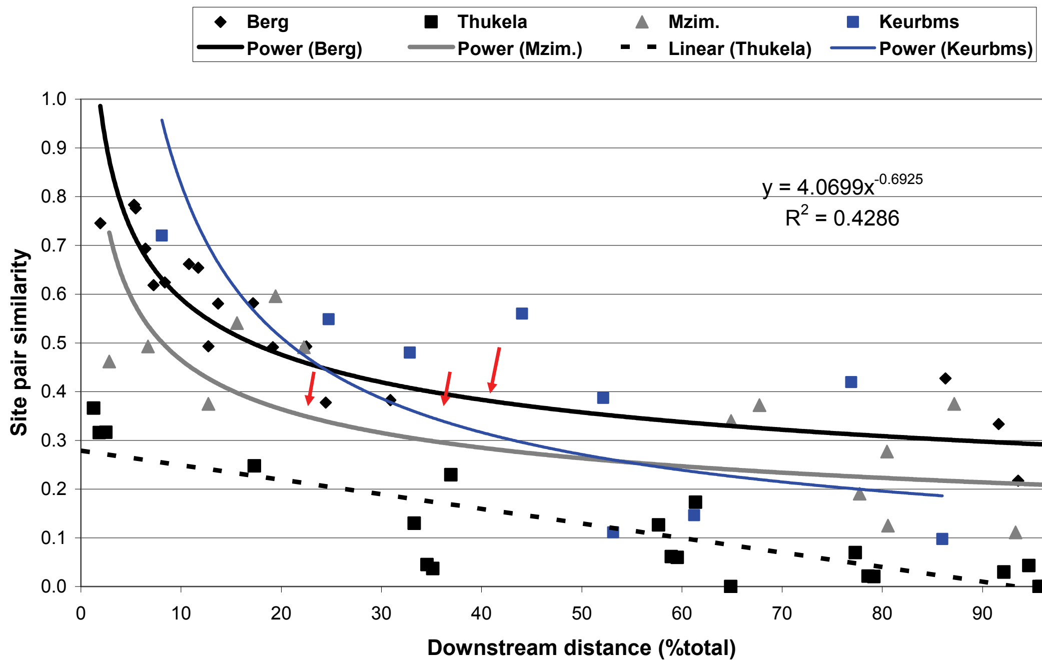

Figure 12 Average beta diversity for total aquatic macroinvertebrate community between site pairs as a function of % downstream distance from source for selected rivers. Red arrows indicate % downstream distance where 50% site similarity is reached.

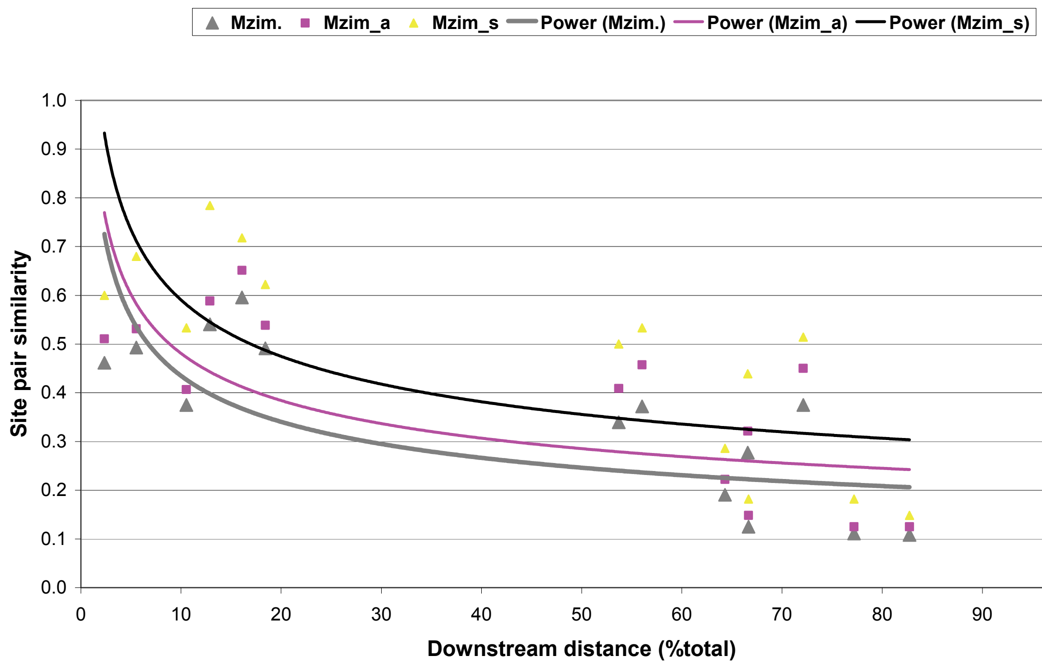

Figure 13 Beta diversity for aquatic macroinvertebrates between site pairs as a function of % downstream distance from source for the Mzimkhulu River, with single occurrence (*_a) and single site (*-s) species removed

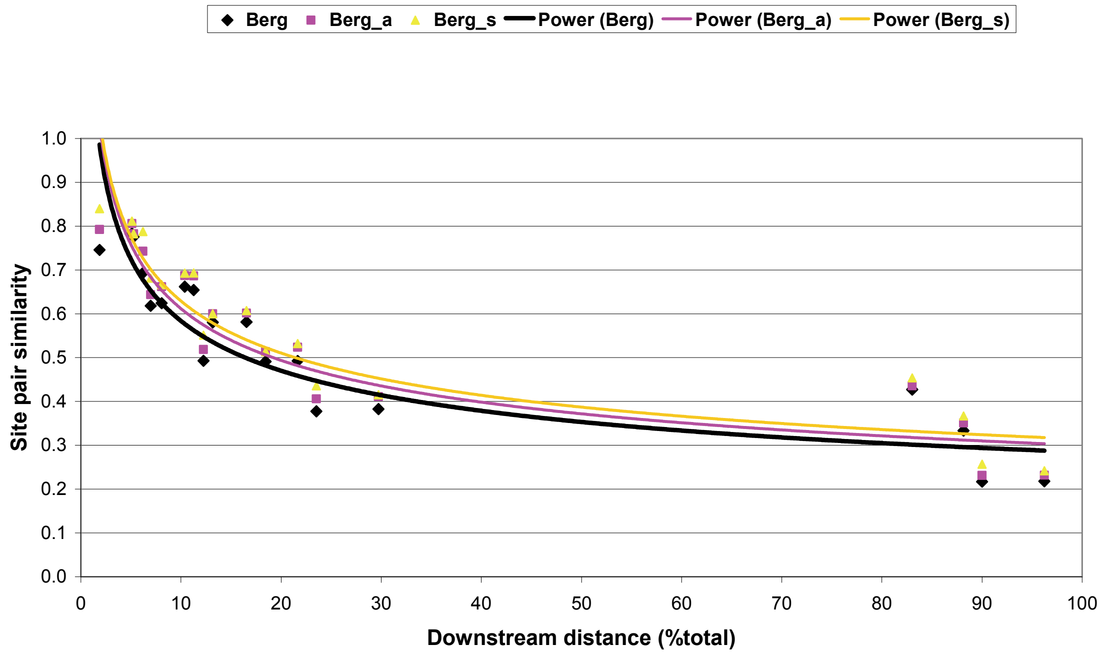

Figure 14 Beta diversity for aquatic macroinvertebrates between site pairs as a function of % downstream distance from source for the Berg River, with single occurrence (*_a) and single site (*-s) species removed

Table 7 Effect of “very rare” (single occurrences) and “rare” (singe sites) species on rates of species turnover for the Mzimkhulu and Berg Rivers

River	Species filtering	Equation	R^2
	All species	$y = 0.981x^{-0.354}$	0.46
Mzimkhulu	Very rare species removed	$y = 1.015x^{-0.324}$	0.41
	Rare species removed	$y = 1.221x^{-0.315}$	0.42
	All species	$y = 1.198x^{-0.312}$	0.80
Berg	Very rare species removed	$y = 1.247x^{-0.309}$	0.82
	Rare species removed	$y = 1.261x^{-0.302}$	0.84

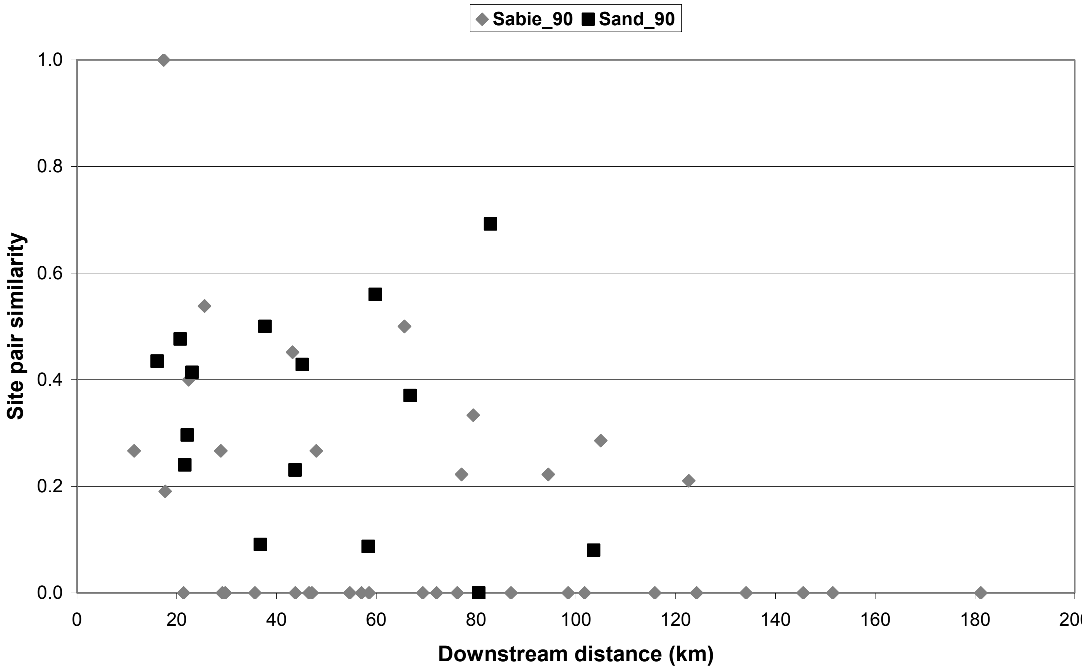

Figure 15 Beta diversity for fish between site pairs as a function of % downstream distance from source for selected rivers

Average species turnover model

The three rivers showing the highest R^2 values for negative exponential decay curves (Berg, Mkuze and Mzimkhulu Rivers) were used to develop a model to estimate the probability of a downstream site not being representative (i.e. site pair similarity ≤50%) of an upstream source site as a function of downstream distance. A binomial logistic regression function (χ^2 probability < 0.001; 299 d.f.) provided the tool to estimate the probability of one site being representative of a second site further downstream (Equation 5; Figure 16).

From the model, the prediction is that on average, there is complete turnover 20% of a river's length away from a source zone. The coefficient of *d* (-0.48) was used to calculate the odds ratio of a downstream site being representative of an upstream source site (Equation 6), viz. that a downstream site is, on average, 6.2 times more likely to be non-representative (similarity < 50%) of an upstream site for every 10% river length.

This figure compares favourably with the species turnovers assumed to occur based on river types as surrogates for macroinvertebrate communities (Figure 17; Table 8). However, this does not take into account the exponential nature of decay in site similarities, such that turnover in the upper reaches is more rapid than turnover in the lower reaches.

$$p = \frac{e^{6.54-0.48d}}{1+e^{6.54-0.48d}} \qquad [5]$$

where *d* is % downstream distance.

$$\Psi = e^{-0.48} \qquad [6]$$

where Ψ is odds ratio

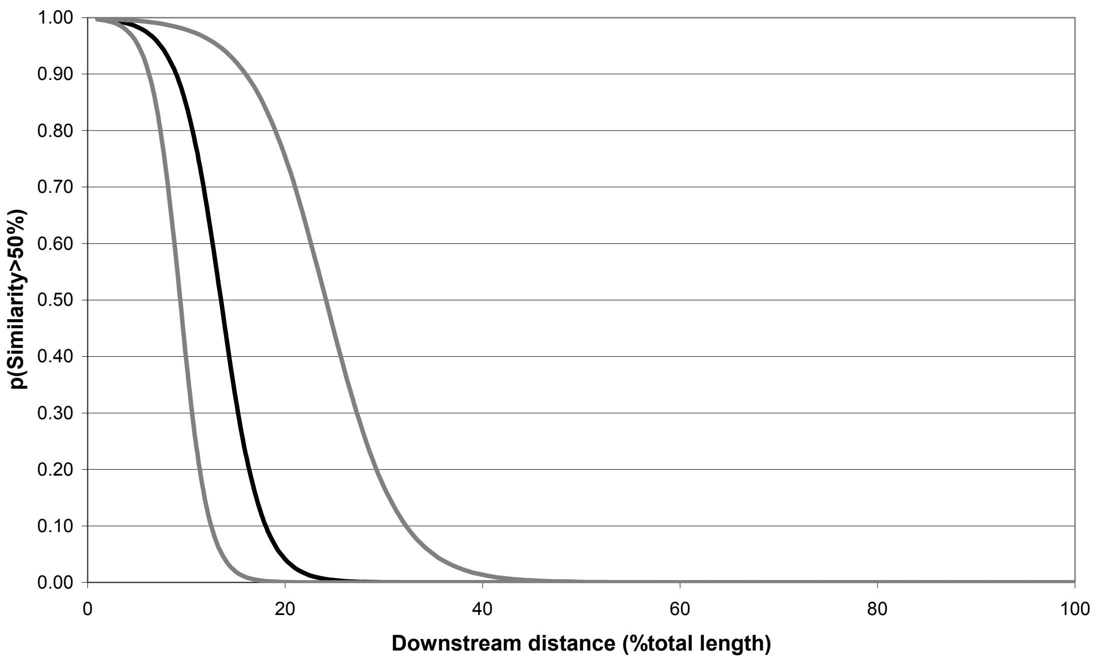

Figure 16 Probability (±95% confidence intervals) of a source site being representative (i.e. site pair similarity ≥50%) of a downstream site

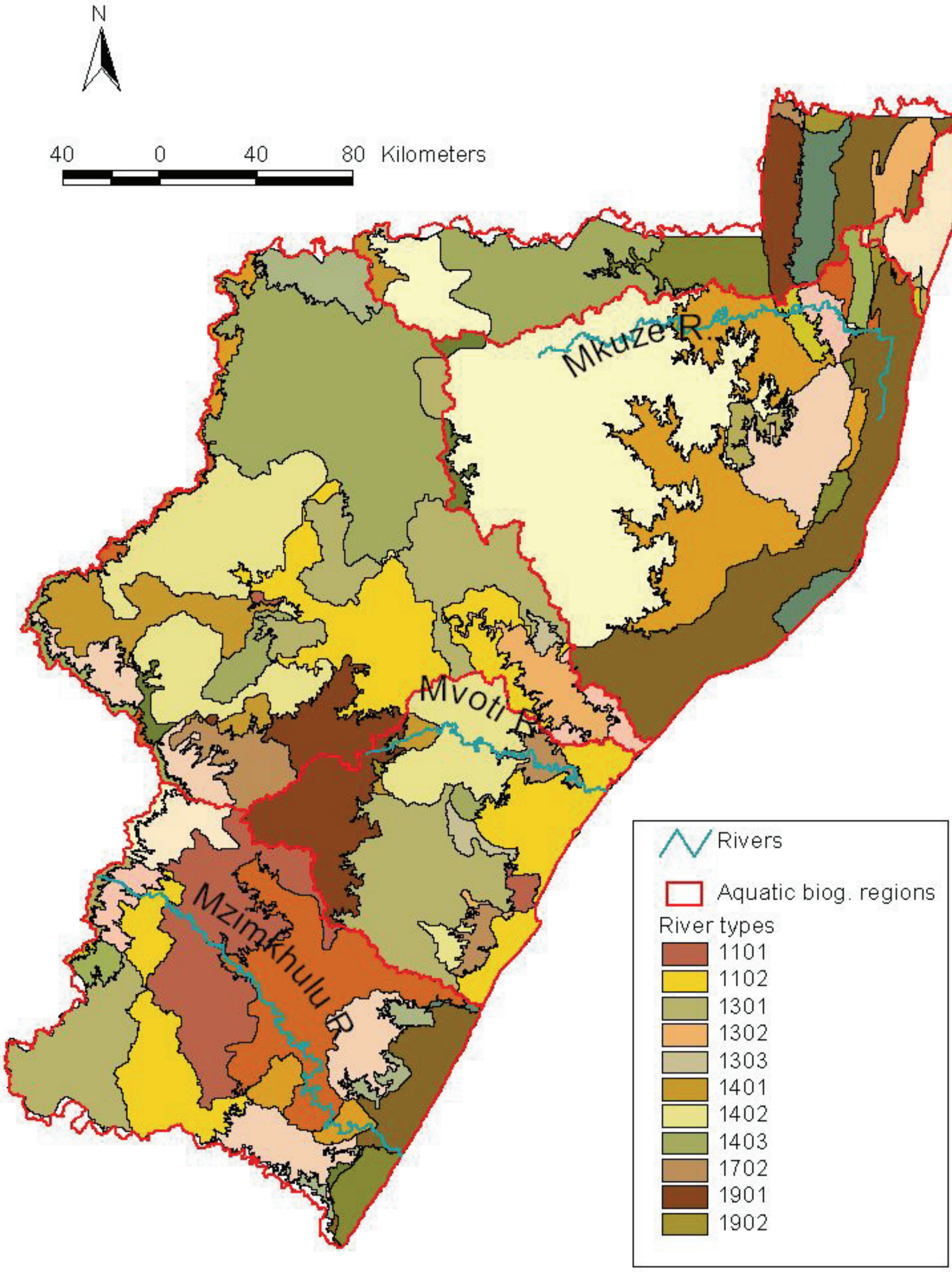

Figure 17 River types as aquatic biodiversity surrogates for KwaZulu-Natal, based on a three-level hierarchical classification from Rivers-Moore and Goodman (2010), and showing the three rivers sampled during this study. Eleven of the 74 provincial river types are illustrated in the legend. The code assigned to river types is a composite number based on the three levels: 10^3 for level I based on six possible aquatic biogeographic regions, 10^2 for level II (11 potential landform and topography types) and 10^1 for level III (four hydrology and low types).

Table 8 River type lengths (% total length) for three river systems in KwaZulu-Natal

	Mkuze	**Mvoti**	**Mzimkhulu**
No. river type reaches	6	5	7
Range of reaches	2.54-33.05	3.73-41.12	0.87-55.86
Mean reach length	16.67	20.00	14.29

Drivers of turnover

Environmental gradients

Principal component analyses of physical, water temperature and flow metrics *vs.* sites on the Mkuze, Mvoti and Mzimkhulu Rivers revealed that all three river systems have unique habitat templates (Figures 18-20; Tables 9-11). Site groups and distributions were different depending on the abiotic templates used to describe them. Based on physical habitat and water quality (Figure 18 and Table 9), sites separated out into clear, high altitude rivers versus turbid, low altitude rivers (Axis 1) with a secondary contribution of narrow, shallow, sandy-bottomed rivers to wider, deeper and rockier rivers (Axis 2).

Sites followed a progressive downstream trend when characterised by water temperatures (Figure 19 and Table 10), with axis 1 contributing 1.3 times more to explaining variation than axis 2. Sites followed the predictions of the river continuum concept, with sites being ranked from cool sites with a wider range of seasonal temperatures (higher coefficient of variability) to warmer less variable sites (Axis 1). Less variation (30.4%) was explained by predictability (which does not preclude a high coefficient of variability) and early summer (November/December) onset of maximum temperatures to later summer maximum temperatures (January).

Finally, for flow patterns as a descriptor of site grouping (Figure 20 and Table 11), axis 1 explained three times more variability than axis 2 (55% vs. 19%). Sites could be grouped as ranging from being more predictable (high predictability, % floods in 60 day period and Base Flow Index) to less predictable on the first axis, with less variation being explained by the number of high pulses which were negatively correlated with different metrics of zero flows (axis 2). The BFI provides a measure of the proportion of flow as baseflow and is an index of short-term variability. Thus rivers with a high BFI are less variable than those with a low BFI (Hughes and Hannart, 2003).

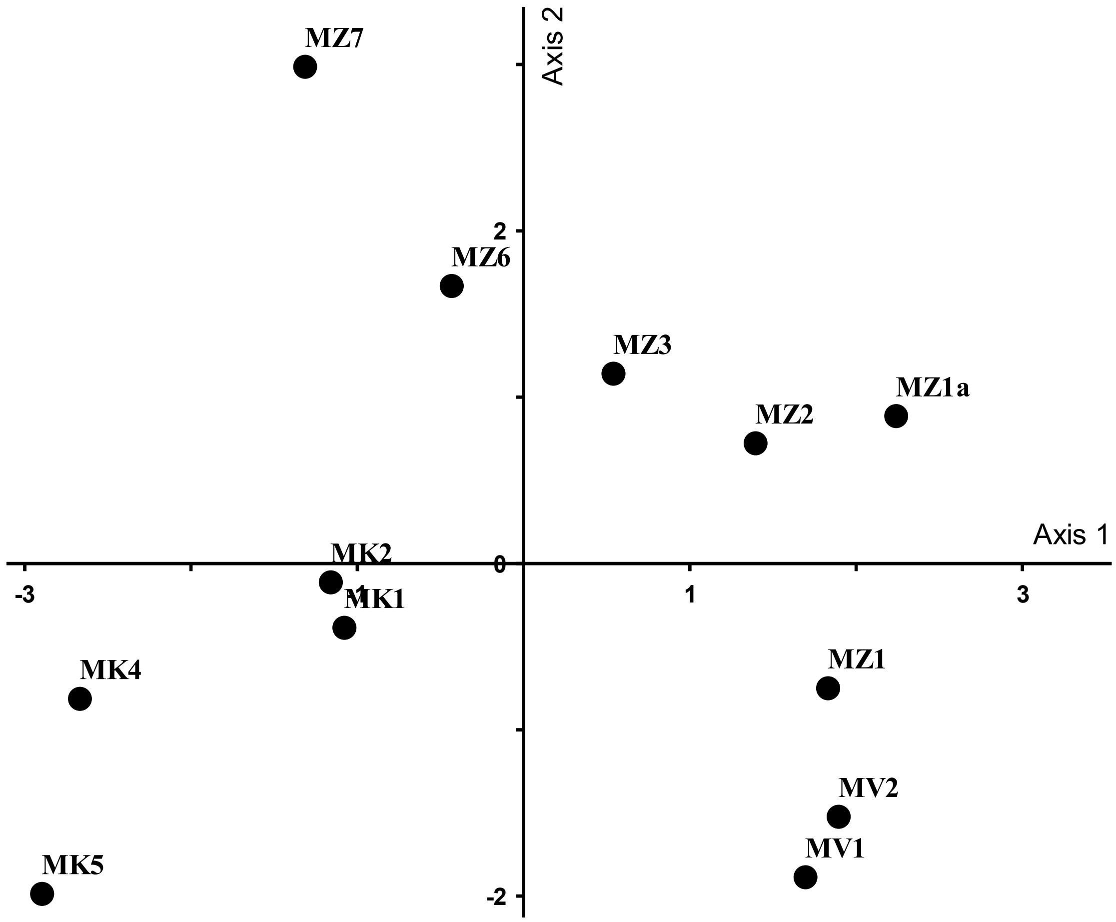

Figure 18 PCA plot of 12 survey sites on the Mkuze, Mvoti and Mzimkhulu Rivers based on physical habitat and water quality.

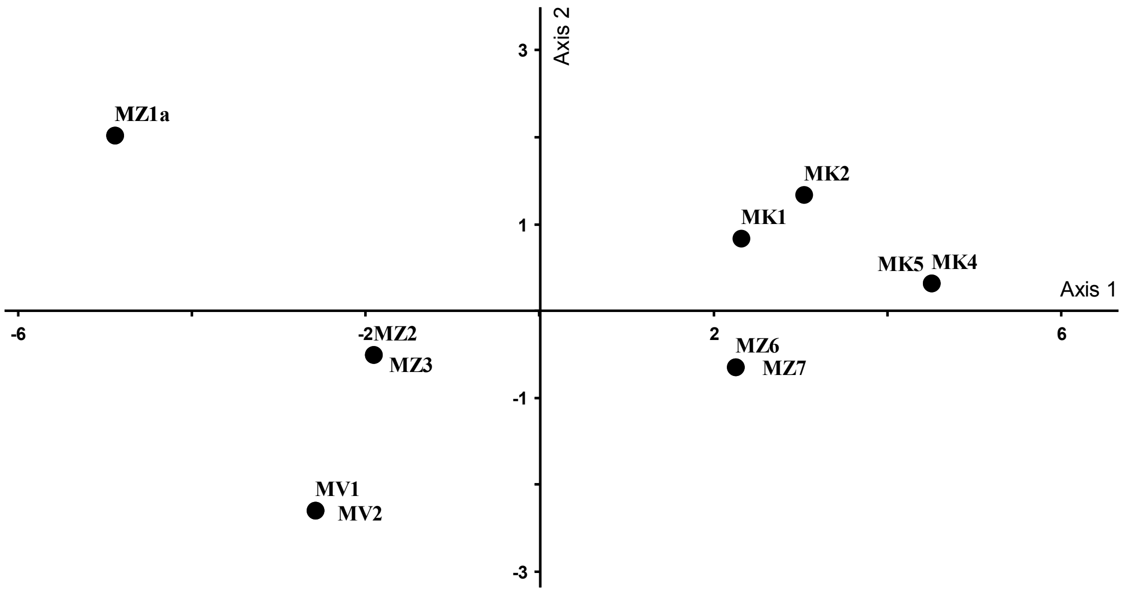

Figure 19 PCA plot of survey sites on the Mkuze, Mvoti and Mzimkhulu Rivers based on water temperature metrics

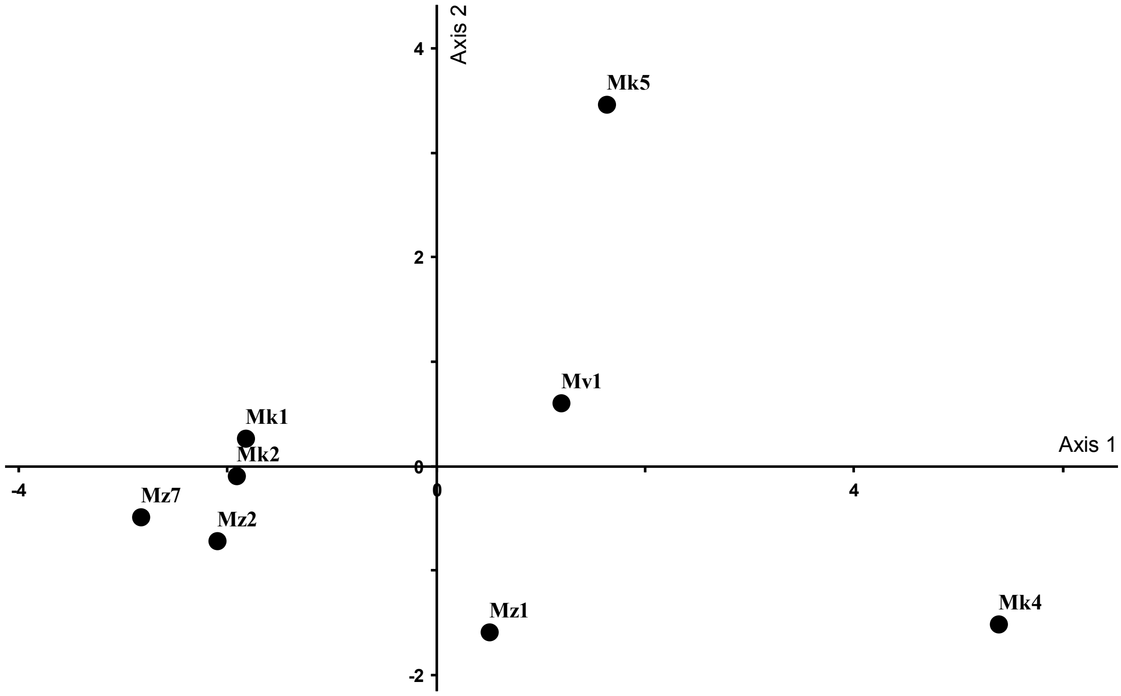

Figure 20 PCA plot of survey sites on the Mkuze, Mvoti and Mzimkhulu Rivers based on flow metrics

Table 9 Eigenvectors of physical variables of sites surveyed in three rivers in KwaZulu-Natal showing the major factors contributing to the ordination.

	Axis 1	**Axis 2**
Eigenvalue	3.08	2.13
% Cum var.	44.06	74.46
Depth	0.04	0.42
Width	0.09	0.59
Turbidity	-0.50	0.20
pH	-0.48	0.19
Conductivity	-0.48	-0.32
Substratum roughness	0.07	0.53
Altitude	0.52	-0.13

Table 10 Eigenvectors of temperature variables of sites surveyed in three rivers in KwaZulu-Natal showing the major factors contributing to the ordination.

	Axis 1	Axis 2
Eigenvalue	11.14	1.89
% Cum var.	74.26	86.87
Mean daily temperature	0.29	0.06
Standard deviation (mean daily temp.)	-0.19	-0.17
Coeff. of variation (mean daily temp.)	-0.30	-0.07
Mean daily temperature range	-0.26	0.21
Mean daily temp - November	0.29	0.08
Mean daily temp - December	0.28	0.18
Mean daily temp. - February	0.30	0.02
Mean daily temp. - April	0.29	0.07
7 day moving average – minimum temp	0.30	-0.02
7 day moving average – maximum temp.	0.28	-0.01
Max. temp. threshold exceed. count	0.29	-0.17
Max. temp. threshold exceed. duration	0.24	-0.39
Julian date of minimum	-0.17	-0.32
Julian date of maximum	0.18	-0.50
Precitability (Colwell, 1974)	-0.13	-0.58

Table 11 Eigenvectors of flow variables of sites surveyed in three rivers in KwaZulu-Natal showing the major factors contributing to the ordination.

	Axis 1	Axis 2
Eigenvalue	6.59	2.24
% Cum var.	54.94	73.64
Mean annual flow	-0.22	-0.12
Coeff. of variation (mean annual flow)	-0.28	-0.04
Predictability (Colwell, 1974)	-0.34	-0.20
% floods in 60 day period	-0.38	0.06
Base flow Index (mean)	-0.35	0.16
Base flow Index (coeff. var.)	0.38	-0.04
Julian date of maximum	0.30	-0.26
High pulse count	0.24	-0.48
Avg. no. days zero flows.year^{-1}	0.25	0.50
Avg. successive days zero flow	0.10	0.60
No flow recurrence interval	-0.13	-0.06
One-year probability (zero flow)	0.32	-0.05

River profiles

River profiles for four rivers in KwaZulu-Natal and the Berg River all showed clear inflection points, separating the rivers into upper and lowland zones (Figures 21, 24). The profiles for the rivers in KwaZulu-Natal also demonstrated a number of convex anomalies indicating previous geological uplift events. When profiles were plotted in conjunction with measures of alpha diversity (Figures 22, 24) and community similarity (from uppermost site and downstream paired sites) (Figures 23, 25), the sites of highest diversity and zones of highest turnover coincide with the profile inflection points.

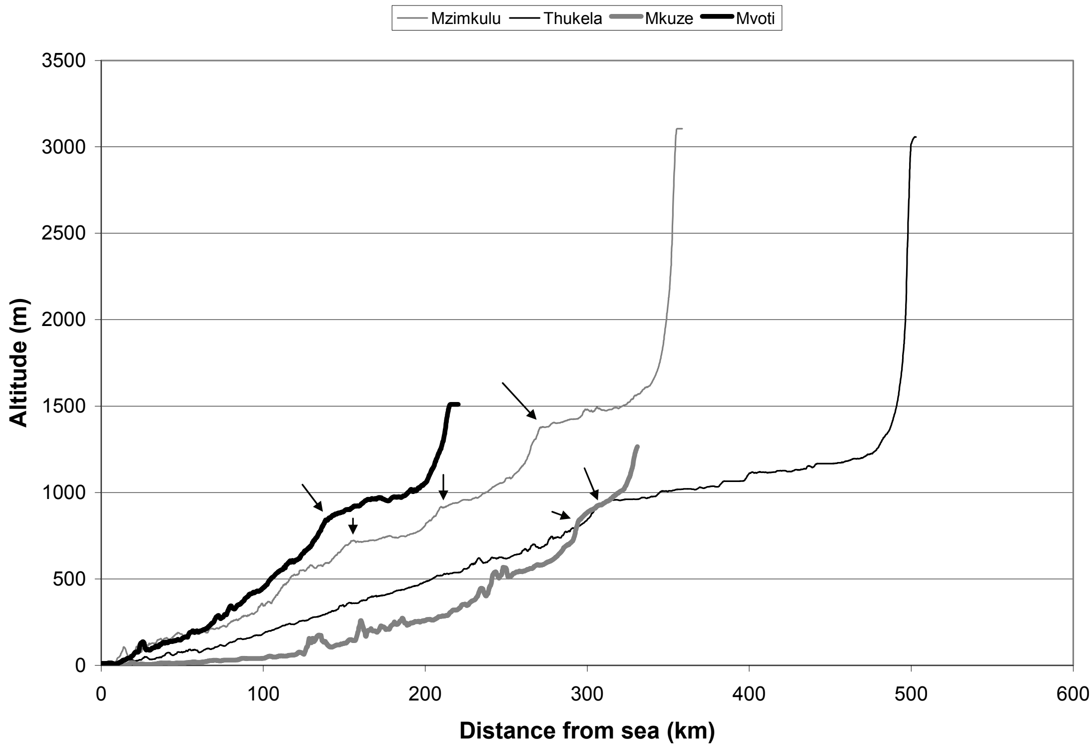

Figure 21 River profiles for the Mzimkhulu, Thukela, Mkuze and Mvoti Rivers in KwaZulu-Natal. Arrows indicate crest of axis of maximum Pliocene uplift (convex upward zones) (after Partridge and Maud, 2000)

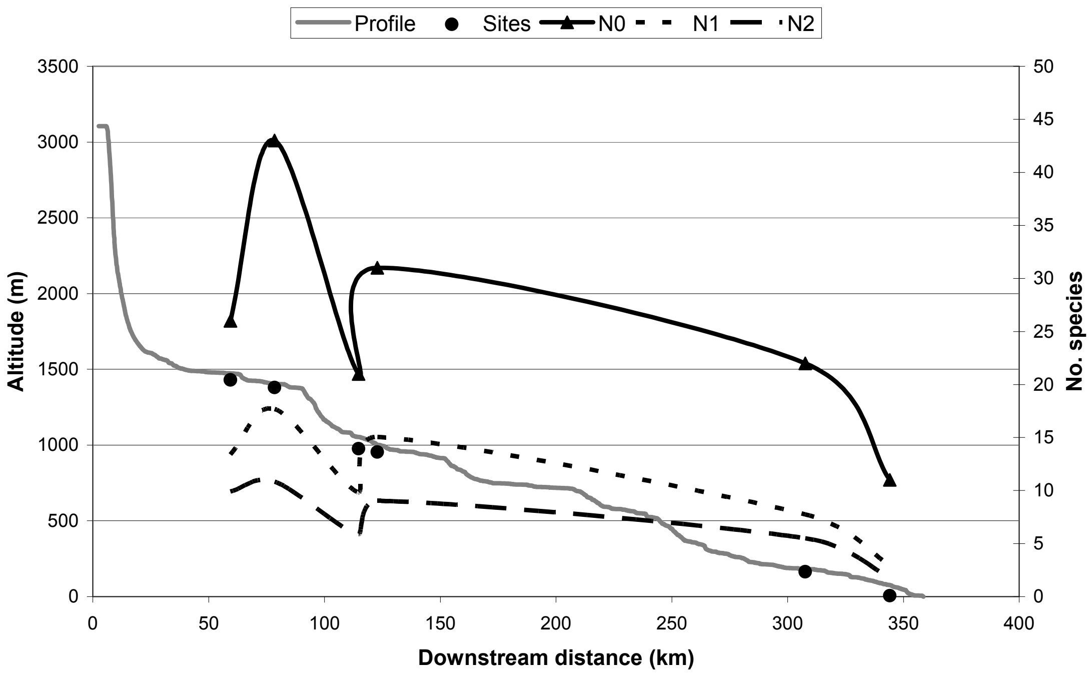

Figure 22 Profile of the Mzimkhulu River plotted correlatively with Hill's measures of alpha diversity

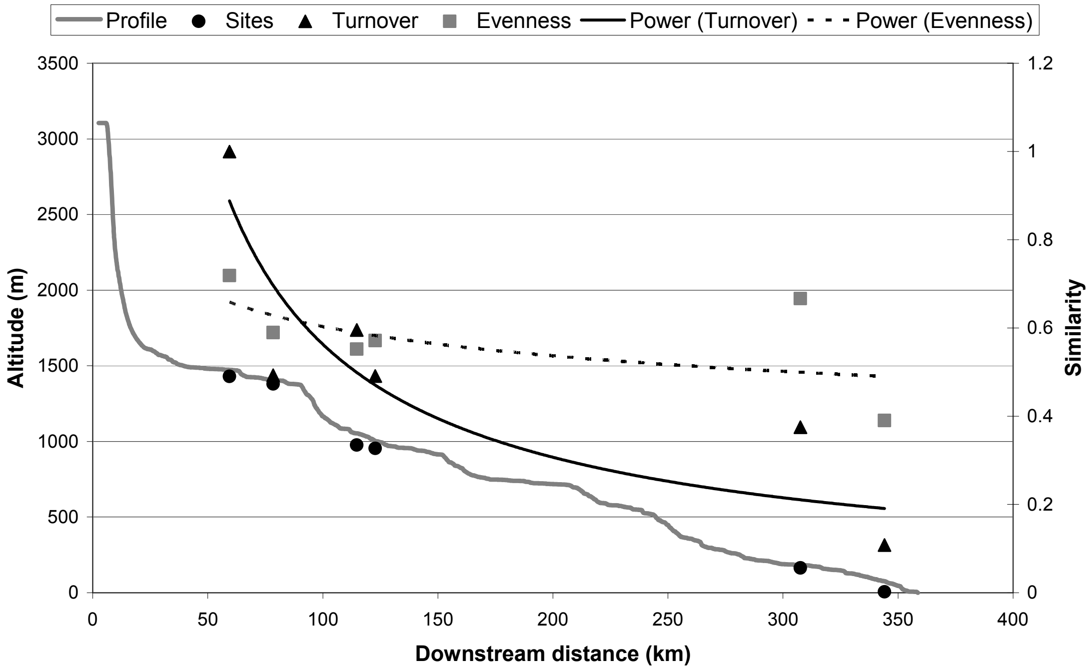

Figure 23 Profile of the Mzimkhulu River plotted correlatively with Hill's evenness index and Sørenson's similarity index (all similarities relative to uppermost site) measures of alpha diversity

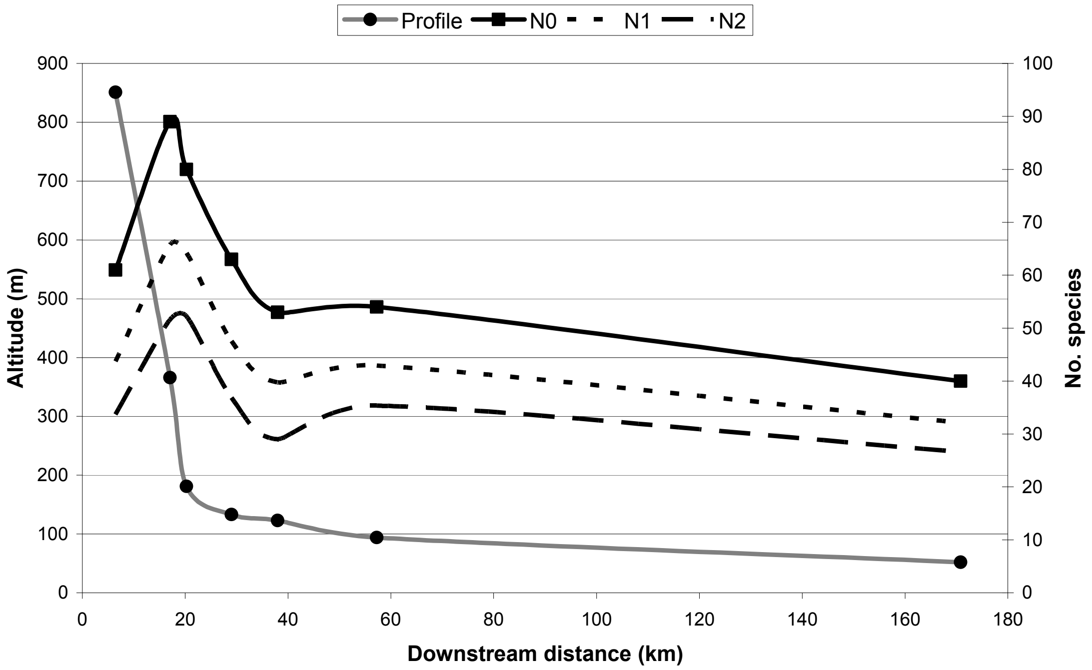

Figure 24 Profile of the Berg River plotted correlatively with Hill's measures of alpha diversity

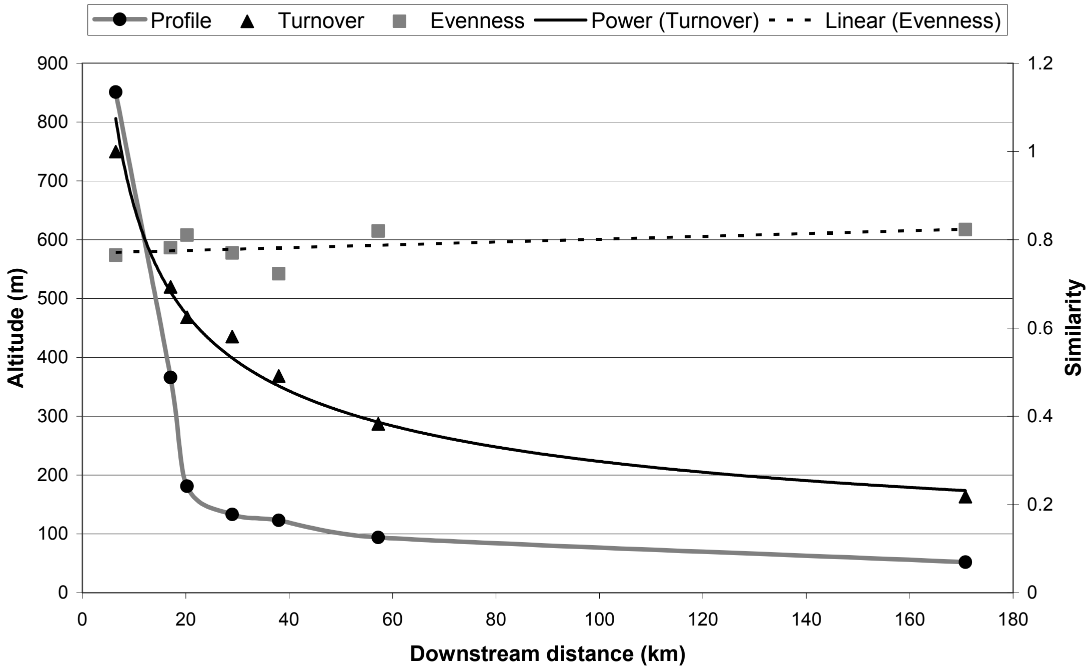

Figure 25 Profile of the Berg River plotted correlatively with Hill's evenness index and Sørenson's similarity index (all similarities relative to uppermost site) measures of alpha diversity

Gamma diversity

As a conservative estimate for four rivers in four different ecoregions (Mkuze, Mvoti, Mzimkhulu and Berg), total river species similarities between paired river systems were 40-50% for river in KwaZulu-Natal, and 5% on average between the Berg River in the Western Cape and the KwaZulu-Natal rivers (Table 12). Gamma diversity was highest for the Mzimkhulu-Berg and Mkuze-Mzimkhulu Rivers, and lowest between the adjacent Mkuze-Mvoti River basins.

Table 12 Gamma diversity values for Mkuze, Mvoti, Mzimkhulu and Berg Rivers

	River	Mkuze	Mvoti	Mzimk.	Berg
Alpha		53	55	81	137
	Mkuze	1.00			
Beta	Mvoti	0.50	1.00		
	Mzimkhulu	0.43	0.51	1.00	
	Berg	0.04	0.03	0.06	1.00
	Mkuze	N/A			
Gamma	Mvoti	81	N/A		
	Mzimkhulu	105	101	N/A	
	Berg	186	189	212	N/A

DISCUSSION

Alpha diversities – selection of focal river reaches

The results of this study, that highest species diversity occurred in mid-order streams and at an intermediate distance down a river's longitudinal axis, are in agreement with northern hemisphere studies (for example, Minshall et al., 1985), and in agreement with the predictions of the River Continuum Concept (Vannote et al., 1980). Within this diversity gradient, community structure is complicated by the relative contributions of rare, abundant, and very abundant species. According to the Fisher Series (Whittaker, 1972), site-specific alpha diversity is typically made up of few very common or very rare species, with many "middling" common ("abundant") ones (Whittaker, 1952). One approach is to calculate the ratio of common to rare species and plot this as a function of downstream distance and stream order. The number of common species peaks in intermediate sections of river axes (Cucherousset et al., 2008), again in agreement with the predictions of the River Continuum Concept, and that common species provide a better approximation of overall species patterns as opposed to rare ones. Pragmatically, conservation targets for rivers could focus on the common and widespread species, with rare and threatened species targeted individually. However, what should guide the selection of target river zones are the conservation planning goals (Rondinini and Chiozza, 2010): Are the goals for rarity or maximum species number (pattern), or process (which would target the more common species which are driving system energy dynamics). Not accounted for in this study was seasonal effect on alpha diversity, where highest species diversity has been recorded from summer samples, which coincide with periods of greatest temperature variability (Minshall et al., 1985).

Beta diversity – how much river should be conserved?

In this study, fish were not a useful measure of determining river conservation targets, while aquatic macroinvertebrate species patterns exhibited predictable patterns of turnover with downstream distance, and are valuable in setting conservation targets. This anomaly may be due to fish being long-lived, density-dependant and typically dynamic and in a non-equilibrium state due to river system resets. Conversely, aquatic macroinvertebrates are relatively short-lived, density-independent and in equilibrium with a changing seasonal environment (Minshall et al., 1985). Beta diversity is partly driven by dispersal ability of fauna between stream networks (Clarke et al., 2010), with many aquatic macroinvertebrates having an adult flight stage.

This research showed that average species turnover happens at predictable rates, and that these rates could be decomposed into turnover of common ("core") species, which are further accelerated by rare species (single occurrences) and narrow range species (single site occurrences). Moreover, what drives this turnover with downstream distance are break-points and river geomorphology. The detection of boundaries (ecotones), which typically coincide with an increase in species diversity, is an essential ecological issue, and qualitative data (presence/absence) facilitates the location in space where species turnover is highest. The concept of beta diversity turnover related to environmental gradients, and half-turnover (which evaluates the number of species in common at the two extremes of a gradient: Fortin and Dale, 2006) was well-established in early ecological studies (Whittaker, 1952, 1960, 1972; Whittaker and Niering, 1965, 1968). It is recognised that sharp environmental change occurs as a result of geomorphology and topography, while gradual environmental change is driven by geography and climate (Fortin and Dale, 2006). Understanding turnover patterns thus requires a spatially hierarchical understanding of river systems before targets should be set.

To understand the sharper ecotones requires knowledge of geological history and how this translates into different river profiles. The clear differences in turnover patterns between the Berg and Mzimkhulu Rivers, for example, can be partially explained through their different geological histories. According to Skelton (1986), the Berg River versus the KwaZulu-Natal rivers have different biogeographical histories for fish, which is as a consequence of different geological histories. The Berg River falls within the Cape Fold Belt, while the KZN rivers fall within the Karoo sedimentary basin zone (Partridge and Maud, 2000). The latter rivers fall within an erosional landscape characterised by series of waterfalls and rapids. It is noted that the uplift period of the Miocene resulted in river profiles which are typically convex upward, and carry heavy sediment loads (erosion) and deeply incised, and that faunal turnover was a response to geological change (Partridge and Maud, 2000).

The more subtle environmental changes driven by geography and climate were also apparent in this study. A combination of physical habitat, water temperature (magnitude and timing) and flows (predictability, magnitude of high flow events and perenniality) added to the understanding of turnover patterns for the Mkuze, Mvoti and Mzimkhulu Rivers. While Whittaker (1972) predicts that diversities are lower in unstable environments because fluctuation reduces the size of the niche hyperspace, the data from this research do not permit the testing of this hypothesis beyond the principle that turnover was undoubtedly driven by habitat variables at a range of scales.

Disruptions to the river continuum (in-channel – for example, the Great Fish River, and within the catchment) impact on the rate of turnover. The Great Fish River is not a free-flowing river, but is useful heuristically in that it shows what a disturbance does to turnover independent of geomorphological zone because all sites fell within the same geomorphological zone. The response of a system to impact gradients may be linear or non-linear (Allan, 2004; Lindenmayer et al., 2008). The non-linear approach inherently assumes the existence of ecological thresholds, following which there is a significant system change. The amount of natural vegetation at catchment scale has been found to be a good predictor of river habitat integrity (Amis et al., 2007). For example, analyses by Allan (2004) found that streams in agricultural catchments usually remain in good condition until the extent of agriculture exceeds 30-50%. Similarly, for every 10% of altered catchment land use, a correlative 6% loss in freshwater diversity was noted, as a linear relationship (Weitjers et al., 2009). The turnover pattern may thus be clouded by both catchment and river disturbance. The cumulative impact of small dams within a catchment has been shown to impact on water quality and quantity (Mantel et al., 2010a). Similarly, the numbers of opportunistic taxa have been shown to increase in catchments with a high density of farm dams, while taxa sensitive to pollution and disturbance declined (Mantel et al., 2010b).

Consistent with other research on South African rivers, aquatic macroinvertebrate communities in this study could be grouped into upland versus lowland assemblages, and also defined by geomorphological zones (Dallas, 2004). This study also showed that the rate of species turnover in the South African rivers assessed was related to environmental gradients and breakpoints, where the more variable upper sites have more rapid turnover than reaches further downstream. This implies that the upper reaches require more representative conservation zones than the reaches further downstream. However, within this generalisation it is clear that each river system studied was unique, showing different rates of beta diversity turnover with downstream distance. From comparisons with existing conservation target setting approaches, the predicted complete turnover every 20% of the overall total length of river from a source site, implies that there should be at least five specific conservation zones within any river system, although this is a generalization because of the concertina effect in the upstream sections of rivers, as shown by the exponential decay in site similarities. While this figure agrees with the number of river types determined for the Mkuze, Mvoti and Mzimkhulu Rivers from this study (see Rivers-Moore et al., 2011), using a blanket 20% target per river type is thus probably a simplistic approach to setting targets, particularly for the upper river zones with higher species turnover.

Gamma diversity – how many basins should be targeted?

Recent studies continue to make use of the multiplicative relationship between alpha and beta diversity in determining gamma diversity to partition gamma diversity into alpha and beta (Jost, 2007;

Clarke et al., 2010). Such studies are providing surprising insights informing regional conservation planning. For example, beta diversity between eight 1st order headwater streams in Victoria, Australia was found to be low, while the alpha diversity contribution in headwater streams was high i.e. each stream had relatively low irreplacability since each site contained a large portion of shared diversity (Clarke et al., 2010). As only four rivers were assessed in this study, it was difficult to draw definite conclusions on gamma diversity. The basic gamma diversity estimates from this study show that to achieve riverscape-level conservation of aquatic biodiversity, it is necessary to explicitly target as many different primary catchments as possible. Under resource-limited conditions, it is more pragmatic to choose primary catchments further apart than closer together within the conservation planning region. An inverse distance weighting algorithm for primary catchment types would address this issue.

APPLICATION

Conservation of inland water systems is a cross-sector responsibility shared between several sectors of society and departments of government (Roux et al., 2006), which can be achieved through the framework already developed by Roux et al. (2009). In achieving conservation of rivers, it is critical to develop objective methods of setting targets for how much of each biodiversity feature are set aside to act as biodiversity "banks" as protection against future potential attrition of rivers. This directly address the identified goal of inland water conservation:

> *"to conserve a sample of the full variety or diversity of inland water ecosystems that occur in South Africa, including all species as well as the habitat, landscapes, rivers and other water bodies in which they occur, together with the ecosystem processes responsible for generating and maintaining this diversity, for both present and future generations".* (Roux et al., 2006, p. 36)

To meet this goal, five key cross-sector policy objectives have been identified by Roux et al. (2006). This research directly address the first policy objective (*Set and entrench quantitative conservation targets for inland water biodiversity*), which highlights the value of setting conservation targets, by recommending that 20% of each inland water ecosystem type be maintained as a natural class. It was previously recognised that this national target be applied differentially at a sub-national scale, and that these targets should be reviewed every five years. Also, management and conservation of inland water ecosystems must address maintenance or re-establishment of environmental gradients in rivers (Objective 3: *persistence*, Roux et al., 2006, p. 58) The fourth objective (*Establish a portfolio of inland water conservation areas*) advocates choosing biodiversity hotspots which yield highest conservation returns at least cost.

In meeting the aim of this research - to develop a scientific method to set conservation targets for river lengths –three of the five cross-sector policy objectives are directly and indirectly addressed. The methods developed here provide guidelines on how to define differential sub-regional targets, and maintenance of environmental gradients and ecotones (hotspots) are central to application of these targets.

Ideally, given that each river has a unique bio-physical signature, targets should be set per river based on each river's biological data. Often, conservation planners do not have the luxury of collecting new data, and planning must occur using a more generic approach. The methods developed here are based on average rates of turnover with downstream distance, and can be applied in data-rich or data-poor scenarios. For a refined quantitative target-setting approach, it is recommended that the 20% target be adjusted to cater for upland and lowland targets as an initial refinement to the existing 20% targets, with at least a 20% target in lowland zones and a 40% target in the upper zones. This is based on the logic that turnover occurs every 10-20% of a river length.

Given the spatial scales at which river conservation planning is occurring (provincially and nationally), what is required to facilitate planning is to apply the approach developed here in a rule-based, automated GIS conservation planning tool framework. A suitable brief could be phrased as:

> "*We need to target at least x geomorphic zones per system, with at least x% of the length of that system, and within each ecoregion we need to target at least x number of different river systems*" (Nel, 2010, *pers. comm.*)

The first key element to be addressed is to define what is meant by a "river system". Primary catchments are too coarse in their spatial resolution, and incorporate a number of major tributaries whose biological uniqueness will be lost at this resolution (see, for example, the Thukela catchment, which would obscure that value of its major tributaries: Klip, Bushmans, Sundays, Mooi and Buffalo Rivers). Using secondary catchments avoids this pitfall, and this is an appropriate spatial resolution at which to define river systems. Theoretically, gamma diversity between secondary catchment pairs is then calculated, using a suitable river system classification (see Rivers-Moore et al., 2011) (Figure 26), with biological data ideally obtained from a national rivers species database. For example, data from four rivers in this study were spatially represented using the highest gamma diversity paired rivers as the starting reference point (Berg/Mzimkhulu Rivers: γ = 212), and applied iteratively for subsequent pairs (Mzimkhulu/Mkuze Rivers: γ = 105; Mkuze/Mvoti Rivers: γ = 81).

The correlation between inflection points in river profiles and aquatic macroinvertebrate ecotones, particularly the upland and lowland division of rivers, identifies aquatic biodiversity "hotspots". These zones can readily be identified for all rivers in South Africa, as calculation of river profiles at a 1:500 000 scale is relatively simple to automate using a grid-based geographical information system. Using the average probability model from this study, the probability of any site upstream or downstream from these focal zones can be calculated using a spreadsheet, and spatially represented using a vector-based geographical information system. This analysis can be undertaken on a per-reach basis (Figure 26, lower left), or iteratively working upstream and downstream of the identified ecotone, with new focal zones being spatially identified whenever the probability of representivity upstream or downstream of an ecotone falls below 50% (Figure 26, lower right). Such an approach can be automated with relative ease, provided a national rivers coverage has been broken down into small enough segments, each with its total downstream length attributed.

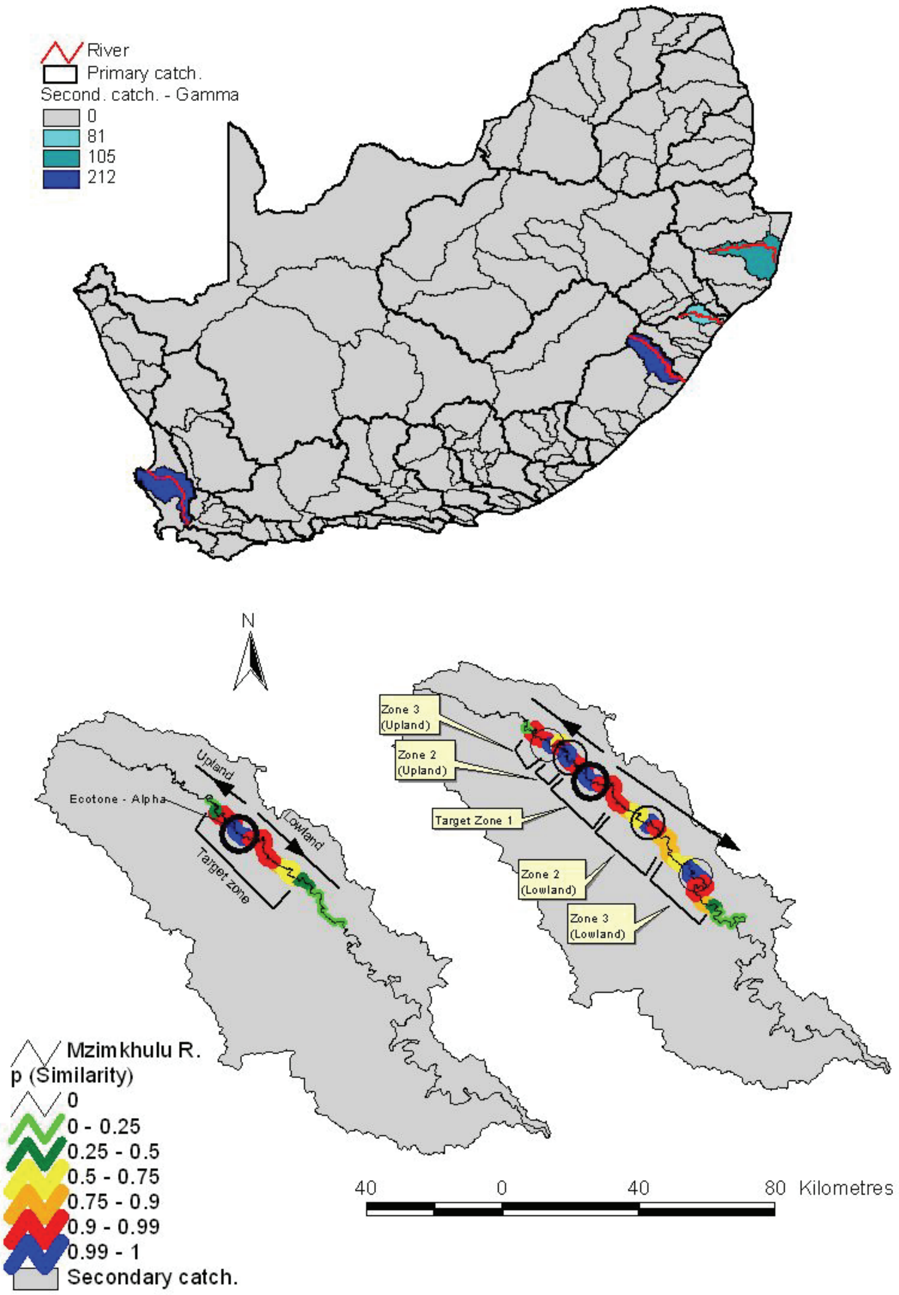

Figure 26 Example of spatial application of river targets using the Mzimkhulu River. Gamma diversity is first calculated for river systems defined at secondary catchment level, using paired rivers (top). The ecotone of highest alpha diversity, coinciding with the profile inflection point separating upland and lowland rivers, is the target starting zone. The probabilities of upstream and downstream sites being representative of this ectonal community are calculated from the model (bottom, left), which identified the target river length. When the probability of representivity falls below 50%, a new focal zone is established, and probabilities of representivity are iteratively recalculated (bottom, right)

RECOMMENDATIONS: FUTURE RESEARCH

- Ongoing refinement of a river classification of river types for South Africa. This should be hierarchical, beginning at the level of a river system (defined here as the mainstem in a secondary catchment), and sub-quaternary, focussing on biotope heterogeneity, geomorphology, and intra-annual flow patterns. Implicit in this recommendation is the need to develop explicit aquatic ecoregions for South Africa.
- From the higher level (secondary catchment/river basin) classification (above), selecting a pre-defined set of drainage basins as a focus for river conservation is required, and targets for selected drainage basins based on their gamma diversity need to be defined.
- For each identified drainage basin, developing diversity profiles for the primary river to facilitate setting upland and lowland river targets.
- Ongoing refinement and population of the BioBase (Dallas et al., 1999). This includes the practical elements of custodianship and funding of this critical resource, and the developmental side of being able to query the database per aquatic ecoregion to provide conservation planners with associated species community descriptions.
- Investigating the role of tributaries as aquatic biodiversity refugia, and investigating links between tributary drainage density and aquatic macroinvertebrate community turnover rates.
- Automating the process of setting river targets in a spatial conservation planning system, by including gamma diversity per secondary catchment, ecotone identification and calculation of probability of representivity (turnovers) with downstream and upstream distance from ecotones.
- Refining the average turnover rate model from this research to turnover rates by stream order.

CONCLUSIONS

The percentage target approach is a useful yet flawed one for identifying areas of conservation importance, and the approach of applying a percentage target of the total river length of each river ecosystem type has at least raised awareness of the concept of sensitive freshwater ecosystems, as applied both regionally and nationally (Nel, 2010, *pers. comm*.; Rivers-Moore et al., 2011). While there is no doubt that a blanket 20% “societal agreement” target for different river types is appropriate in the absence of any other data, the question of how to apply targets in a practical sense remains difficult to answer. Should the target (for example, 17-20%) be applied as ecosystem targets: a percentage of each river type assessed, or a percentage of the mainstem river; or should it be applied as a species approach: percentage of rare species occurrences or of “common” species? How much of a river to conserve is ultimately a function of the overall conservation goals – for rare species, narrow range species, common species, or process.

Nuances with respect to alpha, beta and gamma diversity should be catered for to achieve conservation targets more attuned to species patterns in different river systems. The data clearly show that the upper river zones are the key lengths in driving species patterns, and consequently upper river zones should be weighted more heavily in conservation planning than lowland zones. This contention is further reinforced because of the upstream-downstream interdependence of rivers, the finding that each river system studies has slightly different turnover rates in response to different environmental gradients; and because turnover is a negative exponential decay function,. The concept of a “one-size-fits-all” percentage target is not an appropriate approach for rivers. River types assume boundaries and ecotones, and the obvious ecotonal boundary to advocate more than a single generalized target value per river type is the clear distinction in turnovers between the steeper upper river zone and the less steep lowland zone. Ultimately differential targets should be set for different geomorphological zones, using as a basis the hydraulic biotope heterogeneity per zone as the dialectic, as these are one of the key drivers in species turnover. What remains to be quantified are the seasonal effects on alpha diversity; and the mathematics firstly of alpha and beta diversity partitioning and their contributions on gamma diversity, as illustrated for Australian headwater streams (Clarke et al., 2010), and secondly of the ratio of common to rare species as a function of downstream distance and biotope types.

An intermediate, surrogate-based approach is to refine river type classifications for upper river zones (upstream of profile inflections), and focus on selected river systems at a secondary catchment level, rather than a percentage target of types. A practical mechanism for achieving this is to link ecosystem services to level of river health, where catchment stakeholders decide on the level of services they would require or like (a desired state), which is then related back to ecosystem integrity by freshwater ecologists. Such a concept has been entrenched in South African water policy for Water Resource Classification (Dollar et al., 2010). Securing upper catchments are likely to maintain more natural rates of species turnover and maintain river sections where species richness is highest. Implicit in this is necessary major paradigm shift in environmental policy, which reverses the current burden of proof from environmentalists defending natural systems, to developers proving why a development is sustainable and how the stream ecosystem goods and services is not diminished.

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APPENDICES

Appendix A1 Site locations and water quality data for the Mkuze, Mvoti and Mzimkhulu Rivers

River	Site	Lat. (°S)	Long. (°E)	Depth (m)	Width (m)	Turbid.[1]	pH	Cond. (μs)	S-rough[2]	Altitude (m amsl)
Mkuze	**Mk1**	-27.676	31.445	0.50	21.5	1	9.20	354	2.44	500
	Mk2	-27.627	31.642	0.39	22.0	1	9.40	262	2.78	341
	Mk3	-27.580	31.987	0.31	22.3	1	10.29	505	2.11	121
	Mk4	-27.599	32.302	0.59	14.0	1	9.80	664	0.56	51
Mvoti	**Mv1**	-29.202	30.437	0.46	9.0	0	8.25	75	1.56	1050
	Mv2	-29.160	30.627	0.73	6.0	0	7.90	74	1.56	969
Mzimkhulu	**Mz1**	-29.832	29.522	0.54	40.0	0	8.95	35	1.22	1430
	Mz2	-29.883	29.577	0.64	50.0	0	8.60	37	2.89	1380
	Mz3	-30.012	29.732	0.41	54.0	0	9.14	38	2.78	977
	Mz4	-30.038	29.775	0.79	34.0	1	8.85	39	2.78	954
	Mz5	-30.652	30.198	0.70	45.0	1	9.00	80	3.00	165
	Mz6	-30.707	30.396	1.10	60.0	1	10.09	98	2.56	6

[1] Rivers assigned a qualitative value of 0 for clear water and 1 for turbid water

[2] Substratum roughness, calculated using equation A1 (after Statzner et al., 1988)

$$k_v = (5C_1 + 3C_2 + C_3)/9 \qquad \text{[A1]}$$

where k_v is substratum roughness, and the subscripts 1-3 refer to most, second-most and third-most dominant substratum types

Appendix A2 Water temperature (°C) and flow (m^3s^{-1}) metrics for the Mkuze, Mzimkhulu and Mvoti Rivers

River		Mean temp.	Temp. (CV)	Temp. range[1]	Mean flow	Flow (CV)	Predict-ability
Mkuze	**Mk1**	23.59	14.52	13.68	5.97	3.14	0.35
	Mk2	24.56	13.82	14.64	8.15	2.93	0.35
	Mk3	25.38	12.87	12.32	3.19	1.61	0.22
	Mk4	25.38	12.87	12.32	4.68	1.69	0.27
Mvoti	**Mv1**	20.23	17.67	14.48	0.99	1.44	0.31
	Mv2	20.23	17.67	14.48	0.99	1.44	0.31
Mzimkhulu	**Mz1**	19.22	18.13	16.27	7.61	1.66	0.38
	Mz2	19.22	18.13	16.27	7.61	1.66	0.38
	Mz3	19.94	16.59	14.68	8.61	2.07	0.42
	Mz4	19.94	16.59	14.68	8.61	2.07	0.42
	Mz5	23.95	14.12	14.12	34.97	2.57	0.39
	Mz6	23.95	14.12	14.12	34.97	2.57	0.39

[1] Range refers to mean daily temperature range

Appendix B Species matrices for 12 sites sampled for the Mkuze, Mzimkhulu and Mvoti Rivers, where numbers are relative abundances.

Group/Order	Family	Taxon	Mk1	Mk2	Mk3	Mk4	Mv1	Mv2	Mz1	Mz2	Mz3	Mz4	Mz5	Mz6
Coleoptera	Dytiscidae: Colynbetinae: Colymbetini	*Rhantus* sp.			2									
	Dytiscidae: Hydroporinae: Bidessini	*Uvarus peringueyi*?										1		
		Yola sp.		1										
	Dytiscidae: Hydroporinae: Hydrovatini	*Hydrovatus* sp.								5				
	Dytiscidae: Laccophilinae: Laccophilini	*Laccophilus* sp.	1					5		1				
	Elmidae: Elminae	Elminae Type 1 sp.		3			7	1	2	4	8	32		
		Elminae Type 2 sp.					31		1	2	7	6		
		Helminthopsis sp.					1			5				
		Pachyelmis amaena?	1											
		Pseudancyronyx humeralis natalensis?					2							
		Pseudomacronychs? sp.	1											
		Stenelmis prusias?								1		1		
	Gyrinidae: Gyrininae: Gyrinini	*Aulonogyrus* sp.			4		5					7		
	Gyrinidae: Gyrininae: Orectochilini	*Orectogyrus* sp.					5						1	
	Heleophoridae	*Helophorus* sp.				1								
	Hydrophilidae: Hydrophilinae: Berosini	*Berosus* sp.								4	1			
	Hydrophilidae: Hydrophilinae: Laccobiini	*Laccobius* sp.			1									
	Psephenidae	*Afrobrianax ferdyi*?	1	2			2				3		1	
	unknown	Coleoptera sp.	1				1							
Collembola	Entomobryidae	Entomobryidae sp.							1					
Decapoda	Atyidae	*Caridina africana*	17	14	19			17					29	
		Caridina nilotica	1			12	101							66
	Palaemonidae	*Macrobrachium rude*												6
	Potamonautidae	*Potamonautes clarus*									2			
		Potamonautes dentatus												1
		Potamonautes sidneyi						1						
Diptera	Ceratopogonidae: Ceratopogoninae	*Bezzia* sp.		1				1						
	Chironomidae: Chironominae: Chironomini	*Polypedilum* spp.		3			3		3	4	4		2	
	Chironomidae: Chironominae: Tanytarsini	*Stempellina* sp.		4			3			1			1	
	Chironomidae: Orthocladiinae	*Cardiocladius* sp.					5		3					

		Cricotopus spp.		2			45	4	9		1	4	1	1
		Limnophyes sp.						1						
		Orthocladiinae sp.					12		1	1				
		Paraphaenocladius sp.						1						
		Rheocricotopus capensis							5	23		3		
		Thienemanniella sp.										1		
	Chironomidae: Tanypodinae	*Conchapelopia* sp.					1			2				
	Simuliidae	*Simulium* (Anasolen) *dentulosum*								2				
		S. (Edwardsellum) *damnosum s.l.*		2						2				
		S. (Meilloniellum) *adersi*	2	8										
		S. (Meilloniellum) *hirsutum*								2		2		
		S. (Meilloniellum) *sp.*						1			3			
		S. (Metomphalus) *albivirgulatum*							5					
		S. (Metomphalus) *chutteri*			11				1				4	
		S. (Metomphalus) *hargreavesi*					101		43	66				
		S. (Metomphalus) *medusaeforme* group								2		6		
		S. (Metomphalus) *sp.*					101						12	
		S. (Nevermannia) *nigritarse? s.l.* group							50		1			
	Tipulidae: Limoniinae	*Antocha* sp.					12						1	
		Limnophila sp.										6		1
		Limonia (Dicranomyia) capicola			1							1		
	unknown	Diptera sp.	5							6				
Ephemeroptera	Baetidae	*Acanthiops erepens?*							29				17	
		Afrobaetodes sp.			4									
		Afroptilum sp.								18				
		Baetidae sp.								13				
		Baetis spp.	15	65			38		75	101	39	67		
		Centroptiloides bifasciata?					1							
		Cheleocloeon mirandei						6						
		Cloeon/Procloeon sp.					6							
		Dabulamanzia sp.					7							
		Demoreptus sp.	1				4		31	12		2		
		Labiobaetis/Pseudocloeon spp.	30	9	29	8	15	120		50		33	7	2

		Pseudocloeon glaucum										8		
	Caenidae	*Caenis* sp.	6	4		4	4	52	1	9	1	1		
	Heptageniidae	*Afronurus barnardi*	7	4			3		13	11	32	5	4	
	Leptophlebiidae	*Adenophlebia auriculata*	6											
		Euthraulus sp.		3	3		8	2	1		4			
	Oligoneuriidae	*Oligoneuriopsis elizabethae?*							1	2				
	Prosopistomatidae	*Prosopistoma* sp.								2				5
	Tricorythidae	*Tricorythus* sp.		1			9		19	3	1	1	44	1
Hemiptera	Corixidae: Micronectinae	*Micronecta* sp.										2		
	Naucoridae	Naucoridae sp.											1	
	Naucoridae: Naucorinae	*Macrocoris* sp.	4											
		Naucoris obscuratus		6	17	1	15	12		26		4		
	Nepidae: Ranatrinae	*Ranatra* sp.											1	
	Notonectidae: Anisopinae	*Anisops* sp.							1					
	Notonectidae: Notonectinae: Nychiini	*Nychia limpida*											2	
	unknown	Hemiptera sp.			1									
	Veliidae: Microveliinae	*Microvelia* sp.												1
	Veliidae: Rhagoveliinae	*Rhagovelia* sp.	1	11	2	1	6					4		
	Veliidae: Veliinae	Veliinae sp.								5				
Lepidoptera	Crambidae: Nymphulinae	*Nymphula* sp.					2							
Mollusca	Ancylidae	*Burnupia* sp.								74				
		Ferrissia sp.					6		21		3	4	83	
	Lymnaeidae	*Lymnaea natalensis*	1			1								
	Planorbidae: Bulininae	*Bulinus africanus* group								21				
	Thiaridae	*Melanoides tuberculata*	4	13		79								
Odonata:	Aeshnidae	*Aeshna subpupillata*					3							
Anisoptera		*Anax* sp.												1
	Corduliidae	*Phyllomacromia bifasciata?*		1										
	Gomphidae	*Onychogomphus supinus?*										3		
		Paragomphus sp.			1	1		1						
	Libellulidae	*Macrodiplax cora?*		1										
		Olpogastra fuelleborni?	1											
		Sympetrum fonscolombii						1						

		Tetrathemis polleni?		1									
		Trithemis sp.			1							1	
		Zyxomma atlanticum?		1									
Odonata:	Calopterygidae	*Phaon iridipennis*			3								
Zygoptera	Coenagrionidae	Coenagrionidae sp.										1	
		Pseudagrion sp.	4		1	6	15		8		2	1	
Plecoptera	Perlidae	*Neoperla* sp.				1		2	5	5	24	2	
Polychaeta	Capitellidae	*Dendronereis arborifera*											3
Trichoptera	Hydropsychidae: Hydropsychinae	*Cheumatopsyche afra*	11	2	15		4	13	5				
		Cheumatopsyche maculata								1			
		Cheumatopsyche sp.		45		6		6	6	4	11	25	
		Cheumatopsyche thomasseti	5	16	3								
		Hydropsyche longifurca?				23			1	3	7		
		Hydropsychidae sp. adults							3				
	Hydropsychidae: Macronematinae: Macronematini	*Leptonema natalense*	4	4		3							
		Macrostemum capense				3							
	Leptoceridae	*Athripsodes corniculans?*							1				
		Athripsodes harrisoni group sp.	1				1		1				
		Homilia knysnaensis					4						
		Leptocerus inflatus?							3				
		Oecetis sp.				4							
		Setodes squamosus?								1			
		Triaenodes sp.					1						
	Philopotamidae	*Chimarra* sp.		1		5		9	3	4	2		
Turbellaria	Tricladida	*Dugesia* sp.	2	2					1		7		

Appendix C Fish sampled for the Mkuze, Mzimkhulu and Mvoti Rivers from previous studies and present study, with species names arranged alphabetically, as opposed to taxonomically. The letter "P" indicates presence of fish from historical database, while numbers in brackets indicate abundance of fish caught during this study. Numbers of species at each site from the historical database and from current survey are indicated. Catch per unit effort was not calculated, but total time sampled is indicated.

Site	Mk1	Mk2	Mk3	Mk4	Mv1	Mv2	Mz1	Mz3	Mz6
Time fished	N/A	09:08	11:47	N/A	09:27	12:30	15:55	09:26	24,00
Acanthopagrus berda									(1)
Amphilius natalensis					(1)				
Anguilla mossambica						P		P	(1?)
Awaous aeneofuscus									P
Barbus anoplus							(1)	P (1)	
Barbus viviparus			(5)			P (2)			
Brycinus lateralis			P	P					
Eleotris fusca									P (1)
Glossogobius callidus									P (1)
Labeo molybdinus	P	(3)	(3)						
Labeobarbus natalensis		(3)			P (4)	P		P	P
Microphis brachyurus									P
Microphis fluviatilis									P
Micropterus punctulatus					P				
Monodactylus falciformis									(1)
Myxus capensis									(5)
Oncoryhnchus mykiss							(7)		
Oreochromis mossambicus	P	(2)							P
Tilapia sparrmanii						P			
No. species	2 (N/A)	N/A (3)	1 (2)	1 (N/A)	2 (2)	4 (1)	N/A (2)	3 (1)	7 (6)

Appendix D Observed ("raw" alpha diversities – N_0-obs) and expected species numbers (N_0-exp)for four rivers. Percentage underestimates of expected species numbers per site and averaged per river are indicated.

River	Sites	N_0-obs	N_0-exp	% unobs	Means
Berg	B1	61	67	9.8	
	B3	89	95	6.7	
	B5	80	81	1.3	
	B9	63	74	17.5	
	B10	53	55	3.8	
	B12	54	55	1.9	
	B18	40	40	0.0	5.8
Mkuze	Mk1	26	50	92.3	
	Mk2	30	51	70.0	
	Mk3	18	28	55.6	
	Mk4	9	28	211.1	107.2
Mvoti	Mv1	41	76	85.4	
	Mv2	21	45	114.3	99.8
Mzimkhulu	Mz1	26	34	30.8	
	Mz2	43	61	41.9	
	Mz3	21	38	81.0	
	Mz4	31	45	45.2	
	Mz5	22	31	40.9	
	Mz6	11	28	154.5	65.7
Mean				56.0	
SD				55.8	