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Influence of Stream Order on Compositional and Structural Riparian Biodiversity in south-western Kruger National Park

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A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfillment of the requirements for the degree of Master of Science

Johannesburg, July 2011

I declare that this dissertation is my own, unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.



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Abstract

Riparian zones harbour different species pools from the surrounding landscape and are thus important to biodiversity conservation. However, riparian zones are highly variable. Network characteristics, morphology, flow-sediment interactions, biophysical connectivity and biological characteristics all vary along the length of a river. It could therefore be expected that the biodiversity characteristics of different riparian zones may also be variable. To investigate this, this study quantified compositional and structural diversity in 1st, 2nd, 4th, 5th, and 7th stream order rivers in south-western Kruger National Park (KNP). A suite of measures, chosen to encompass the variety, balance, and disparity properties of diversity, was used to quantify woody vegetation and bird compositional and structural diversity within each stream order.

Woody plant species richness and species diversity was highest in the 7th order river and similar in the 1st through 5th order rivers. Likewise the woody vegetation community composition of the 7th order river was distinct from those in the other stream order rivers. Bird species diversity was similar in all five stream orders considered. Bird community composition of the 7th order river was distinct from the bird community composition of the 4th and 5th order rivers, which in turn was distinct from the bird community composition of the 2nd and 1st order rivers. Woody vegetation height, canopy width and diameter diversity tended to be highest in the 4th and 5th order rivers, while number of stem (NoS) diversity was generally highest in the 1st order rivers and decreased along the stream order sequence to the 7th order river. Bird body mass diversity was highest in the middle of the stream order sequence, while bird wing length/body length (WL/BL) and leg length diversity was similar along the entire stream order sequence. Overall, a variety of patterns of change in biodiversity along the stream order sequence were observed

The lack of a consistent pattern along the stream order sequence among the different elements of compositional and structural diversity illustrates that no single measure can properly characterise the biodiversity of an area, and thus researchers and managers need to be explicit about which aspect of biodiversity they are aiming to study/conserve. Additionally, the unique combination of biodiversity found in each of the stream orders illustrates that each contributes importantly to overall

regional biodiversity, and thus there is need to consider the role of entire drainage networks in the landscape, rather than simply focusing on perennial rivers. Finally, this study illustrates the need to consider the heterogeneous nature of biodiversity itself.

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Chapter 1:

Introduction

1.1 Basis for the study

A common notion in ecology is that riverine corridors are more species rich than their upslope landscape counterparts (Gregory *et al.* 1991; 1993). This elevated richness is thought to be related to variable flood regimes, geomorphic channel processes, altitudinal climate shifts, and upland influences on the fluvial corridor (Naiman *et al.* 1993). Higher species richness in riparian zones has been observed in some systems (Woinarski *et al.* 2000; Catterall *et al.* 2001; Brown & Peet 2003) but not in others (McGarigal & McComb 1992; Pearson & Manuwal 2001; Schade *et al.* 2003). In a meta-analysis using data collected from seven continents and a range of taxa, Sabo *et al.* (2005) found that riparian zones do not harbour higher numbers of species, but rather support significantly different pools from other parts of the landscape. Thus, while it may not always be correct to assume that riparian corridors are more species rich than the surrounding landscape, they do play an important role in promoting regional species richness.

Riparian corridors are highly variable. Network characteristics (e.g. area drained), morphology (e.g. channel gradient), flow-sediment interactions (e.g.

sediment storage), biophysical connectivity (e.g. between hillslope/channel), biological characteristics (e.g. production) and human impacts (e.g. land use) all vary along the length of a river (Cullum *et al.* 2008). The well-known river continuum concept describes, among other things, how the structure and function of biological communities found within rivers changes from headwaters to mouth (Vannote *et al.* 1980). Considering the variation present within riparian systems, it is logical to hypothesize that the biodiversity characteristics of different parts of these systems will also be variable. However, there is limited knowledge in this regard.

Examination of broad patterns of biodiversity variation associated with changes in riverine characteristics requires similar rivers to be grouped together. The concept of stream order is helpful in this regard and has proven useful in grouping streams of shared geomorphological and ecological properties (Naiman *et al.* 2005). In Strahler's method of stream ordering, all unbranched streams are classified as first order, two first combine to make a second order, two second combine to make a third order, and so on (Strahler 1957). Strahler's method has been used by several authors in the few attempts to quantify biodiversity in different riparian systems.

The distribution of a number of different taxa has been shown to correlate with stream order. Crunkilton and Duchrow (1991) sampled benthic macroinvertebrates in different stream orders in the United States of America (U.S.A) and found diversity to be highest in stream orders 4 and 5 with decreased values in lower and higher order streams. Whiteside and McNatt (1972) and Beecher *et al.* (1988), also working in the U.S.A., found fish species richness to be positively correlated with stream order. Fish species diversity was also positively correlated with stream order (Harrel *et al.* 1967; Barila *et al.* 1981). A similar pattern was shown by birds in the Pacific Northwest where species richness was greater on large rivers (i.e. high stream order) than on smaller rivers (i.e. lower stream order) (Lock & Naiman 1998). Nilsson *et al.* (1994) found that main channels often have higher riparian plant species richness than their smaller tributaries in Sweden.

These examples suggest a positive relationship between biodiversity and stream order, however, this trend has not been thoroughly tested. Furthermore, most of the studies listed above considered only species richness, neglecting the many other aspects of biodiversity. There is a need to more comprehensively understand

how biodiversity in its entirety varies across a wide range of stream orders. To do this it is necessary to understand fully what is meant by the term biodiversity.

Biodiversity as an ecological concept and biodiversity as a measurable entity are often two different things. The United Nations Environment Programme (Heywood 1995, p. 8) defines the ecological concept of biodiversity as "the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic systems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems." Alternatively, in her comprehensive book 'Measuring Biological Diversity', Magurran (2004, p. 8) defines biodiversity as "the variety and abundance of species in a defined unit of study." As an ecological concept, biodiversity is interesting as it has the potential to reflect the nature of the underlying processes and organization that structure a community (Sugihara 1982). Thus, in this context, areas that are highly biodiverse would theoretically perform ecological functions more efficiently and have higher conservation value. However, the relationship between biodiversity and ecosystem functions, such as productivity and nutrient cycling, is still the subject of much debate (Naeem *et al.* 1994; Tilman *et al.* 1996; Huston 1997; Kaiser 2000). Scientists are still searching for a characterization of biodiversity that will most clearly reveal these functional connections. Their search has led to a multitude of measurement techniques (Magurran 2004; Botta-Dukat 2005; Petchey & Gaston 2006) and researchers trying to quantify biodiversity must carefully consider which of these are the most appropriate for their study. Studies are therefore frequently designed to ensure that specific measurement techniques can be used, thereby moving the focus from biodiversity as an ecological concept to biodiversity as a measurable entity. This difficulty led Ricotta (2005, p. 29) to write: "in practice biodiversity has suffered from a great number of definitions that vary with the specific needs of the different researchers, thus making it extremely confusing as an ecological concept." Research should be designed in such a way that a variety of biodiversity measurement techniques can be applied, but importantly, these measurements should still allow biodiversity to be interpreted as an ecological concept.

Recognizing biodiversity as an ecological concept, Noss (1990) described biodiversity as consisting of three components; compositional, structural and

functional diversity, that can be measured at several levels of ecological organization. A comprehensive account of biodiversity should consider all three components, but this is extremely difficult. In practice ecologists choose, or are often forced (by time and/or money constraints), to focus their research upon a specific component of biodiversity at a specific level of organization. The majority of past biodiversity research has been focused upon compositional diversity, with ecologists investigating patterns in the distribution and abundance of species (Naeem 2002). This has changed in recent years and studies concerned with structural (e.g. de Casanave *et al.* 1995; Anten & Hirose 2001; Asner *et al.* 2008) and functional diversity (e.g. Diaz & Cabido 2001; Kinzig *et al.* 2001; Walker & Langridge 2002) are now becoming more common. Nonetheless, structural and functional diversity remain the more poorly understood components of biodiversity, and more research to include these two components is needed.

Diversity is a concept common to a variety of disparate disciplines. Stirling (2007) recognizes three properties of diversity; *variety*, *balance* and *disparity*. Variety answers the question: "how many types of things do we have?" Balance answers the question: "how much of each type of thing do we have?" Disparity answers the question: "how different from each other are the types of things that we have?" It is necessary to include all three of these properties when measuring diversity in any discipline. The examination of biodiversity should thus not only include the study of compositional, structural and functional components, but also measurements of the *variety*, *balance* and *disparity* properties of each of those components.

To further understand how riparian biodiversity might vary with changes in riverine characteristics, this study was designed to examine the relationship between stream order and compositional and structural riparian biodiversity within the Kruger National Park (KNP). Woody vegetation and bird diversity were measured in rivers ranging from first stream order to seventh stream order. Woody vegetation was studied as it plays a major role in defining structural diversity. Birds were chosen as they are a well known component of the biodiversity of this region, and have been shown to respond to differences in vegetation structure (MacArthur & MacArthur 1961; Roth 1976; Wiens & Rotenberry 1981) as well as to differences in floristic composition (Ralph 1985). I measured biodiversity using numerous

techniques ranging from indices to multivariate statistics to simple descriptions, and made sure to include measurements that incorporated the *variety*, *balance* and *disparity* properties thereof. This was done with the aim of describing the pattern of change in biodiversity across stream orders in such a way that the emphasis was upon the ecological concept of biodiversity.

Kruger National Park management aims to "maintain biodiversity in ALL its facets and fluxes, to provide human benefits and build a strong constituency". Riverine areas contribute significantly to regional diversity, and thus the maintenance of riparian biodiversity is of priority to the KNP. Much of the riverine research in the KNP has focused upon the large perennial rivers, and there is a lack of information on the diversity of both fauna and flora in the smaller, lower order rivers. This study contributes significantly in this regard through its description of the distribution of compositional and structural diversity (ALL three properties thereof) across a savanna drainage network.

1.2 Important concepts

This study aims to determine how riparian biodiversity varies along a stream order sequence. In doing so it embraces concepts drawn from the fields of biodiversity and riverine ecology. A brief review of the pertinent concepts in these two fields follows:

1.2.1 Biodiversity

The earth is home to an extraordinary diversity of life which has captured the human imagination for centuries. Indeed it is estimated that some 13 million species exist today (Heywood 1995), although it is recognized that this estimate may be out by more than an order of magnitude (Wilson 1997). The study of this biological diversity (biodiversity) has recently become a scientific specialization in its own right.

Biodiversity: Definition and Components

Simplified definitions of biodiversity, such as those found in general biology textbooks, might define biodiversity as "the number and variety of living organisms" (Solomon *et al.* 1999, p. 1211). A definition such as this is adequate as a description of biodiversity to the general public; however, as an ecological concept the definition of biodiversity is more complex. Biodiversity encompasses all levels of natural variation from the genetic level to the species level to the landscape level. It includes the variation in population structure to the variation in species identities to the variation in landscape processes. A single definition of biodiversity that is simple, comprehensive and operational is thus unlikely to be found. It is perhaps easier to conceptualize biodiversity in the framework provided by Noss (1990).

Noss (1990) provides a hierarchical characterization of biodiversity. He recognizes three components of biodiversity; compositional, structural and functional diversity. Compositional diversity has to do with the identity and variety of elements in a collection. It includes species lists, measures of species diversity and measures of genetic diversity. Structural diversity is the physical organization or pattern of a system, from habitat complexity as measured within communities to the pattern of patches and other elements at a landscape scale. Functional diversity involves ecological and evolutionary processes, including gene flow, disturbances and nutrient cycling. These three components can be measured at several levels of

organization, ranging from the genetic level to the landscape level. This characterization provides a conceptual framework for identifying specific, measurable indicators to assess the overall status of biodiversity. The choice of which component to measure at which level of organization is dependent on the question asked.

What is appropriate for my question? The spatial scale of this study was relatively small, with some of the lower order rivers measuring approximately one kilometer in length. At this scale it was appropriate to measure biodiversity at the species/community level of organization. Other research has examined species richness in rivers of different stream order, but I wanted to expand on this by measuring structural diversity as well as a range of compositional diversity characteristics. Time constraints prevented the inclusion of functional diversity.

1.2.2 Measurement of biodiversity

It is necessary to measure the *variety*, *balance* and *disparity* (Stirling 2007) properties of compositional and structural diversity to understand the complete range of biodiversity present within a riverine system.

Measurement of compositional diversity

Species richness, simply the number of species in a particular area, is the oldest and simplest measure of compositional diversity. At the community level of organization it measures the *variety* property of diversity. A basic problem with this measure is that it is often not possible to enumerate all of the species in a natural community. Furthermore, it also does not take into account that different species may occur in different abundances. Think about two communities that contain 10 species each, but in the first community each species is equally abundant while in the second community one species is dominant and makes up 91% of all the individuals. Would you judge the communities to be equally diverse? *Species evenness* is a diversity measure that takes this into account and quantifies the relative abundance with which each species is represented in an area. Species evenness answers the question: “how much of each type of thing do we have?”

Measures that combine the concepts of species richness and species evenness are known as *species diversity* measures. The most widely used of these are the

Shannon-Wiener index and Simpson's index. Fisher's alpha, or α diversity, is another species diversity index which is becoming increasingly popular (Magurran 2004). However, the use of any species diversity index can be somewhat controversial. It has been argued that different species diversity indices can give virtually the same value for very different patterns of species abundance. Furthermore, it is possible to come up with hypothetical patterns of species abundance which different diversity indices would rank in opposite order (Magurran 1988).

Species diversity, like any statistic, summarizes a certain property of many different objects in a sample. In doing so much information is lost. However, it is still useful as a concise way of describing compositional diversity within a community. Moreover a community can be more completely represented when multiple species diversity indices are used (Huston 1994). The Shannon-Weiner index is recommended when one wishes to weight rare species more (a greater emphasis on richness than composition), while Simpson's index is recommended when one wishes to weight abundant species more (a greater emphasis on evenness than richness) (Krebs 1989). Fisher's alpha is less affected by the abundance of the rarest or commonest species, and depends more on the number of species of intermediate abundance (Magurran 1988). Fisher's alpha has been adjudicated as a good, if not one of the best, species diversity index by several authors (Magurran 2004).

Species diversity is a composite measure of both species richness and species evenness. It does not consider the final property of diversity; *disparity*. Similarity indices describe the similarities between sites in terms of the species they support. In other words (and in the context of this study), similarity indices describe how different from each other two communities are, and they are thus useful for describing *disparity*. Many similarity indices exist. These include the Jaccard, SØrensen, Marczewski-Steinhaus, Bray-Curtis and Morista-Horn. SØrensen's similarity measure is considered the best index that includes only presence-absence data (Southwood & Henderson 2000). Of the those indices that include abundance data, the Bray-Curtis measure is recommended (Magurran 2004)

In this study species richness, species evenness, species diversity and similarity indices were used to describe the full spectrum of compositional biodiversity present within each stream order. The Shannon-Wiener, Simpson's and Fisher's alpha were considered the most appropriate species diversity measures. Bray-Curtis was considered the most appropriate similarity index as it includes abundance data.

Measurement of structural diversity

Variation in vegetation structure is the most common measure of structural diversity, and has been shown to be an important component of a community's overall biodiversity. Changes in vegetation structure have been associated with changes in bird communities (MacArthur & MacArthur 1961; Karr & Roth 1971; Jansen & Robertson 2001), insect communities (Southwood *et al.* 1979; Brose 2003), small mammal communities (Peles & Barrett 1996) and bat communities (Norberg & Rayner 1987). Additionally vegetation structure along forest edges has been found to have important implications for fire encroachment into forests. Dense forest edges buffer the interior from fire, whereas more open edges allow fire through, which can then lead to elimination of the seed bank and increased plant mortality (Didham & Lawton 1999). Structural diversity thus has important functional implications.

Vegetation structure is most often measured as a variety of variables that indicate the horizontal as well as the vertical elements of vegetation pattern. Diameter at breast height (DBH), basal area, canopy width and percentage cover are measures commonly used to describe vegetation structure in the horizontal plane (e.g. de Casanave *et al.* 1995; Anten & Hirose 2001; Neumann & Starlinger 2001). Plant height, foliage height profiles and number of vertical layers are measures commonly used to describe vertical vegetation structure (e.g. Didham & Lawton 1999; Oosterhoorn & Kappelle 2000; Onaindia *et al.* 2004). Canopy density, canopy architecture and growth form describe both horizontal and vertical vegetation structure (Pickett & Kempf 1980; Montgomery & Chazdon 2001). I included measures of both horizontal and vertical structure in this study.

It is problematic to summarize vegetation structural diversity data because many of the variables measured are continuous. *Richness*, *evenness*, *diversity* and

similarity measures all require categorical data and thus cannot be used to summarize height, DBH, canopy width and other continuous structural variables. To counteract this problem many authors have grouped the continuous structural variables into classes. These classes can then be substituted into the traditional diversity indices (e.g. Shannon) in place of "species". For example, MacArthur and McArthur (1961) obtained foliage height profiles by estimating the proportion of total foliage in chosen horizontal layers, and then calculated a foliage height diversity index using Shannon's index. The number of species was replaced by number of layers, and the abundance of each species was replaced with the proportion of foliage in each layer. A similar approach has been used by other authors describing foliage height diversity (Ambuel & Temple 1983; Onaindia *et al.* 2004), and DBH diversity (de Casanave *et al.* 1995; Lähde *et al.* 1999). However, the grouping of continuous structural variables into classes has drawbacks. Categorizing variables means that information about the distribution of each variable is lost and class limits are often somewhat arbitrary. New structural diversity indices capable of including continuous variables have thus been proposed (Neumann & Starlinger 2001; Staudhammer & LeMay 2001), but they are in need of further testing and as yet have not been widely utilized (Neumann & Staudhammer 2001). It seems that at present the use of adapted compositional diversity measures is the best method for describing vegetation structural diversity.

I used *richness*, *evenness*, *diversity* and *similarity* measures to describe the structural diversity of vegetation in each stream order. The same diversity and similarity indices as were chosen for compositional diversity were chosen for structural diversity. These measures encompass the *variety*, *balance* and *disparity* properties of diversity.

Structural diversity is most often measured as variation in vegetation structure, but this need not be the case. The same principles that apply to vegetation structural diversity could be applied to any taxon. For example, the diversity in body length, leg length and body mass of a certain animal taxon could be measured in the same way that the diversity of height, canopy width and DBH of plants is measured. Structural variation in animals is associated with ecological diversity in much the same way that vegetation structural diversity is. For instance, body size affects a wide range of behaviors in animals, such as activity levels, dominance, home range

size, competitive ability, foraging ecology, sexual selection and predation risk (Dial *et al.* 2008). Furthermore, changes in wing morphology have implications for the ecology of flying animals. Both bats and birds hunting among vegetation have short, broad wings that allow for good maneuverability, while those hunting in more open habitats have slightly longer wings which lower the energetic cost of transport and increase flight speed (Norberg & Rayner 1987; Loon & Loon 2005). As a final example, leg length in lizards is related to habitat use, usually correlated with substrate diameter in arboreal species (Kohlsdorf *et al.* 2001). Overall, structural diversity of animal taxa is another relevant measure of community biodiversity.

In this study I examined the structural diversity of birds detected within each stream order. Body mass, a ratio of wing length to body length (WL/BL), and leg length were the structural attributes considered. Structural diversity of the bird assemblage was quantified in the same way as vegetation structural diversity, and included the *variety, balance* and *disparity* properties of diversity.

1.2.3 Riparian areas as highly diverse components of a landscape

Ecological theory would suggest that, in general, riparian areas are highly diverse because of their wide range of landscape elements, natural disturbance regime, presence of refugia, and large species pool. I elaborate on the theory before considering empirical evidence.

Riverine corridors in the natural state are characterised by a diverse array of landscape elements, including surface waters, the fluvial stygoscape, riparian systems and geomorphic features (Ward *et al.* 2002). Surface waters include lotic (running), semi-lotic and lentic (still) waters. The fluvial stygoscape refers to the subterranean extension of the riverine landscape and, while traditionally thought of as rather homogenous, is now known to exhibit high levels of heterogeneity (Ward *et al.* 2002). Vegetation growing along the river corridor comprise riparian systems, which form a complex mosaic in response to gradients of elevation, disturbance and inundation (Gregory *et al.* 1991; van Coller *et al.* 1997b). Many geomorphic features are found within the riparian corridor, including bars, islands, ridges, levees, deltas, fringing floodplains and woody debris deposits. The wide range of landscape elements present would theoretically lead to a high diversity of species and ecological processes in riparian areas.

Fluvial action (erosion, transport, deposition) constitutes the natural disturbance regime of riparian corridors (Ward *et al.* 2002). Flooding is common and may lead to the destruction (e.g. bars) or creation (e.g. floodplain) of landscape elements. Similarly periods of low flow may either support or discourage the formation of geomorphic features. The continual creation/destruction of landscape elements makes riparian areas highly dynamic and theoretically highly diverse.

Riparian corridors act as refuges for organisms and processes under certain circumstances (Naiman *et al.* 2005). Firstly the formation and disintegration of islands within the channel creates a broad range of disturbance and environmental conditions, and thus provides a diversity of habitats supporting many successional stages and ecological processes. Secondly, during periods of widespread environmental shifts riparian corridors often act as safe havens for a variety of fauna and flora (Naiman *et al.* 2005).

The species pool in riparian areas is large as it draws from both terrestrial and aquatic communities. The natural disturbance regime suppresses competitive exclusion, and thus many species are able to persist. Some species occur solely in the riparian corridor, while others perform certain parts of their lifecycle therein (Decamps & Tabacchi 1992). Hypothetically riparian areas should be highly diverse because of the large species pool from which they may draw.

Overall ecological theory suggests that riparian areas should be more diverse than the adjacent upland habitats, but are there data to support this hypothesis? This pattern has been observed in several studies. In the southern Appalachians riparian areas were found to have more exotic and native plant species than upland areas (Brown & Peet 2003). Bird species richness and total abundance was significantly greater in riparian zones than in matched non-riparian areas in Australia's Northern Territory (Woinarski *et al.* 2000), and a similar pattern was observed for trees, birds and litter invertebrates in south-east Queensland (Catterall *et al.* 2001). Maritz and Alexander (2007) found herpetofaunal species richness and abundance to be higher in riparian areas than non-riparian areas in an agricultural landscape in South Africa. In other cases this pattern has not been observed. Hughes and Cass (1997) and Goebel *et al.* (2003) found no significant difference in tree and shrub species richness, while Pearson and Manuwal (2001) found no difference in bird species

richness, between riparian areas and adjacent uplands. Bird species richness, diversity and total abundance was found to be higher in upslope areas than in riparian zones in the central Oregon Range (McGarigal & McComb 1992), as was plant species richness in the Sonoran desert (Schade *et al.* 2003). These conflicting results in empirical studies make it difficult to definitively judge whether riparian zones are more diverse than adjacent upslope areas.

In an attempt to clarify the matter Sabo *et al.* (2005) conducted a meta-analysis to answer the question: "Does average richness (reflecting α–diversity) differ between riparian and upland habitats across all replicated studies examining this question?" They found that riparian habitats do not harbor higher numbers of species, but rather support significantly different species pools altogether. In this way they increase regional richness (over upland habitats) by 38% on average (Sabo & Soykan 2006).

In conclusion, ecological theory suggests that riparian zones are highly diverse and thus should support higher numbers of species than upland areas, but this hypothesis is not always corroborated by empirical evidence. Riparian zones are however highly important in promoting regional diversity, and therefore they remain vital components in a landscape.

1.2.4 The concept of stream ordering

Stream ordering provided a suitable method for grouping similar rivers in this study. The Strahler method of stream ordering, in which all unbranched streams are classified as first order, two first combine to make a second order, two second combine to make a third order, and so on (Strahler 1957), is commonly used and was chosen for this study. It has been shown that rivers of different stream order demonstrate different physical characteristics.

Catchment size is positively correlated with stream order (Gordon *et al.* 1992). Hillslope geomorphology, as well as number of geomorphic boundaries on these hillslopes, is significantly different between rivers of different stream order (Khomo & Rogers 2009). Hillslope geomorphological complexity increases with increasing stream order, as does the number of geomorphic boundaries. It has also been shown that fluctuations in physicochemical conditions decrease as stream order

increases (Whiteside & McNatt 1972). Along with physical characteristics, it has also been shown that rivers of different stream order possess different biological characteristics. Fish species richness (Whiteside & McNatt 1972; Beecher *et al.* 1988), fish diversity (Harrel *et al.* 1967; Barila *et al.* 1981), plant species richness (Nilsson *et al.* 1994), the structure and productivity of riparian vegetation (Spoonseller & Fisher 2006) and bird diversity (Lock & Naiman 1998) are all positively correlated with stream order.

The aim of this study was to describe possible differences in biodiversity associated with variation in riverine characteristics. The concept of stream ordering permits the grouping of rivers with similar physical and biological characteristics, and thus was deemed an appropriate method of categorization for this study.

Chapter 2:

Methodology and approaches to data analysis

2.1 Study Site

This study was conducted within the Kruger National Park (KNP), a 2-million hectare conservation area in the north-east of South Africa. More specifically, biodiversity was measured in rivers located in the south-western part of KNP, near Skukuza rest camp (Fig. 2.1). All sites were positioned within the Skukuza Land System (Venter 1990), which is characterised by granotoid rocks associated with the Basement complex, moderately to slightly undulating plains with a typical convex/concave land surface, and a mean annual rainfall ranging between 500 and 740 mm. At a lower level, my sites were located within the Skukuza and Renosterkoppies land types (Venter 1990), which are similar in their geology (granite/gneiss of the Nelspruit granite suite), geomorphology (moderately undulating plains sloping downwards towards the Sabie River) and valley bottom soils (complex association of deep brown sand to clay, clayey soils are frequently calcareous) . Rainfall is slightly higher in the Renosterkoppies land type (600-700mm in Renosterkoppies opposed to 500-600mm in Skukuza), but as most sites were positioned near the transition zone between these two land types and were all within 20km of one another this is considered negligible. The overall similarity in the underlying physical template between sites allowed for an investigation of the

influence of stream order on riparian biodiversity without climate and geology as confounding factors.

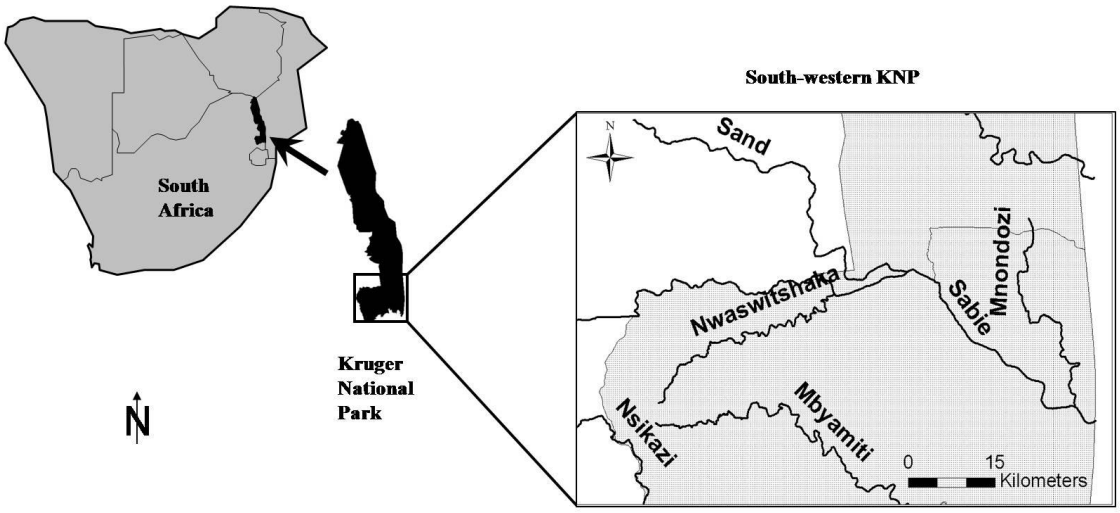

Figure 2.1: The study area within KNP

Rivers of 1st, 2nd, 4th, 5th and 7th stream order were investigated during this study. The Sabie River, one the five perennial rivers flowing the KNP, was the 7th order river considered. The Sabie River is a semi-arid, bedrock influenced river with a catchment area of approximately 7096km^2. It rises in the Drakensberg to the west of the KNP, descends rapidly onto the flat lowveld and Lebombo zones to the east before flowing into the Incomati River in Mozambique. A hierarchical geomorphological classification has been developed and applied to the Sabie River (Van Niekerk *et al.* 1995). The largest-scale feature that is repeated in the KNP section of the river is the channel type. Five different channel types have been recognized according to their proportion of bedrock and alluvial influence. The single thread channel type shows no bedrock influence and is characterized by a single channel with deep alluvial pools. The braided channel type also has no bedrock influence, but this alluvial channel type exhibits channel splitting and rejoining over short distances. Pools separated by bedrock rapids is characteristic of the pool-rapid channel type, while multiple channels flowing through alluvium on a bedrock base is characteristic of the mixed anastomosing channel type. Finally the bedrock anastomosing channel is characterized by multiple channels flowing through bedrock fissures. I used this classification to place my sites in different channel types in an effort to cover the recognized variability.

The 5th order Nwaswitshaka River originates within the KNP and joins the Sabie River at Skukuza rest camp. This river flows in most but not all years, and only in the summer months. Joining the Nwaswitshaka are many smaller rivers ranging from 1st to 4th stream order in which aboveground flow is highly episodic. The 5th, 4th, 2nd and 1st stream order sites were situated in these rivers.

2.2 Field methods

2.2.1 Site selection

Compositional and structural diversity of woody vegetation and the bird community were measured at 15 sites, three per stream order (Fig. 2.2; Table 2.1). 1st, 2nd, 4th, 5th and 7th order rivers were sampled (Fig. 2.3 – 2.7). Each site was approximately 1.5 kilometers long to allow for adequate bird sampling to take place. All sites were located within the Skukuza Land System (Venter 1990) and had similar geology and climate. The Sabie River was the 7th order river sampled, and three sites were situated along its length. Each of these sites was placed in a different channel type; bedrock anastomosing, braided and pool-rapid. Three sites were located along the 5th order Nwaswitshaka River. Each site was situated immediately downstream of a confluence of a 4th order river with the Nwaswitshaka. A site was positioned, near the confluence to allow easier movement between sites, in each of three 4th order tributaries joining the Nwaswitshaka, . Smaller tributaries of these rivers provided three 2nd order sites and three 1st order sites. To ensure consistency in the choice of 1st and 2nd order sites, I selected only those rivers that flowed directly into a river of the same stream order. In other words I chose 1st or 2nd order rivers that flow into other 1st or 2nd order rivers respectively, rather than, for example, a 1st order river that flows directly into a 5th order river.

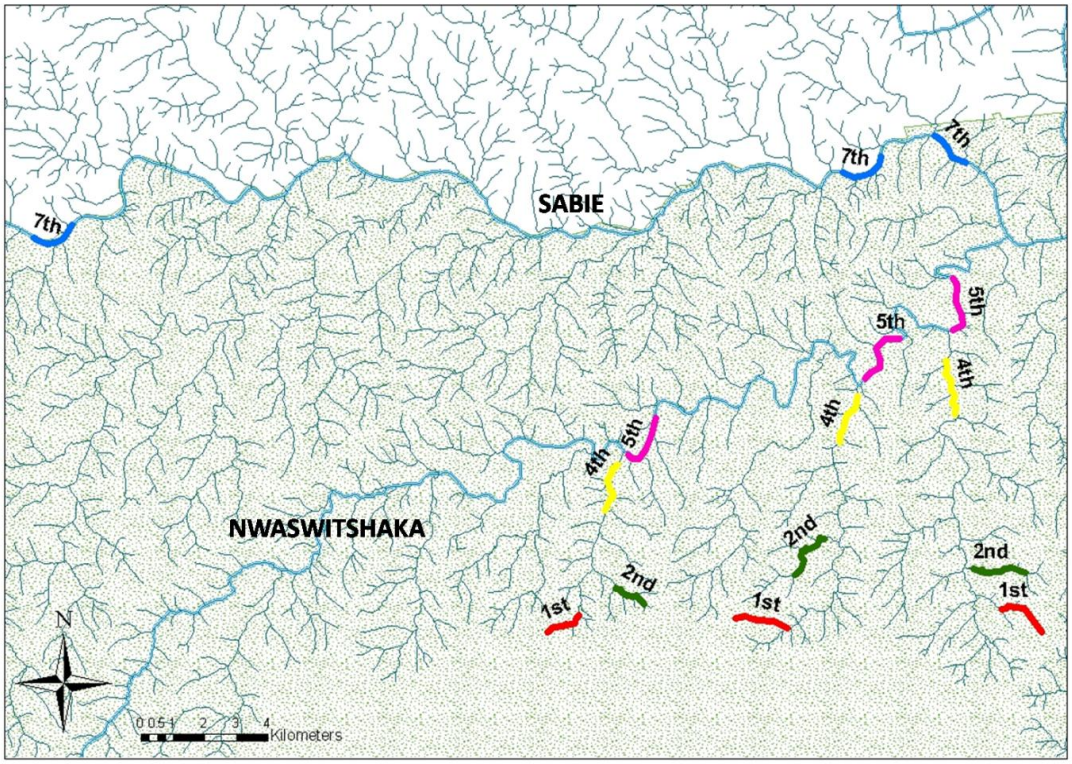

Figure 2.2: Map of study area showing sampling sites. Sites within each stream order where labeled a-c (i.e. 1a, 1b, 1c … 7c) from right to left.

Table 2.1: GPS co-ordinates for the start and end of each of the fifteen sites. The co-ordinates are given in decimal degrees.

Site	Start Point		End Point	
1a	31.586211	-25.093654	31.597460	-25.099322
1b	31.518014	-25.098523	31.503258	-25.095467
1c	31.443796	-25.098620	31.452593	-25.095236
2a	31.593036	-25.083886	31.577323	-25.082833
2b	31.521057	-25.083773	31.530076	-25.074084
2c	31.472973	-25.090969	31.464819	-25.086515
4a	31.569033	-25.024975	31.571885	-25.037933
4b	31.541578	-25.033701	31.535633	-25.046157
4c	31.465931	-25.052162	31.462508	-25.064307
5a	31.572209	-25.002288	31.571881	-25.015161
5b	31.551863	-25.017008	31.544128	-25.028480
5c	31.477912	-25.041866	31.472976	-25.049960
7a	31.566673	-24.961865	31.573333	-24.968367
7b	31.538092	-24.971619	31.549683	-24.968075
7c	31.294127	-24.986069	31.283981	-24.986963



Figure 2.3: Example of a 1st stream order river



Figure 2.4: Example of a 2nd stream order river



Figure 2.5: Example of a 4th stream order river



Figure 2.6: Example of the 5th stream order river



Figure 2.7: Example of the 7th order river

Lower order rivers are numerous and it was possible to find three separate replicates. However, the N'waswitshaka River is the only 5th order river, and the Sabie River the only 7th order river, in this catchment. This meant that to obtain three sites in 5th and 7th order rivers I needed to sub-sample these two rivers. Such pseudoreplication represents a perennial problem in scaled studies. Oksanen (2001) illustrates the point that the appropriate scale for a study should always have priority over replication, and that replication can also be obtained afterwards by conducting studies with basically similar design in different areas and using meta-analysis. In the case of this study, it was not possible to maintain both its scaled nature and at the same time avoid pseudoreplication.

2.3 Woody vegetation diversity

2.3.1 Woody vegetation census method

The collection of woody vegetation diversity data took place during summer between 16 February 2007 and 28 April 2007. Woody vegetation was sampled in a plot that extended from the middle of each river channel up until the edge of the riparian zone. The edge of the riparian zone was decided subjectively, based upon changes in dominant vegetation, changes in slope and often the presence of a game trail (Fig. 2.8). A single plot was situated in approximately the centre of each site, and on the right hand side of the channel when facing downstream. The plots in the 4th, 5th and 7th order rivers were 100m long while plots in the 1st and 2nd order rivers were 150m long because of their narrower riparian zones. I used species accumulation curves to verify that plots of these sizes were adequate to sample the community in each stream order. A species accumulation curve is a plot of the cumulative number of species discovered as additional area is sampled, and the point where this curve reaches a horizontal asymptote represents the area needed to be sampled in order to detect most of the species. When the three sites in each stream order are combined into one dataset, the corresponding species accumulation curves begin to asymptote (see Fig. 3.1 in Chapter 3), and thus plots were judged to be sufficiently large.



Figure 2.8: Example of the boundary between a riparian zone and upland. The blue line indicates the point at which changes in dominant vegetation, slope and the presence of a game trail defined the upper boundary of the riparian zone.

2.3.2 Collection of woody vegetation compositional diversity data

Each plot was divided into 5m wide bands to make sampling more manageable. All woody plants greater than 1m in height encountered within each band were identified to species and counted. The identity of all the species and their abundances was used to calculate compositional diversity within each site.

2.3.3 Collection of woody vegetation structural diversity data

Plant height, canopy width, DBH and number of stems (NoS) were measured to evaluate structural diversity within each site. Plant height (height from the ground to the top of the canopy), canopy width (width of the canopy at its widest point), DBH and NoS are all common measures of plant structure (e.g. Sussman & Rakotozafy 1994; Anten & Hirose 2001; Montgomery & Chazdon 2001). These measurements were taken on the first 50 individuals greater than 1m in height encountered within each plot. Height was measured with a graduated pole (shorter trees) or a clinometer (taller trees), DBH was measured with a DBH tape and canopy width was measured with a tape measure.

2.4 Bird diversity

2.4.1 Bird census

The point count and the transect method are two of the most common techniques for bird sampling (John Ralph *et al.* 1993). The point count method was deemed appropriate for this study as it allows the researcher to study differences in species composition between habitats as well as abundance patterns of birds (John Ralph *et al.* 1993). This is in line with the overall aims of the study. The transect method is more commonly used in open habitat (e.g. grasslands) and bird abundance patterns are not as easily estimated. In addition, the point count method has been used successfully in several other studies investigating riparian bird communities (Sanders & Edge 1998; Saab 1999; Jansen & Robertson 2001).

2.4.2 Sampling protocol

Bird censuses were conducted during summer between 16 February 2007 and 28 April 2007. Point counts were conducted every 250m down the length of each site. I attempted to carry out 7 point counts within each site (i.e. a total site length of 1.5km), but this was not always possible in some of the shorter, lower order streams. In these streams I placed as many point counts as their length allowed (Table 2.1) In addition only 5 point counts were conducted along one of the Sabie River sites (7a) as its length was constrained by Skukuza rest camp downstream (within 250m) and a private game lodge upstream (within 250 m). Each site was visited on 5 separate days during the study period, with a random number of days separating each visit. From the literature it appears that between 4 and 6 visits per site are required to accurately assess the bird community present (Schieck *et al.* 1995; Saab 1999; Skowno 2000). On some days (6/42) it was not possible to conduct the maximal number of point counts because of dangerous animals or rain, but this was uncommon.

Table 2.2: Details of the point counts conducted in each site

Stream Order		Number of days site was visited	Maximum number of point counts possible	Total number of point counts conducted
1	a	5	6	29
1	b	5	7	33
1	c	5	6	30
2	a	5	7	35
2	b	5	7	35
2	c	5	6	30
4	a	5	7	35
4	b	5	7	33
4	c	5	7	35
5	a	5	7	35
5	b	5	7	33
5	c	5	7	32
7	a	5	5	24
7	b	5	7	35
7	c	5	7	33

Point counts were 5 minutes in duration and conducted between sunrise and approximately four hours thereafter to allow for consistent bird detection rates. Usually two sites were censused per day, the first site sampling beginning at sunrise and the second site sampling beginning approximately 2 hours thereafter. A schedule was organized so that all sites were sampled either thrice in the early session and twice in the later session, or vice versa.

Except for two days, there were two observers present on each day of sampling. I was present every day. Sampling was generally conducted in warm, still and sunny conditions and thus bird detection rates were relatively constant throughout. Sampling was not conducted in rain, strong winds, or cold conditions.

2.4.3 Collection of bird compositional diversity data

During each point count I recorded all bird species seen or heard that were actively utilizing the riparian zone. Birds actively utilizing the riparian zone were those feeding, calling, resting, perching or displaying within the riparian zone; birds flying over the river were not recorded. Additionally the number of individuals of each bird species detected was recorded. This was sometimes difficult when a species was only heard and not seen. In these cases knowledge of a species' habit was utilized to approximate the number of individuals present. Species heard that are usually solitary (e.g. Whitebrowed Robin-Chat) were recorded as single

individuals, while I actively sought out gregarious species (e.g. Arrowmarked Babbler) to count the number of individuals after the point count was finished. The identity of all species and their abundances was used to calculate compositional diversity within each site.

2.4.4 Collection of bird assemblage structural diversity data

Body mass, a ratio of wing length to body length (WL/BL), and leg length were examined to evaluate the structural diversity of birds within each site. These structural attributes were chosen as measurements thereof are readily available in the literature and because of their association with ecological processes. Body mass affects a wide range of behavior in animals (Dial *et al.* 2008), WL/BL is correlated with foraging behavior (Loon & Loon 2005) and leg length is linked to habitat use. It was not possible to physically capture and measure all of the birds observed, and thus measurements for each of these attributes were obtained from Roberts Birds of Southern Africa VII (Hockey *et al.* 2005), the most comprehensive book on southern African birds available. Roberts VII provides measurements of body mass, wing length, body length (billtip to tailtip with the bird stretched out), and leg length (tarsus). These measurements are usually presented as a range and mean. The mean was used in these analyses. In the few cases where only a range was supplied, the median was used. In cases where there is a gender difference in the attribute measurements, the larger value was utilized.

2.3 Approaches to data analysis

After fieldwork was completed I had for each site: species lists and abundances for woody plants and birds, records of structural attributes for 50 individual trees, and structural attribute information for all the bird species observed. There were three points to consider before analyzing these data.

2.3.1 Unequal sample sizes

The width of the riparian zone was different in each of the rivers sampled, and thus the area of each woody vegetation plot or the effective radius around each point count was different in each site. While the use of species accumulation curves and guidance from literature allowed me to be satisfied that adequate sampling had taken place, the differing areas sampled in each site meant that it was possible to sample many more individual woody plants or birds in larger sites for no other

reason than they spanned a greater area. It was necessary to compensate for this, considering that an increase in the number of individuals recorded generally translates into an increase in the number of species recorded (Ambuel & Temple 1983). Two techniques were employed to do this.

Sample-based rarefaction (expected species accumulation curves) is a method for calculating the number of species expected in each sample if all samples were of a standard size. Rarefying a sample estimates its expected species richness at different values of n samples or n individuals from the pooled total species richness, by repeatedly and randomly re-sampling (without replacement) the pool of N samples or N individuals (Gotelli & Colwell 2001). These estimates of expected species richness can then be plotted to produce rarefaction/expected species accumulation curves. In other words the rarefaction curve is the statistical expectation of the corresponding classic species accumulation curve. A larger dataset can then be compared to a smaller dataset at the point on its rarefaction curve where it matches the sample size of the smaller dataset (see Fig. 3.1 in Chapter 3). In this way many differently sized datasets can be compared without having to disregard any of the information contained within them. EstimateS (Colwell 2005) computes sample-based rarefaction curves, which I used to compare species richness between stream orders. Additionally, EstimateS computes several other diversity statistics which can also be plotted as accumulation curves. In cases where the program does not directly compute a certain diversity measure (e.g. evenness) the appropriate outputs can be utilized to calculate the measure and construct the corresponding accumulation curve. I used rarefaction/ accumulation curves produced by EstimateS or from its outputs to compare richness, evenness and diversity between stream orders at a common sample size. These techniques were employed to compare woody vegetation and bird compositional diversity measures and bird assemblage structural diversity attributes.

A second way of compensating for unequal sample size was needed before calculating similarity between sites. Apart from the woody vegetation structural diversity data (which already had equal sample sizes), each dataset was standardized so that the total abundance of woody plants or birds within each site was equal to one. This standardization is recommended when dealing with plots of unequal area (Quinn & Keough 2002).

2.3.2 Low replication

Time constraints limited the total number of sites that could be sampled during this study, and thus I was forced to choose between sampling more sites in fewer stream orders, or fewer sites in more stream orders. The aim of this study is to investigate how riparian biodiversity might vary across a stream order sequence, and meeting this aim requires that biodiversity be measured in a wide range of stream orders. Thus it was decided to measure biodiversity in five different stream orders, at the expense of having only three replicate sites in each. However, the low replication of sites within each stream order posed a problem when conducting many traditional statistical procedures with these data, because obtaining a significant p-value with so few replicates was difficult. It was therefore important during this study to explore other statistics that do not make use of p-values (such as certain multivariate statistics) as well as to describe patterns in the data. Simple line graphs, similarity indices, cluster analyses and multidimensional scaling (MDS) are examples of methods which don't rely on a p-value used to describe patterns in the data.

2.3.3 Grouping/Partitioning of data

Data collection was designed in such a way that measurements of compositional and structural diversity were obtainable for each site individually, and each site could then be compared to any other site/group of sites. A second way of analyzing the data was to combine the records from the three sites in each stream order into one larger dataset. The five datasets generated in this manner were termed "*order*" datasets, and this approach allowed examination of the data from a new perspective. This approach provided greater confidence that the majority of the community had been sampled and it was easier to discern patterns, but the lack of replicates prohibited the use of certain statistical techniques. Throughout the analysis of the data I made use of both the *sites individually* approach and the *order* approach.

2.4 Data analysis

The broader approaches that were taken towards the analysis of the data have been dealt with. The specific techniques used will now be described.

2.4.1 Species Richness, Species Evenness and Species Diversity

EstimateS (Colwell 2005) was used to calculate a multitude of diversity measures, including species richness, species richness estimators and species diversity indices. Additionally outputs from the program were used to calculate species richness indices, species evenness indices and further species diversity indices. This provided a wide range of diversity metrics to choose from, but it was necessary to limit the number of biodiversity measures included, and to ensure that the measures chosen match the aims of this investigation. In the end seven different biodiversity measures were chosen.

The first two biodiversity measures chosen deal with the richness aspect of diversity. Species richness is the most intuitive measure of biodiversity and is simply the number of species recorded in each site. It is however unlikely that all the species potentially present within a site are recorded during sampling, and thus total species richness estimators can also be used. A non-parametric species richness estimator developed by Chao (1984) was used in this study. The estimate is calculated by EstimateS and, along with other nonparametric species estimators, represents "probably the most significant advance in diversity measurement in more than a decade" (Magurran 2004). It is termed nonparametric because it is not based on the parameter of a species abundance model that has previously been fitted to the data. Instead, it is a function of the ratio of singletons and doubletons recorded within a sample and will exceed observed species richness by ever greater margins as the relative frequency of singletons increases. In EstimateS the estimate is referred to as Chao 1, and is calculated as:

$$S_{Chao1} = S_{obs} + \frac{F_1\ (F_1 - 1)}{2(F_2 + 1)}$$

where S_{obs} = the number of species in the sample; F_1 = the number of observed species represented by a single individual (singletons); and F_2 = the number of observed species represented by two individuals (doubletons).

Shannon, Simpson and Fisher's alpha species diversity indices were chosen. The Shannon diversity index is widely used in ecological studies and, while it has been criticized, is chosen to allow for comparison with other work. Simpson's and Fisher's alpha diversity indices are well understood and intuitively meaningful, and

are recommended as perhaps the best species diversity measures (Magurran 2004). All three species diversity indices were calculated in EstimateS using the following equations:

- *Shannon diversity index*

$$H' = -\sum p_i \ln p_i$$

where p_i = the proportion of individuals found in the *i*th species.

- *Simpson's diversity index*

$$D = \sum \left(\frac{n_i[n_i - 1]}{N[N-1]} \right)$$

where n_i = the number of individuals in the *i*th species, and N = the total number of individuals. As D increases, diversity decreases, and so in this study Simpson's index is expressed as 1/D.

- *Fisher's alpha diversity index*

$$\alpha = \frac{N(1-x)}{x}$$

Where N = the total number of individuals and x is estimated from the iterative solution of:

$$S/N = (1-x)/x[-\ln(1-x)]$$

Where S = the total number of species

Finally two species evenness measures were chosen. The Shannon evenness measure is commonly used and complementary to the Shannon diversity index. It is calculated as follows:

$$J' = \frac{H'}{\ln S}$$

Simpson's measure of evenness is also recommended, particularly if Simpson's species diversity is used (Magurran 2004). It is derived by dividing the reciprocal form of the Simpson's diversity index by the number of species in the sample:

$$E_{\frac{1}{D}} = \frac{(1/D)}{S}$$

2.4.2 Similarity indices

As was the case with biodiversity measures, I calculated numerous similarity indices, including Jaccard, Sørensen, Bray-Curtis and Morista-Horn. The results obtained from each of these indices were similar, even though some (Jaccard, Sørensen) were based on only presence/absence data, while the others took abundance into account. Thus only the Bray-Curtis results are presented, as it is recommended as the most useful index that includes abundance data (Magurran 2004). The similarity indices were computed using EstimateS and CAP.

2.4.3 ANOSIM

ANOSIM's were performed to test for significant differences in the community composition between the different stream orders. The concept behind an ANOSIM is that if samples (sites) within an assigned group (in this case sites were grouped by stream order) are meaningful, then samples within groups should be more similar in composition than samples from different groups. If the ANOSIM test statistic (R_{ANOSIM}) has a value greater than zero then the most similar samples are found within the same group, and thus there are differences in composition between groups.

Chapter 3:

Compositional diversity

3.1 Introduction

Compositional diversity, as an understanding of the species present in a location and their abundance distributions, is the primary focus of most studies concerned with biodiversity. However, compositional diversity is often only measured as species richness (*variety*) (e.g. Myers *et al.* 2000), and the *balance* and *disparity* properties of compositional diversity are neglected. In this chapter I examine how compositional diversity, in this broader sense, varies along a stream order sequence.

What might I expect to observe? The compositional diversity of riparian vegetation, birds, and fish has been shown to be elevated in higher order rivers (Harrel *et al.* 1967; Whiteside & McNatt 1972; Barila *et al.* 1981; Beecher *et al.* 1988; Nilsson *et al.* 1994; Lock & Naiman 1998; Spoonseller & Fisher 2006), and thus an increase in compositional diversity along the stream order sequence might be expected in this study. However, no other studies encountered have investigated the change in compositional diversity associated with different stream orders in a savanna landscape, and so new insights may emerge.

Catchment size has been positively correlated with stream order (Gordon *et al.* 1992) and thus, in areas of comparable rainfall, more water flows through higher,

than lower, order rivers. Furthermore, average river bed slope is negatively correlated with stream order (Gordon *et al.* 1992), and so while erosional processes dominate low order rivers, depositional processes increase in importance in higher order rivers. This leads to more depositional geomorphic features (e.g. sandbars, floodplains) in higher order rivers increasing physical heterogeneity of the river bed. Finally, hillslopes associated with lower order rivers have a simpler geomorphology than hillslopes associated with higher order rivers (Khomo & Rogers 2009). Thus higher order rivers thus provide a wider range of potential habitats, and so it can be expected that diversity will increase along the sequence from 1st to 7th stream order.

Overall, I expect compositional diversity to increase along the stream order sequence from 1st to 7th order rivers.

3.2 Methods

The methods for determination of species diversity metrics, similarity indices and ANOSIM, and the approaches to data analysis were described in Chapter 2. Here I discuss only those methods specific to the analysis of compositional diversity. All the methods apply to analyses conducted at the species level of organization.

3.2.1 Deciding if a species is *common, intermediate* or *rare*

A simple method for categorizing species based on their abundance can be obtained from Hill's numbers (Williams *et al.* 2005). Hill's numbers are a series of diversity measures arranged by their propensity to emphasize either species richness or evenness (Magurran 1988). N_0 equals the total number of species (S), while N_1, N_2, and N_∞ measure the number of abundant, very abundant and most abundant species respectively in a sample. Williams *et al.*. (2005) then defines the number of *rare*, *intermediate* and *common* species in the following way:

common $\approx N_\infty$;

intermediate $\approx N_1 - N_\infty$; and

rare $\approx N_0 - N_1$.

"*Rare*" species are those species found at low abundances within the sample, and are not necessarily endangered. I utilized this method to classify all the species of trees and birds observed during this study as *common*, *intermediate* or *rare*.

3.2.2 Investigating which species contribute most to dissimilarities in community composition using Simper analysis

After comparing the similarity in community composition between stream orders using Bray-Curtis and Sørensen's similarity indices, a SIMPER analysis was performed to analyze which individual species contributed most to the observed dissimilarities. This analysis breaks down the contribution of each species to the observed dissimilarity (or similarity) between samples, and identifies those species that are most important in creating the observed pattern of dissimilarity. The method uses the Bray-Curtis measure of similarity, comparing in turn, each site in each stream order with each site in all other stream orders. I performed a SIMPER analysis using Community Analysis Package 3.1 (2004) to identify the woody plant and bird species that contributed most to the observed dissimilarity between the stream orders. Examining the overall abundance (*common, intermediate, rare*) and riparian affinity of the species identified in this way provided further insight into the pattern of change in community composition along the stream order sequence.

3.2.3 Determining the "riparian affinity" of woody plant and bird species

To further investigate some of the patterns observed I examined how groups of trees and birds with different riparian affinities varied in abundance along the stream order sequence. To do this it was necessary to classify each woody plant and bird species according to how specific it is in utilizing riparian zones as a preferred habitat. Recently published, well known reference books were used to establish the preferred habitats for every species observed during this study. For woody vegetation, *Trees and Shrubs of Mpumalanga and the Kruger National Park* (Schmidt *et al.* 2002) and *Palgrave's Trees of southern Africa (*Coates-Palgrave 2002*)* were used, and for birds *Robert's VII* (Hockey *et al.* 2005) was used. Based on their preferred habitats, I then applied certain criteria (Table 3.1; 3.2) to categorize all species as either *riparian specialist*, *near-riparian specialist*, *loosely associated with riparian areas*, or *upland* species.

Table 3.1: Criteria used to categorize woody vegetation species based on riparian affinity

Riparian affinity categorization	**Criteria**
Riparian specialist	A tree where the only preferred habitat mentioned is riparian areas
Near-riparian specialist	A tree which occurs mainly in riparian areas but occasionally is found elsewhere in the landscape e.g. termite mound
Loosely associated with riparian areas	A tree which has riparian areas listed as one of several preferred habitats
Upland species	A tree which does not have riparian areas listed as a preferred habitat

Table 3.2: Criteria used to categorize bird species based on riparian affinity

Riparian affinity categorization	**Criteria**
Riparian specialist	A bird where the only preferred habitat mentioned is riparian areas
Near-riparian specialist	A bird which is closely associated with fresh water. Either Roberts VII states this or riparian areas is listed as one of two preferred habitats
Loosely associated with riparian areas	A bird which has riparian areas listed as one of several preferred habitats
Upland species	A bird which does not have riparian areas listed as a preferred habitat

3.3 Results

A total of 6519 woody plants of 121 different species, and 4916 individual birds of 140 different species were recorded from all the sites combined. Species diversity metrics and similarity indices were applied to these records to investigate how the *variety*, *balance* and *disparity* properties of compositional diversity varied along the stream order sequence.

3.3.1 Species diversity metrics

Species richness

Generally, more individual trees and birds were recorded in the higher order rivers, and thus sample-based rarefaction was used to correct for unequal sample size and compare species richness between sites and *orders* (Fig. 3.1; 3.2). The curves are plotted with individuals on the x-axis so that species richness in its conventional sense is displayed; plotting the curves with samples/area on the x-axis results in a comparison of species density. The curves can be compared to one another by drawing a vertical intercept at the size of the smallest sample.

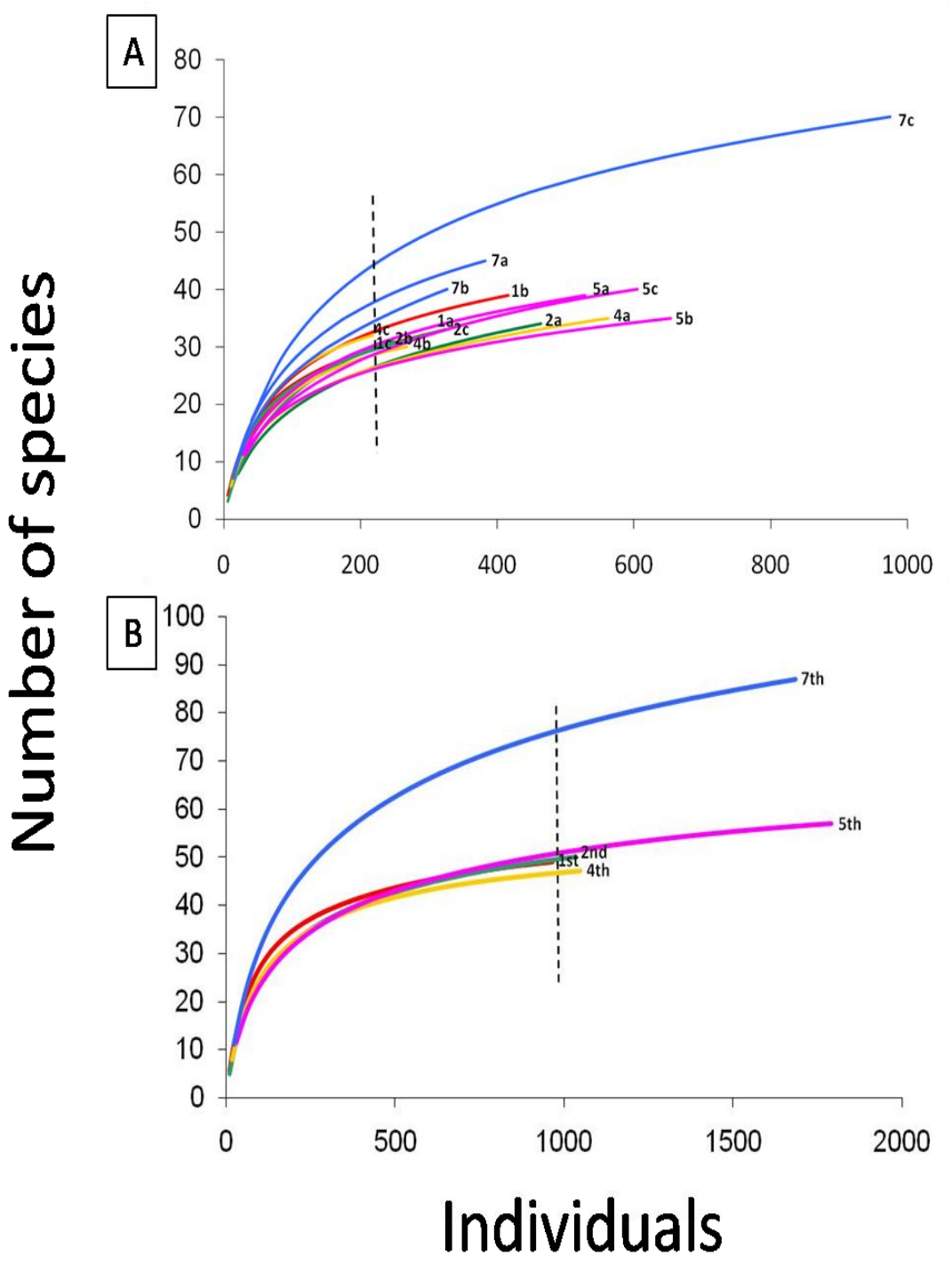

Figure 3.1: Sample-based rarefaction curves showing woody plant species richness in (A) each site and (B) each *order*. In both graphs blue = 7th order, purple = 5th order, yellow = 4th order, green = 2nd order and red = 1st order. The dotted lines in each graph show the point at which the separate rarefaction curves should be compared.

Woody vegetation:

Woody plant species richness was highest in the 7th order rivers, and similar in the 1st through 5th order rivers (Fig. 3.1). This pattern was most pronounced at the *order* level of organisation, but indeed each of the three 7th order sites individually showed a higher species richness than any of the other sites. Results from an ANOVA and Fisher LSD post-hoc tests support this pattern; the 7th order river supported a significantly higher species richness than all the other orders ($F_{(4,10)} = 5.66$, $p<0.05$), while there was no significant difference between the 1st through 5th order rivers.

Birds:

There was no clear distinction in bird species richness between the five stream orders (Fig. 3.2). On average bird species richness was highest in the 1st order rivers (41.13 species), but this was not substantially greater than the lowest average species richness (38.67 species) observed in the 2nd order rivers. The highest and lowest bird species richness recorded were in two separate 5th order sites. There was also no clear distinction in bird species richness between the stream orders at the *order* level of organisation (Fig. 3.2 B). Overall there was no significant difference in bird species richness between the five stream orders ($F_{(4,10)} = 0.21$, $p>0.1$).

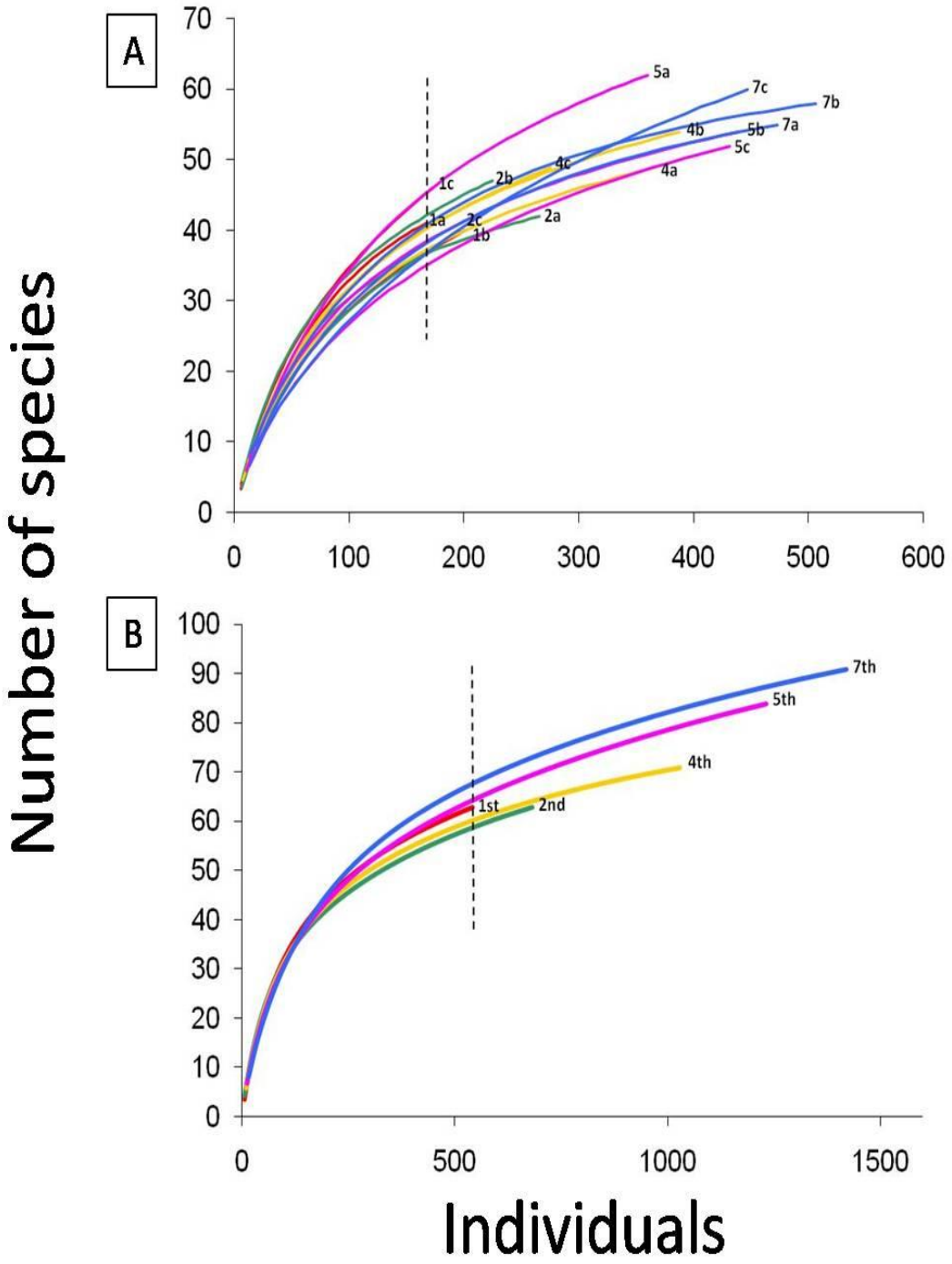

Figure 3.2: Rarefaction curves showing bird species richness in (A) each site and (B) each *order*. In both graphs blue = 7th order, purple = 5th order, yellow = 4th order, green = 2nd order and red = 1st order. The dotted lines in each graph show the point at which the separate rarefaction curves should be compared.

Species richness estimators, species evenness and species diversity

Species accumulation curves were used to overcome the problem of unequal sample sizes for other measures of compositional diversity. It is not feasible to present the multitude of curves produced, so summaries of single values from each site/*order* taken from each curve at the appropriate sample size (see an example of this with the dotted line in Fig. 3.1; 3.2) are displayed.

Woody vegetation:

The estimated woody plant species richness (Fig 3.3 A) showed a similar trend to observed species richness along the stream order sequence, being significantly different ($F_{(4,10)}=8.97$, $p<0.05$) and highest in the 7th order river (Fisher's LSD, $p<0.5$) and similar in the 1st through 5th order rivers (Fisher's LSD, $p>0.05$). Estimated species richness was consistently higher than observed species richness for all stream orders. Furthermore, the proportional difference between the estimated and observed richness ranged between 20-22% and 6-9% in the 1st through 4th order rivers for the individual site and *order* datasets respectively, increased in the 5th order river (individual site 28%, *order* 15%), before peaking at 31% and 20% in the 7th order river. This indicates that a higher proportion of species occurred at very low abundances (1 or 2 individuals) in the higher order rivers.

There was no significant difference in Shannon's evenness ($F_{(4,10)}=1.72$, $p>0.1$) or Simpson's evenness ($F_{(4,10)}=0.94$, $p>0.1$) between the five stream orders. This pattern was repeated for both indices at both the individual sites and the *order* level of organisation (Fig 3.3 B; C). Shannon's evenness is more strongly affected by species richness than Simpson's evenness, and yet both indices produce similar patterns. This emphasizes that the abundance distributions of woody plant species were similar in all five stream orders.

Fisher's alpha diversity (Fig. 3.3 D) was significantly different ($F_{(4,10)}=6.12$, $p<0.05$) and highest in the 7th order river (Fisher's LSD, $p<0.05$), and similar in the 1st through 5th order rivers (Fisher's LSD, $p>0.1$). In this way it demonstrates a similar pattern to species richness, and appears to be highly influenced by it. A weakly significant difference in Shannon's diversity (Fig. 3.3 E) was shown between the stream orders ($F_{(4,10)}=6.12$, $p=0.069$), but this difference was primarily between the 7th and 2nd, and the 7th and 4th, order rivers (Fisher's LSD, $p<0.05$). Shannon's

diversity places increased emphasis on infrequently observed species, and so indicates that an increased number of species found in low abundance caused the increase in diversity in the 7th order river, corresponding with the results from the species richness estimator. Simpson's diversity (Fig. 3.3 F) showed no significant difference between the five orders ($F_{(4,10)}$=1.94, p=0.179). Simpson's diversity places emphasis on frequently observed species, and so is more influenced by evenness. The lack of differentiation with regards to Simpson's diversity reiterates that evenness is equivalent between stream orders.

The general trend from all three species diversity indices is that diversity was highest in the 7th order river, mainly due to its elevated species richness and not due to differences in evenness. Furthermore species diversity was similar in the 1st through 5th order rivers.

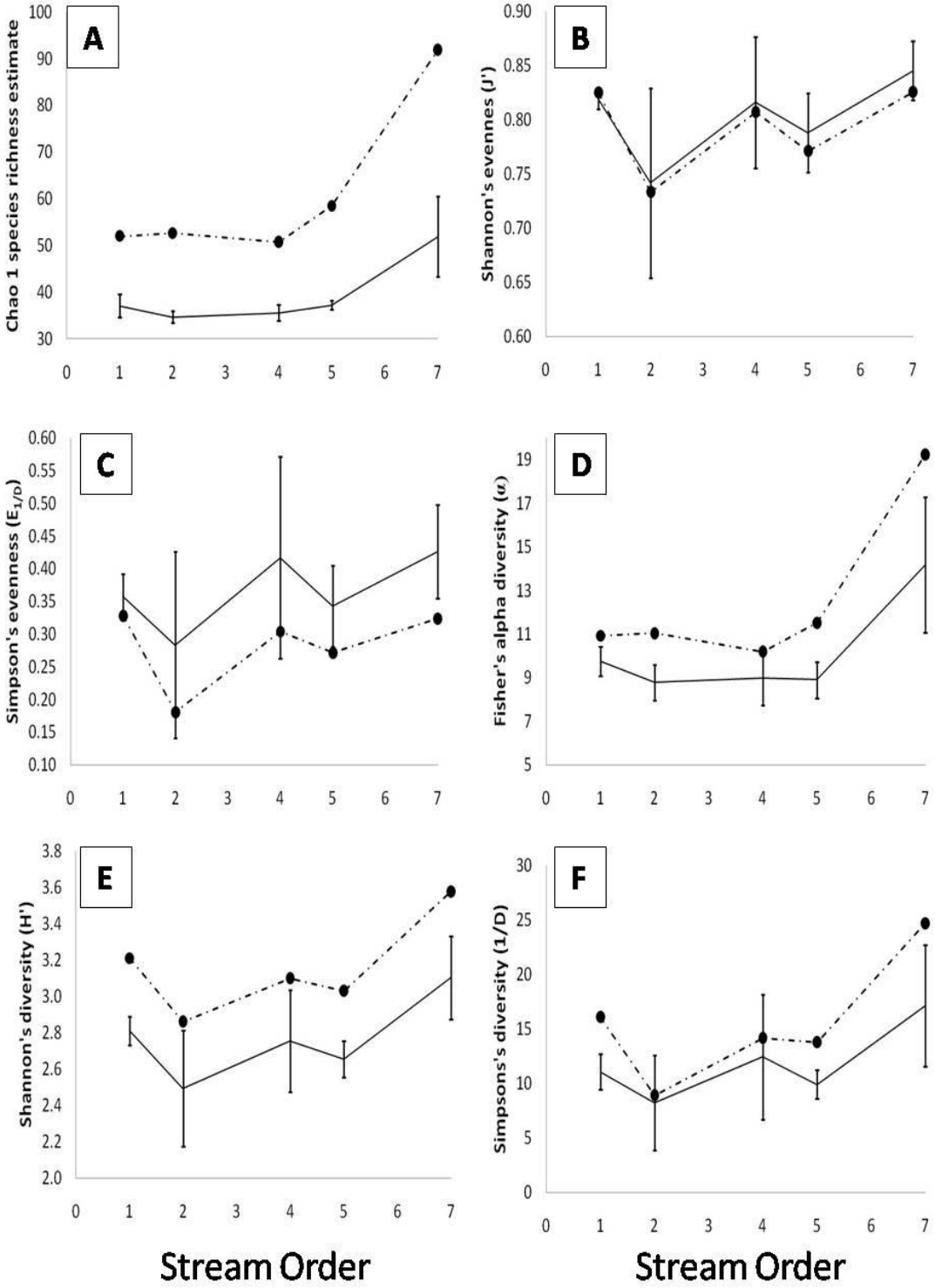

Figure 3.3: Measures of woody plant diversity along the stream order sequence, showing (A) Chao 1 species richness estimate, (B) Shannon's evenness, (C) Simpson's evenness, (D) Fisher's alpha diversity index, (E) Shannon's diversity index, and (F) Simpson's diversity index. In each graph the solid line represents the average diversity per site in each separate stream order with the associated standard deviation, and the dashed line represents the single value from each *order* dataset.

Birds:

No significant differences in any of the six diversity metrics were found between the stream orders.

Chao 1 estimate of bird species richness was comparable in all five stream orders (Fig. 3.4 A), displaying a similar trend to observed species richness. Unlike woody vegetation the proportional difference between estimated and observed richness remains relatively constant across all stream orders, indicating a similar proportion of species that occur at very low abundances was observed in each stream order.

Shannon's and Simpson's evenness tended to be lower in the 5th and 7th order rivers, and highest in the 4th order rivers (Fig 3.4 B; C), however, variation in the evenness values blurs a clear differentiation between stream orders. The high variation in evenness values was probably caused by the observation of larger flocks of birds at some sites. When a larger, monospecific flock was observed, dominance by that particular species increased and hence evenness decreased; when no large flock was observed evenness values were higher.

There was no clear differentiation in Fisher's alpha, Shannon's and Simpson's diversity between the five stream orders (Fig. 3.4 D; E; F). Fisher's alpha showed elevated diversity in the 7th and 5th order rivers at the stream *order* level of organization, a pattern paralleled by the two richness statistics, but this was not seen at the individual site level. Shannon's and Simpson's diversity emphasize evenness to a greater extent and so reported lower diversity indices in the 5th and 7th order rivers, however, the variation surrounding each value was high.

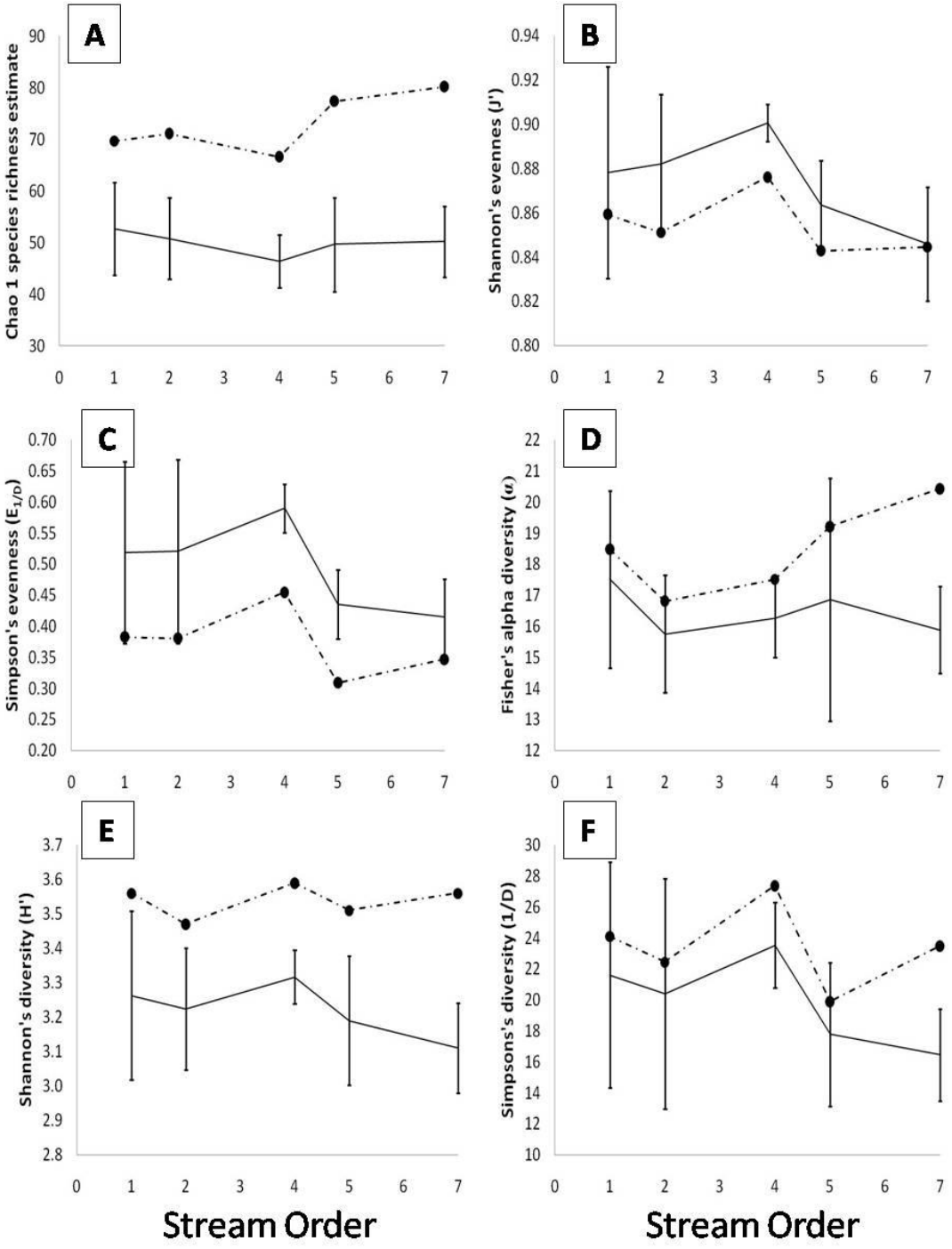

Figure 3.4: Measures of bird diversity along the stream order sequence, showing (A) Chao 1 species richness estimate, (B) Shannon's evenness, (C) Simpson's evenness, (D) Fisher's alpha diversity index, (E) Shannon's diversity index, and (F) Simpson's diversity index. In each graph the solid line represents the average diversity per site in each separate stream order with the associated standard deviation, and the dashed line represents the single value from each *order* dataset.

3.3.2 Community Composition (Similarity indices)

The diversity metrics covered thus far have revealed information regarding how the *variety* and *balance* aspects of diversity change along the stream order sequence. The *disparity* aspect of compositional diversity is now examined using cluster analyses. Cluster analyses combine similar objects into groups or clusters which are then displayed as a dendrogram. The clusters in this case are computed from a Bray-Curtis similarity matrix in PRIMER. All cluster analyses were performed on standardized data. Results from ANOSIM's are used to validate the patterns revealed in the dendrograms. This section reveals how community composition varies across the stream order sequence.

Woody vegetation community composition:

The most distinct woody plant community was found in the 7th order sites (Fig. 3.5), being significantly more similar to one another than to sites in any of the other stream orders (Table 3.3). This pattern is repeated at the *order* level of organization (Fig. 3.6). There was no clear division in community composition between the remaining 1st through 5th order rivers. There was some indication of differentiation in community composition between the 5th order river and the rest at the *order* level of organization, however the difference was small (Fig. 3.6). Results from an ANOSIM indicated a significant difference in community composition between the 5th order sites and the 2nd order sites only (Table 3.3). Overall, the pattern in community composition mirrored those of the species diversity metrics, showing the 7th order as different, and the 1st through 5th order rivers as similar.

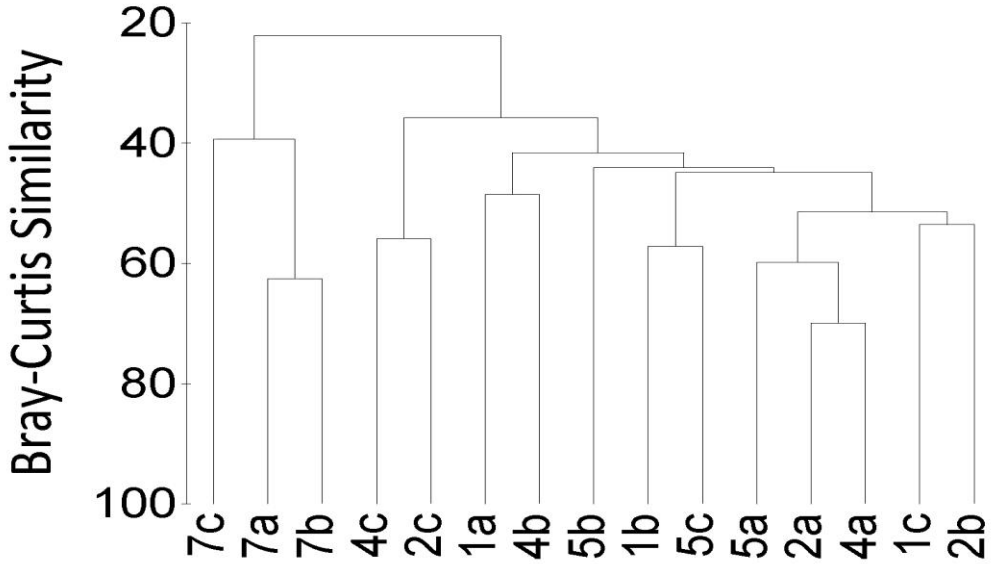

Figure 3.5: Similarity in woody plant community composition between sites. The figure depicts an average-linkage hierarchical cluster dendrogram based upon a Bray-Curtis similarity matrix.

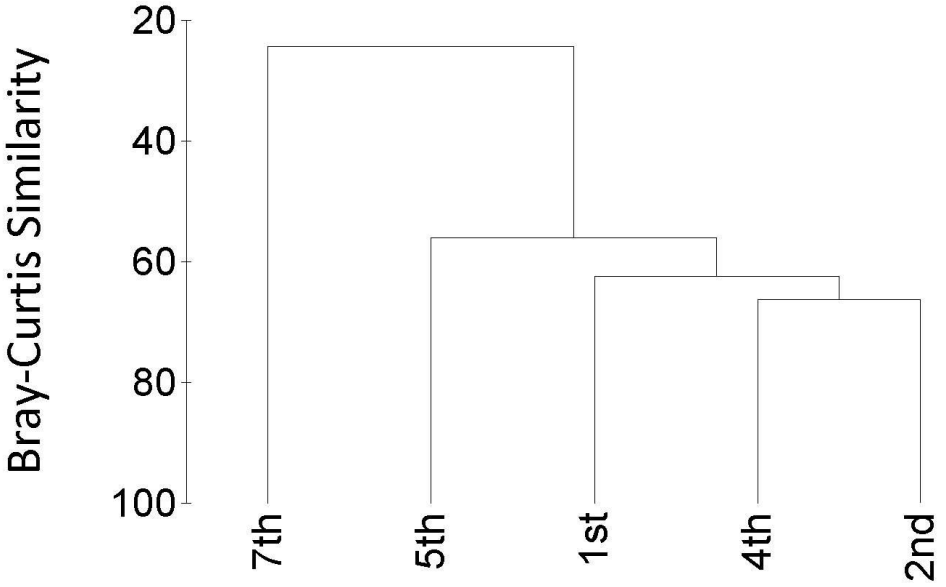

Figure 3.6: Similarity in woody plant community composition between *orders*. The figure depicts an average-linkage hierarchical cluster dendrogram based upon a Bray-Curtis similarity matrix.

Table 3.3: Results from an ANOSIM testing for significant differences in woody vegetation composition between stream orders. Above the table are the global test statistic and the associated p-value. Within the table, numbers on top and to the right are the pairwise R(ANOSIM) test statistics; numbers on the bottom and to the left are the associated p-values. Significant p-values are coloured red.

$R_{(ANOSIM)}$ 0.416
p 0.001

	1	**2**	**4**	**5**	**7**
1		-0.111	-0.148	0.370	1
2	*0.75*		-0.074	0.556	0.963
4	*0.55*	*0.55*		0.074	0.556
5	*0.25*	*0.05*	*0.25*		0.889
7	*0.05*	*0.05*	*0.05*	*0.05*	

Bird community composition:

As was the case with woody vegetation, the 7th order sites held the most distinct bird community (Fig. 3.7), with their community composition being significantly different from sites in all the other stream orders (Table 3.4). Results at the *order* level of organization (Fig. 3.8) corresponded with this finding. Unlike woody vegetation, a second differentiation in bird community composition was discernable, with the 5th and 4th order rivers separating from the 1st and 2nd order rivers (Fig. 3.7; 3.8). The pattern was further supported by ANOSIM results which showed significant differences in community composition between stream orders in all but two pairwise comparisons (Table 3.4), meaning that the sites within a specific order were more similar to one another than to any of the sites from other stream orders. Unlike the species diversity metrics, bird community composition differed between the different stream orders.

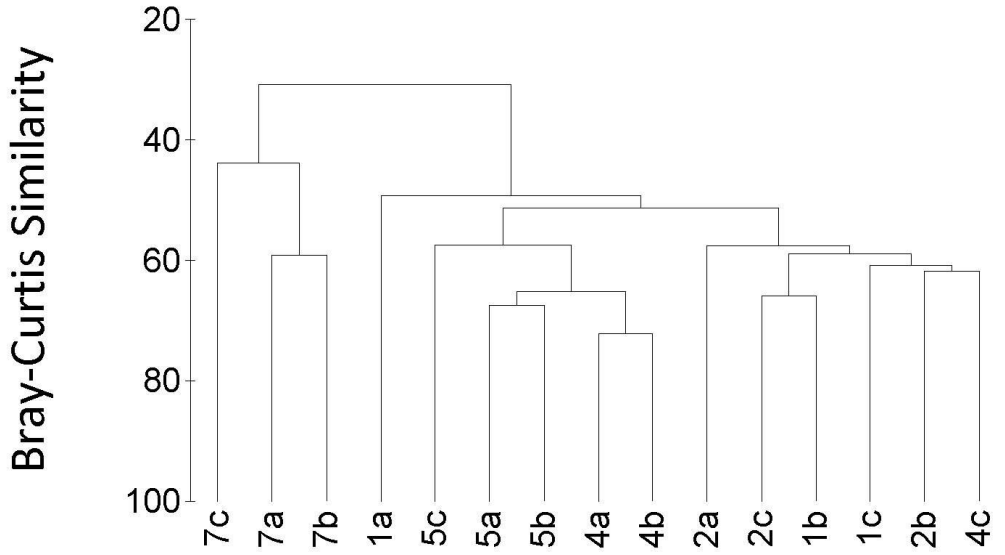

Figure 3.7: Similarity in bird community composition between sites. The figure depicts an average-linkage hierarchical cluster dendrogram based upon a Bray-Curtis similarity matrix.

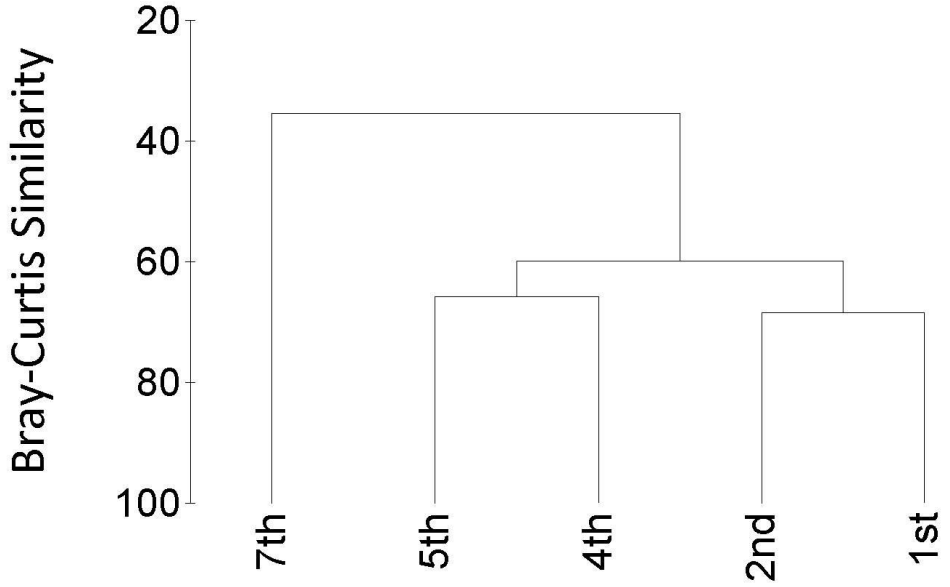

Figure 3.8: Similarity in bird community composition between *orders*. The figure depicts an average-linkage hierarchical cluster dendrogram based upon a Bray-Curtis similarity matrix.

Table 3.4: Results from an ANOSIM testing for significant differences in bird composition between stream orders. Above the table are the global test statistic and the associated p-value. Within the table, numbers on top and to the right are the pairwise $R_{(ANOSIM)}$ test statistics; numbers on the bottom and to the left are the associated p-values. Significant p-values are coloured red

$R_{(ANOSIM)}$ 0.578
p 0.001

	1	**2**	**4**	**5**	**7**
1		0.111	0.370	0.778	1
2	*0.25*		0.519	1	1
4	*0.15*	*0.05*		0.333	0.889
5	*0.05*	*0.05*	*0.05*		0.778
7	*0.05*	*0.05*	*0.05*	*0.05*	

3.3.3 How does species composition of communities differ between stream orders?

Thus far the broad patterns of community composition change along the stream sequence have been examined. I now investigate how community composition changed by considering the individual species found within each stream order. In this section it is easier to examine woody vegetation and birds simultaneously.

Some interesting patterns emerge when examining a simple diagram listing all of the woody plant/bird species observed, as well as the stream order/s in which they were found (Fig. 3.9; 3.10). Firstly there is a group of "generalist" species that occur in all five stream orders; 23 (19%) of the woody plant species and 33 (23.6%) of the bird species encountered were "generalists". These unique species were normally observed in higher abundances than the other species. Secondly, a large number of "unique species", or species that were found in only one stream order, are observed. Forty five (52%) woody plant species and 30 (33%) bird species were found only in the 7th order, while this number ranged between 2 (4%) and 5 (8.8%) and 4 (6%) and 11 (13%) respectively for the other four orders (Fig.3.9; 3.10). These species, more often than not, were found in low abundances, with the only exceptions being certain species found in the 7th order river (e.g. *Breonadia salicina*, Reed Cormorant). Finally, 9 of the 10 alien woody plant species observed during this study occurred exclusively along the 7th order river.



Figure 3.9: Woody plant species observed in each stream order. Species listed to the left of the figure were encountered in more than one stream order, with the orders in which they occurred represented by coloured blocks. Species encountered in only one stream order are written in white in the black bars above the appropriate order. Alien species are in grey coloured blocks. This figure represents data that have not been standardized for unequal sample sizes.



Figure 3.10: Bird species observed in each stream order. Species listed to the left of the figure were encountered in more than one stream order, with the orders in which they occurred represented by coloured blocks. Species encountered in only one stream order are written in white in the black bars above the appropriate order. No alien bird species were recorded. This figure represents data that have not been standardized for unequal sample sizes.

From a presence/absence perspective, "generalist" species will contribute to similarity and "unique" species to dissimilarity in community composition between the different stream orders. When abundance is considered however, this need not be the case. Variation in the abundance of frequently encountered "generalist" species may contribute more to dissimilarity than the presence of infrequently encountered "unique" species. It is thus informative at this point to quantitatively examine how many *rare*, *intermediate* and *common* species were observed in each stream order.

A high proportion of *rare* species was found in all five stream orders; with 50% or greater of all the woody plant species encountered within each order, and 40% or greater of all bird species encountered within each order, considered *rare* (Fig. 3.11). Correspondingly, there was a low proportion of *common* species in all five stream orders; approximately 10% of the woody plant or bird species observed in each order were considered *common*.

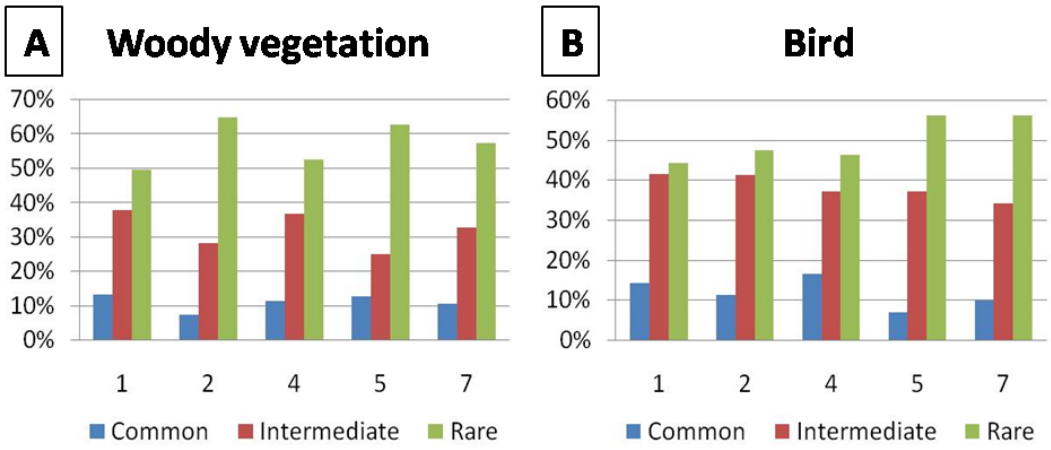

Figure 3.11: The proportion of *common*, *intermediate* and *rare* (A) woody plant species, and (B) bird species observed within each stream order. The categories are derived from Hill's numbers' where *common* $\approx N_{\infty}$; *intermediate* $\approx N_1 - N_{\infty}$; and *rare* $\approx N_0 - N_1$.

To further understand how the species composition of communities differed between stream orders I questioned whether it was the small number of *common* species or the larger number of *rare* species which played a more important role in causing the observed dissimilarity between the five stream orders.

The results of a SIMPER analysis indicate that it was the varying abundances of the *common* species which contributed most to the observed dissimilarity. All of the 7 woody plant species (*Spirostachys africana, Gymnosporia senegalensis, Euclea divinorum, Pterocarpus rotundifolius, Dichrostachys cinerea, Acacia burkei, Diospyros mespiliformis*) and 6 bird species (Red-faced Mousebird, Cape Turtle-Dove, Arrow-marked Babbler, African Green-Pigeon, Dark-capped Bulbul, White-fronted Bee-eater) that contributed most to the dissimilarity between the stream orders were found in high abundances.

Since *common* species were important in creating differences in community composition, I next investigated how the abundance of all the frequently observed species changed along the stream order sequence. A species was defined as frequently observed if 50 or more individuals were encountered during the study. For both woody plants and birds three major patterns emerged. Firstly there was a group of species whose abundance increased along the sequence from 1st to 7th stream order (Fig. 3.12 (A), (B)). Secondly there was a group of species whose abundances decreased along the sequence from 1st to 7th stream order (Fig 3.12 (C), (D)). Finally there was a group of species that showed a humped distribution across the stream order sequence and were most abundant in the 4th or 5th order rivers (Fig. 3.12 (E), (F)).

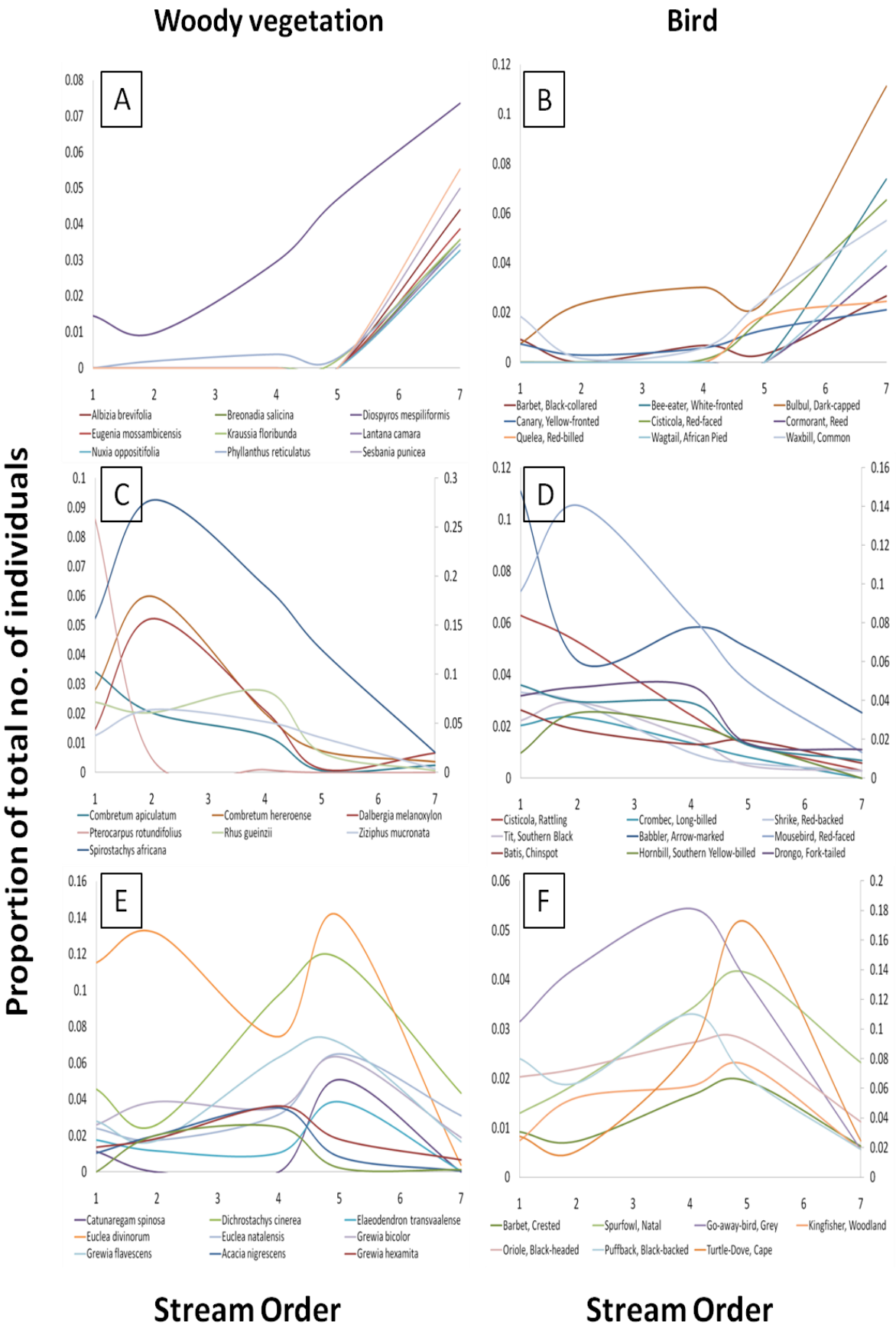

Figure 3.12: Changes in the proportional abundance of frequently observed (A, C, E) woody plant species, and (B, D, F) bird species. A species was considered to be frequently

observed in 50 or more individuals were encountered during the study. (A) and (B) show species whose abundance increases in higher order streams. (C) and (D) show species whose abundance decreases in higher order streams. (E) and (F) show species that are most abundant in 4th or 5th order streams. The secondary axes in (C), (D) and (F) represent the proportional abundances of *Spirostachys africana*, Red-faced Mousebird and Cape Turtle-Dove, respectively.

To further understand these patterns, the change in abundance along the stream order sequence of both woody plant and bird species with differing riparian affinities was examined (Fig. 3.13). In both cases it was observed that the proportional abundance of riparian specialists showed a sharp increase in the 7th order rivers. Near-riparian specialists showed a more gradual increase in proportional abundance along the stream order sequence from 1st through to 7th order rivers. The proportional abundance of those species loosely associated with riparian areas and upland species generally decreased along this same sequence.

Relating this to the frequently observed species, it was found that the majority (12/19) of those frequently occurring species whose abundance increased along the stream order sequence were classified as either riparian specialists or near-riparian specialists. The majority (12/17) of those frequently occurring species whose abundance decreased along the stream order sequence were classified as upland species, and finally, the majority (12/17) of those frequently occurring species who showed a humped distribution along the stream order sequence were classified as loosely associated with riparian areas.

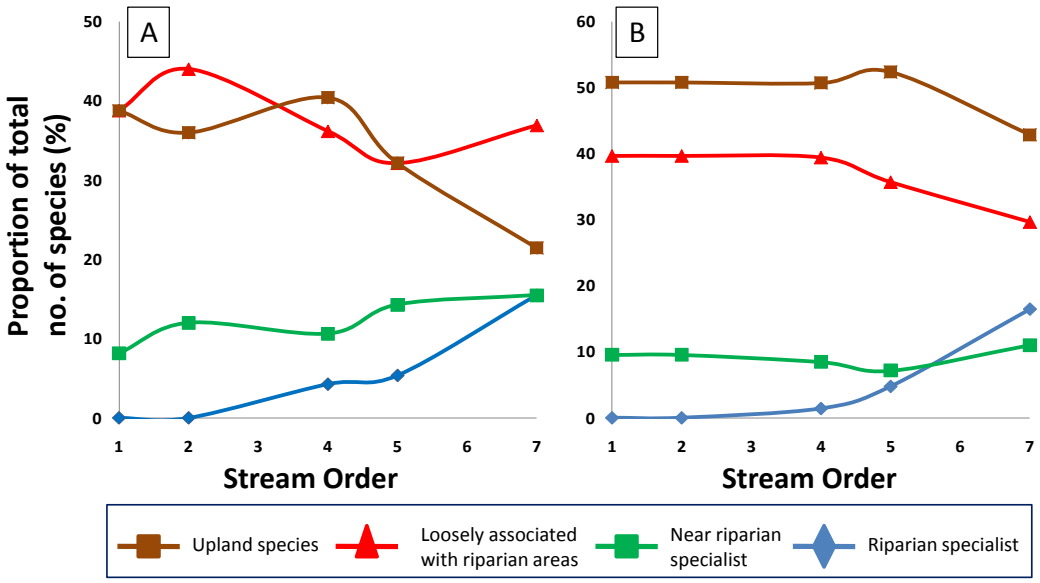

Figure 3.13: Changes in the proportional abundance of groups of (A) woody plant species, and (B) bird species, with different riparian affinities. The brown line with squares represents the group "upland species", the red line with triangles the group of species "loosely associated with riparian areas", the green line with squares the group of "near-riparian specialists", and the blue line with diamonds the group of "riparian specialists".

3.4 Discussion

This study provides insight into the variation in biodiversity along a stream order sequence in a semi-arid savanna landscape. The initial expectation was that compositional diversity would increase incrementally along the stream order sequence from 1st to 7th order rivers because of an increase in the underlying physical heterogeneity. In some instances this expectation was met, but not in others.

Woody plant species richness and species diversity (*variety* and *balance*) were highest in the 7th order river, but similar in the 1st to 5th order rivers. The consensus in the literature (Naiman *et al.* 2005) is that plant diversity increases downstream (implying an incremental increase in diversity with increasing stream order), but I only observed an increase in compositional diversity in the 7th order river. Thus the woody plant species diversity results only partially corresponded with initial expectations. One of the reasons for the elevated number of woody plant species observed in the 7th order river was primarily due to the addition of riparian specialist species to the species pool. These species (e.g. *Nuxia oppositifolia, Combretum erythrophyllum, Ficus sycomorus*) are restricted to the riparian zone

because they require geomorphic features present only in riparian areas of perennial rivers. For example, *Breonadia salicina* seedlings, another species observed only in the 7th order river, have been found to grow only on patches of exposed bedrock along the Sabie River (DeFontaine & Rogers 1995). Additionally, species richness in the 7th order river was enhanced by the presence of alien species (e.g. *Chromolaena odorata*, *Lantana camara*, *Sesbania punicea*), with nine of the ten alien species encountered during this study present only in the Sabie River. Riparian zones of large perennial rivers within the KNP are highly prone to invasion by alien plants due to the continuous influx of alien propagules from the poorly managed upper reaches of the major river catchments, combined with the capacity of river systems to facilitate invasions (Morris 2008).

Bird species richness and species diversity (*variety* and *balance*) were similar in all five stream orders, results which disagree with my initial expectations. This disagreement illustrates the great importance of all riparian zones to birds, with bird diversity being exceptionally high in each of the stream orders considered. At the order level of organization, Shannon's diversity was greater than 3.4 in all five stream orders. These values are all at the high end of the usual range for this index, which typically falls between 1.5 and 3.5 (Magurran 2004). The total number of bird species (140) recorded during this study is also high. It is problematic to compare this value to other studies which took place in different parts of the world because their regional species pools differ in size, but to provide some context, only 64 species were recorded in 50 sites in south-eastern Australia (Jansen & Robertson 2001) and 40 species were recorded over two years of sampling at 6 sites in the Pacific Northwest, U.S.A. (Lock & Naiman 1998).The high bird diversity recorded in each stream order shows the great importance of riparian zones to birds in the semi-arid KNP, and indicates that when overall diversity is particularly high the effect of stream order is dampened.

Patterns of change in both woody vegetation and bird community composition *(disparity*) generally matched my initial expectations. The perennial 7th order river held the most distinct woody vegetation and bird community composition, and further differentiation in bird community composition was evident between the 5th and 4th order rivers and the 1st and 2nd order rivers. The reasons for these observed correspondences with initial expectations are threefold.

Firstly, upland species (e.g. *Pterocarpus rotundifolius, Combretum apiculatum,* Rattling Cisticola, Blue Waxbill) or those loosely associated with riparian zones (e.g. *Spirostachys africana, Ziziphus mucronata,* Arrow-marked Babbler, Southern Yellow-billed Hornbill) were found in higher abundances in the lower order rivers. The increased similarity in the community composition between lower order rivers and their adjacent upland areas, as compared to higher order rivers, is a pattern common to several studies (Lock & Naiman 1998; Woinarski *et al.* 2000). The riparian zone of lower order rivers is narrower and thus more permeable to typically upland species, particularly when considering the highly mobile nature of birds, and so upland species constitute a larger proportion of the overall community. On the other hand, the riparian zone of the 7th order river is wider than any of the other stream orders, and thus there is more area available for riparian specialist species to establish themselves and prevent the recruitment of other species. Upland /loosely associated with the riparian zone plant species are restricted to a narrow band near the boundary with the upland, and thus their proportional abundance is lower. A similar pattern was observed by van Coller *et al.* (1997a) who described a *Spirostachys africana* vegetation type, which included a high proportion of species typically found in the surrounding savanna, along the highest elevation of the macro-channel bank along the Sabie River.

The second factor responsible for the 7th order community being distinct is the increased abundance of near-riparian specialists (e.g. *Diospyros mespiliformis, Phyllanthus reticulates,* White-fronted Bee-eater, Common Waxbill) within this stream order. This factor was more important for woody vegetation community composition, with plant near-riparian specialists making use of the wider riparian zone as well as access to permanent water in the highest order river. While the abundance of the bird near-riparian specialists was highest in the higher order rivers, their presence was more consistently detected along the entire stream order sequence. The bird species classified as near-riparian specialists were less dependent upon the water provided by rivers and more on the habitat provided by riparian woodlands (e.g. Purple-crested Turaco, White-browed Robin-Chat). Finding near-riparian specialists in all five stream orders is indicative of the highly mobile nature of birds, as well as the difficulty in defining specialist riverine organisms, a problem encountered in many other studies (Buckton & Ormerod 2002).

Finally, the presence of unique riparian specialist species (e.g. *Nuxia oppositifolia, Breonadia salicina,* Reed Cormorant, Pied Kingfisher*)* in high abundances in the 7th order river leads to its community composition differing from the other four stream orders. Unique species were recorded in every stream order, however, in the 1st through 5th order rivers these unique species were *rare* and so didn't contribute greatly to the overall community composition. Conversely in the 7th order river several of these unique species were found in higher abundances and so changed the overall community composition.

Why, in a broader sense, were initial expectations regarding the pattern of change in woody vegetation and bird compositional diversity along the stream order sequence not fully met? I consider the semi-arid savanna context of the study before discussing whether study design may have played a role.

3.4.1 Implications of the observed pattern of change in compositional diversity along the stream order sequence for our understanding of riparian biodiversity in a semi-arid savanna context

The KNP falls within a semi-arid region of South Africa (Du Toit *et al.* 2003). The 7th order river considered in this study was a perennial river, while the 1st to 5th order rivers were all ephemeral. There are no perennial rivers of lower stream order anywhere within the KNP. This work contrasts strongly with studies (Knopf *et al.* 1985; Nilsson *et al.* 1994; Lock & Naiman 1998; Goebel *et al.* 2003) in temperate North America and Europe, upon which the initial expectations for this study were based, where the low and high stream order rivers were all perennial. Since much of the present knowledge regarding diversity in riparian areas is gleaned from work done in these temperate regions, this study offers new insight into the patterns of change in biodiversity in rivers with variable hydrological characteristics. It is known that the importance of riparian zones to birds differs depending upon landscape context and the characteristics of the riparian zone itself (Woinarski *et al.* 2000), and that riparian zones perform an essential and unique function in areas where water availability is limited (Lock & Naiman 1998). The overall importance of all riparian zones in semi-arid areas may thus override the effects of stream order, and so the differences in diversity between low and high order rivers are not always

observed. This study shows that in the semi-arid KNP the switch from an ephemeral to a perennial river, rather than simply an increase in stream order, is highly important in creating the observed patterns of change in compositional diversity along the stream order sequence.

3.4.2 Critical evaluation of methods

Nine of the ten alien plant species observed during this study occurred only in the 7th order river and contributed to the observed increase in woody vegetation compositional diversity (in particular to the *richness* property) in that river. The Sabie River is the only river considered during this study whose catchment includes area outside of KNP, and thus alien species were far more likely to occur there than in any of the other rivers (Morris 2008). This is important to be aware of as it means that the 7th order river had a larger potential species pool, and from this alone I may expect diversity to be higher therein. However, an inherent characteristic of 7th order rivers is that they are long, generally longer than rivers of a lower stream order, and this increased length means they are always more likely to flow through poorly managed areas before reaching protected areas. Thus access to a greater pool of potential species can be considered as an inherent characteristic of 7th order rivers, and thus the inclusion of alien species in the diversity estimates is appropriate.

Another inherent characteristic of 7th order rivers is that they have wider riparian zones than rivers of a lower stream order. This meant that the area of each woody vegetation plot or the effective radius around each bird point count was higher in this stream order than in any of the other stream orders. Thus one might expect diversity to be higher in this order than in any of the others simply because an increase in sample area usually correlates with an increase in diversity (Connor & McCoy 2001). Sample-based rarefaction curves were utilized to overcome this problem and allowed for comparison between stream orders at a common sample size (common number of individuals recorded). This study provides a good example of the value of this method, and I recommend it to be used in other studies where similar sample size issues are encountered.

I chose to use similarity indices as a measure of the disparity property of diversity because they could easily be applied to both the compositional and structural diversity data. However, taxonomic distinctness is another measure of

disparity which could have been applied to the compositional diversity data. This is a possible avenue for future research.

Another possible route for future research would be to conduct a similar study during winter. While woody species composition should remain similar throughout the year, literature suggests that bird habitat associations are more defined in the winter rather than in the summer months (John Ralph *et al.* 1993). Thus new or perhaps clearer patterns may emerge if this study were to be replicated during winter.

Chapter 4

Structural diversity

4.1 Introduction

Structural diversity, particularly at the community level of organization, is probably the component of biodiversity which receives the least attention, yet it plays a fundamental role in all ecosystems. Increased structural diversity is associated with increases in compositional (MacArthur & MacArthur 1961; Jansen & Robertson 2001; Brose 2003) and functional diversity (Norberg & Rayner 1987; Dial *et al.* 2008). Furthermore, in forest ecosystems where it is most commonly studied, measures of community level structural diversity are important for predicting future stand growth (Staudhammer & LeMay 2001). In this chapter I examine how the structural diversity of woody plant and bird species varies along a stream order sequence.

Very few studies have explicitly measured structural diversity in rivers of different size. In the Sonoran Desert, canopy volume of velvet mesquite and overall plant cover were found to increase along larger (higher order) rivers (Spoonseller & Fisher 2006), and in the Pacific Northwest, U.S.A. large rivers were found to support significantly more deciduous vegetation coverage in midstory and canopy layers than smaller rivers (Lock & Naiman 1998). No study examining structural diversity in any animal taxon in rivers of different stream order or size was

encountered. The lack of existing knowledge means that this study contributes significantly to our understanding of the variation in structural diversity among rivers of different stream order, especially with regards to bird (animal) structural diversity.

What might I expect to observe? In the previous chapter it was hypothesized that physical heterogeneity within the riparian zones would increase along the sequence from 1st through to 7th order rivers, and the logic behind this explained. An increase in physical heterogeneity would mean an increase in the variety of patch types present in a river, and thus a greater potential for woody plants with different growth forms, sizes and life history strategies to be present, and therefore a greater potential for higher woody vegetation structural diversity. Based upon this reasoning I expected woody vegetation structural diversity to increase along the stream order sequence from 1st to 7th order. Changes in vegetation structure have been associated with changes in bird communities (MacArthur & MacArthur 1961; Karr & Roth 1971; Jansen & Robertson 2001), and therefore it is expected that an increase in woody vegetation structural diversity would lead to an increase in bird assemblage structural diversity. Thus I also expected bird assemblage structural diversity to increase along the stream order sequence from 1st to 7th order.

4.2 Methods

The methods of field work, determination of species diversity metrics, similarity indices and ANOSIM and the approaches to data analysis have been covered in Chapter 2. Here I discuss only those methods specific to the analysis of structural diversity.

4.2.1 Categorization of structural attributes

Diversity metrics (e.g. richness, diversity indices) require categorical data (i.e. partitioned into species). All except one (NoS) of the structural attributes measured during this study; plant height, canopy width and DBH for woody vegetation, and body mass, WL/BL and leg length for birds; are measured on a continuous scale. It was thus necessary to categorize these measurements.

There were several considerations for categorizing the structural diversity data. Firstly the total number of categories needed to be decided upon. I required

enough categories so that differences in *richness* (i.e. the number of categories filled) would be noticeable between orders, however, not too many that each category became sparsely populated and thus differences in *evenness* were indistinguishable. Secondly, the bin size needed to match the accuracy of measurement for each attribute. For example, plant height data could not be binned into 10cm groups if the potential error in measurement was 20cm. Finally, for bird body mass, it was necessary to vary the bin size. The range of body mass values varied by several orders of magnitude (10g to 5.5 kg), but with the majority of species concentrated at the lower end of the spectrum. Additionally, the accuracy of measurement decreased as weight increased. It was therefore necessary to have narrower bin widths at the lower end of the spectrum, and to increase bin size as body mass increased. This allowed for a meaningful number of categories to be created and these categories matched the accuracy of measurement. Variable bin sizes are common to several studies of structural diversity (e.g. MacArthur & MacArthur 1961; Onaindia *et al.* 2004). The categories chosen for each structural diversity attribute are presented below (Table 4.1).

Table 4.1: Summary of structural attribute categories of woody vegetation and birds

Structural Attribute	**Bin Size**	**Minimum category**	**Maximum category**	**Total no. of categories**	
Woody Vegetation					
Height	1m	1m – 2m	19m – 20m	19	
Canopy width	1m	0m – 1m	19m – 20m	20	
DBH	2cm	0 – 2cm	>50cm	26	
NoS	1 stem	1 stem	≥ 20 stems	20	
Birds					
Body mass	10g	0 - 10g	90-100g	10	28
	50g	100g – 150g	450g – 500g	8	
	500g	500g – 1kg	5kg – 5.5kg	10	
WL/BL	0.02	0.34 – 0.36	>0.78	23	
Leg length	5mm	10mm – 15mm	>100mm	19	

4.2.2 Testing for differences in the distribution of structural attribute measurements between stream orders.

Kolmogorov-Smirnov two-sample tests were used to test for differences in the distribution of structural attribute measurements between stream orders. The test is based on the unsigned differences between the relative cumulative frequency distributions of the two samples. The null hypothesis of this non-parametric test is that the two samples under consideration have the same distributions, and thus the test is sensitive to differences in location, dispersion, skewness and so forth (Sokal & Rohlf 1981). Finding significant differences between the two samples indicates that they have different distributions.

4.3 Results

Overall structural diversity comprises the diversity of several separate attributes, unlike overall compositional diversity which involves the diversity of a single attribute (species). Thus in this chapter the structural diversity of woody vegetation and birds are considered separately. Results at both the individual site as well as the order level of organization are considered.

4.3.1 Structural diversity of woody vegetation

It is informative to examine the woody vegetation structural data in a simple format to observe broad patterns, before these data are converted into more complicated diversity metrics. Several patterns emerge when simply examining the proportion of trees in each of the height, canopy width, DBH and NoS categories (Fig. 4.1).

- A high proportion (at least 80%) of all the trees measured fell within the smaller (<4m height, <4m canopy width, < 10cm DBH) size classes for all four structural attributes. The clearer differences in woody vegetation structure between stream orders were in the measurements of medium and large (>4m height, >4m canopy width, >10cm DBH) trees, which made up only a small proportion of all the trees measured. Thus differences in structural diversity between stream orders may be dampened by a high proportion of structurally similar smaller woody plants.

- The 1st order rivers lacked large (>7m height, > 7m canopy width, > 20cm DBH) trees, and showed a different distribution of height, canopy width and DBH measurements from the 4th, 5th and 7th order rivers (Kolmogorov-Smirnov, $p<0.025$). There were no individuals with a height or canopy width greater than 7 metres, or a DBH greater than 25cm.

- The distribution of trees within the NoS categories was different in the 1st order rivers from all other stream orders except 4th (Kolmogorov-Smirnov, $p<0.001$). There is a more even spread of individuals across the NoS categories in the 1st order rivers. The lowest proportion of trees with a single stem and the highest proportion of individuals with 19 or more stems were found in the 1st order rivers.

- The distributions of height, canopy width and DBH measurements in the 4th order rivers was different to those in the 1st, 2nd, and 7th order rivers (Kolmogorov-Smirnov, $p<0.025$). These differences can be attributed to the higher number of medium (4-7m height, 4-7 canopy width, 10-20cm DBH) and large trees observed within this stream order. In the 4th order sites 34 individuals greater than 4m high were encountered, approximately three times more than the number observed in the 1st and 7th order sites. Similarly, 21 trees with a DBH greater than 10cm were encountered in the 4th order rivers, compared with 7, 16 and 13 in the 1st, 2nd and 7th order rivers respectively. The increased number of size classes filled and the more even distribution of trees within these different size classes suggests that structural diversity will be higher in the 4th order rivers.

- There were few medium sized trees in the 7th order river. Measurements of height, canopy width and DBH all show a sharp increase from small trees to large trees with very few individuals in between. The distribution of trees for each of these attributes was different in the 7th order compared to all the other stream orders (Kolmogorov-Smirnov, $p<0.025$).

The broad patterns observed in this simple format provide context for the results obtained from the diversity metrics.

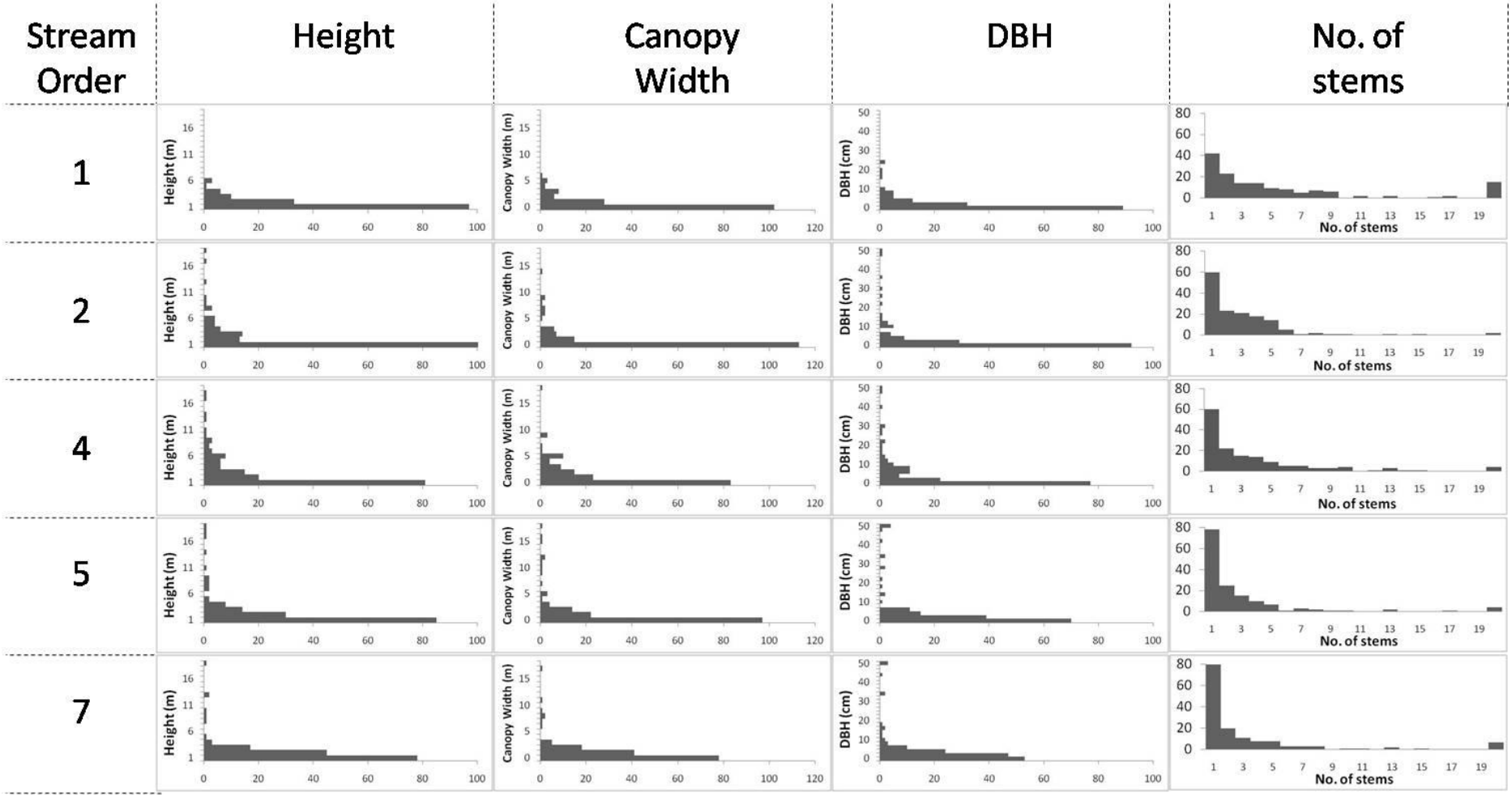

Figure 4.1: Counts of trees in each of the height, canopy width, DBH and NoS categories in each stream order.

Structural diversity metrics

The diversity metrics presented are category richness, Simpson's evenness and Simpson's diversity. Category richness measures the *variety* property of diversity, Simpson's evenness the *balance* property of diversity, and Simpson's diversity a combination of the two. Simpson's diversity was chosen as it is widely used and provides a good estimate of diversity at relatively small sample sizes. Simpson's evenness is complementary to Simpson's diversity and thus it was the evenness measure included.

Category richness was highest in the 4th order rivers for all attributes when considering each site separately, and highest in the 4th order rivers for all attributes except canopy width at the stream order level of organization (Fig. 4.2 (A)). This corresponds with the broad patterns observed above; the presence of more medium sized trees in the 4th order rivers increased diversity therein. Also corresponding with the broad patterns observed above, height, canopy width and DBH category richness was generally lowest in the 1st and 7th order rivers (Fig. 4.2). In the 1st order rivers this was due to a lack of large trees, while in the 7th order river it was due to a lack of medium sized trees.

Simpson's evenness reveals a different pattern to category richness. Evenness values for height, canopy width and DBH tended to be highest in the 1st and 7th stream orders, both when considering each site individually and at the stream order level of organization (Fig. 4.2 (B)). Evenness values for NoS were highest in the 1st order rivers, matching up with more even distribution of NoS measurements in the 1st order rivers detected above, before steadily decreasing down the stream order sequence to the 7th order river. Overall the values for Simpson's evenness were low; indicating that a high proportion of each stream order's tree population was found in only a few size classes.

There were no significant differences in height, canopy width or DBH Simpson's diversity between the five stream orders (Height: $F_{(4,10)} = 0.87$, $p>0.1$; Canopy Width: $F_{(4,10)} = 0.91$, $p>0.1$; DBH: $F_{(4,10)} = 1.40$, $p>0.1$). It is probable that the similarly high proportions of trees found in the smallest category sizes in each stream order contributes to the observed similarities in diversity. Simpson's diversity, as applied to the NoS measurements, decreases along the stream order

sequence from 1st to 7th order streams (Fig 4.2 (C)). NoS diversity in the 1st order rivers was particularly high, significantly higher than the NoS diversity measured in either the 5th or 7th order rivers (Fisher's LSD, $p<0.05$).

Woody plant structural composition (Similarity indices)

The diversity metrics presented thus far have dealt with the *variety* and *balance* aspects of diversity. Similarity indices will now be used to consider the *disparity* aspect of structural diversity.

There is no clear distinction in height, canopy width and DBH structural composition between stream orders (Fig. 4.3). In all three cases, sites within the same stream order did not house a similar combination of structural characteristics and thus did not cluster out together. Results from ANOSIM reveal that sites within the same stream order are no more similar to one another in structural composition than to sites between stream orders (Height: $R_{ANOSIM} = 0.00$, $p>0.1$; Canopy Width: $R_{ANOSIM} = 0.01$, $p>0.1$; DBH: $R_{ANOSIM} = 0.08$, $p>0.1$). NoS displays a different pattern of structural composition, where the first two clusters separate out two of the three 1st order sites (Fig 4.3). All 1st order sites tend to hold a higher proportion of multi-stemmed trees, and thus were different in their structural composition from higher order streams. These results are supported by an ANOSIM ($R_{ANOSIM} = 0.08$, $p = 0.07$).

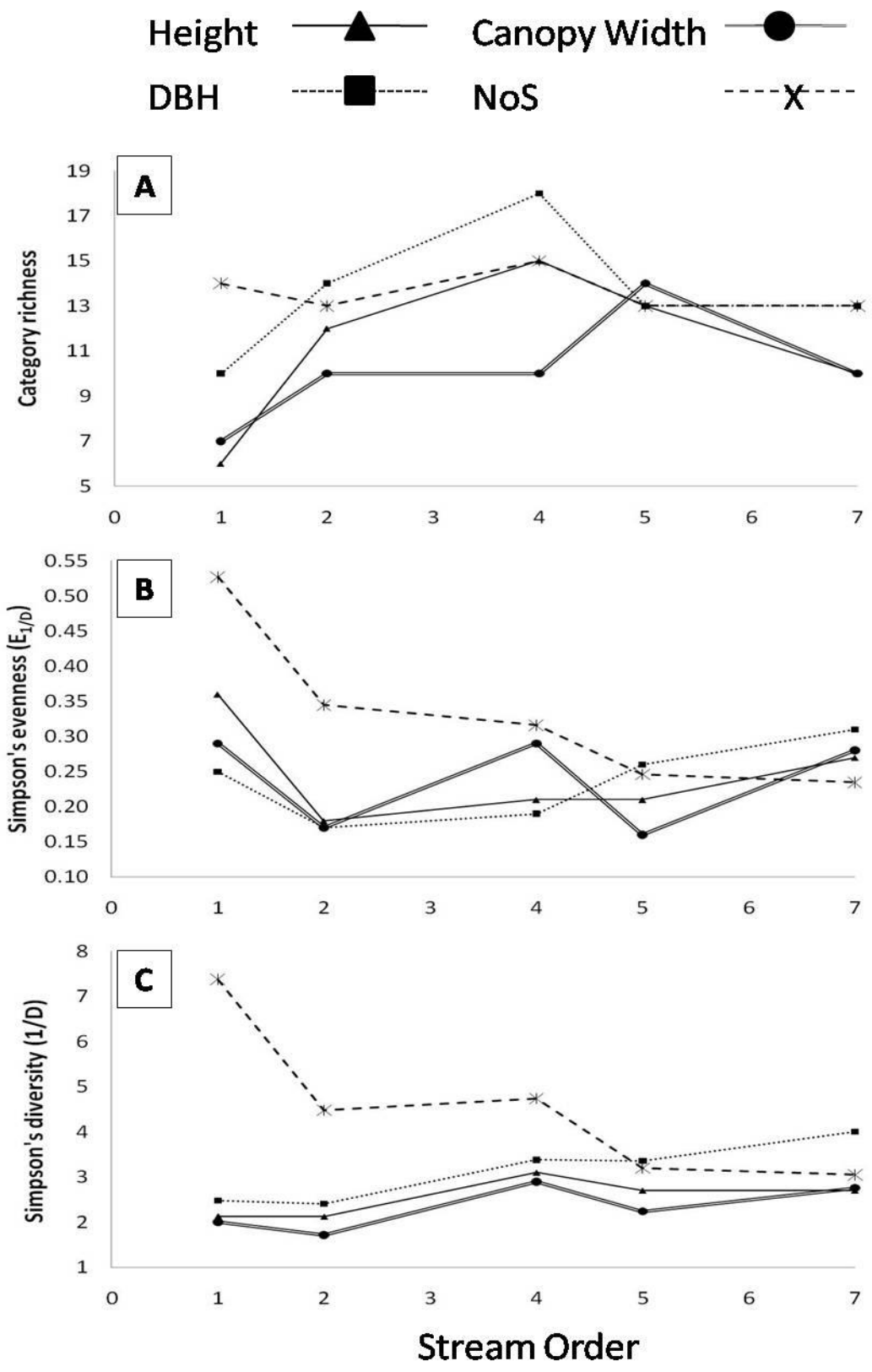

Figure 4.2: Measures of woody vegetation structural diversity across a stream order sequence, showing category richness (A), Simpson's evenness (B) and Simpson's diversity (C) for four separate structural attributes; height, canopy width, DBH and NoS. The values are obtained from the "order" datasets.

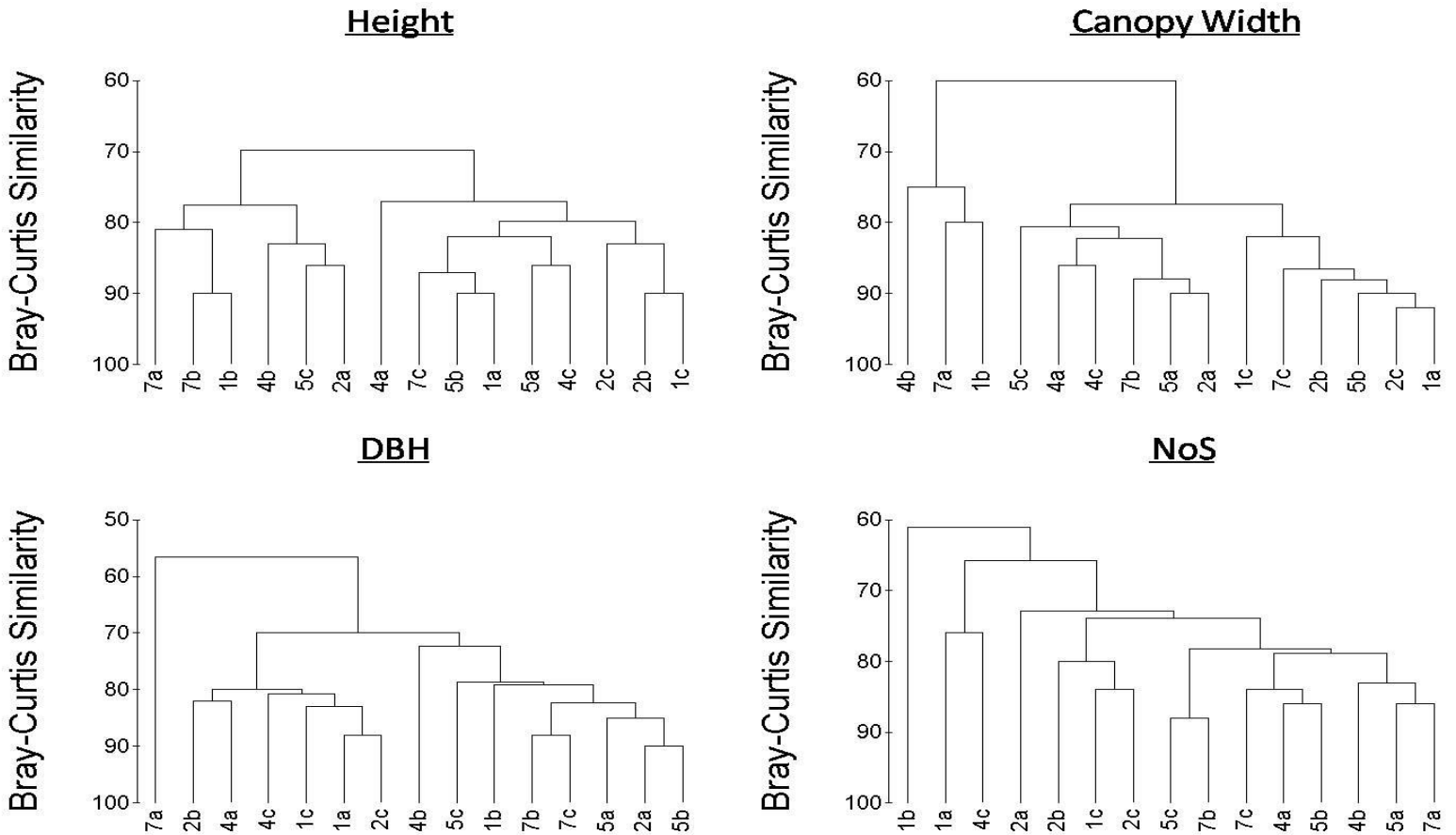

Figure 4.3: Similarity in woody vegetation structural composition between sites for four different attributes; height, canopy width, DBH and NoS. The figures depict average-linkage hierarchical cluster dendrograms based upon Bray-Curtis similarity matrices.

4.3.2 Structural diversity of the bird species assemblage

Examining bird assemblage structural diversity data in a simple format, as the proportional abundance of birds in each of the body mass, WL/BL and leg length categories (Fig. 4.4), reveals broad patterns which provide context for the results from the diversity metrics.

For all three attributes, a higher proportion of measurements falls within the same smaller (body mass <100g, WL/BL < 0.5, leg length , 25mm) size categories. Differences in bird assemblage structural diversity between the stream orders are thus most pronounced in the higher size classes.

There were a greater proportion of heavier birds in the higher order rivers (4th - 7th). Average body mass increased from 64g and 84g in the 1st and 2nd order rivers respectively, to 144 g, 145 g and 125 g in the 4th, 5th and 7th order rivers respectively. This was due to the occurrence of both large raptors (e.g. Wahlberg's Eagle, Verreaux's Eagle-Owl, White-backed Vulture) and large water birds (e.g White-breasted Cormorant, Goliath Heron, Egyptian Goose) and means that a greater number of body mass categories was occupied in the higher order rivers. The distribution of body mass measurements was significantly different between all stream orders (Kolmogorov-Smirnov, $p<0.001$), except between the 4th and 5th order rivers (Kolmogorov-Smirnov, $p>0.1$).

The distribution of WL/BL measurements was also significantly different between all stream orders (Kolmogorov-Smirnov, $p<0.005$). The differences were more pronounced in the shape of the distributions, implying differences in evenness, rather than that the distributions were spread over different categories, implying differences in richness. There was a greater proportion of birds with a low WL/BL ratio in the 7th order river. In the 1st to 5th order rivers 1-2% of the bird species observed had a WL/BL ratio less than 0.4, compared to 11% in the 7th order river. The presence of White-breasted Cormorant and Reed Cormorant in the 7th order river contributed significantly to this observed difference.

A similarly high proportion (47-52%) of birds in all five stream orders had a leg length between 20 mm and 25 mm. The proportional abundance of birds in the other leg length categories was more variable and it is these differences which will

account for dissimilarities in evenness between the stream orders. Indeed overall there was a significant difference in the distribution of leg length measurements between all stream orders (Kolmogorov-Smirnov, $p<0.005$), except between 1st and 2nd (Kolmogorov-Smirnov, $p>0.1$). There are also differences in the total number of leg length categories occupied between the stream orders. There were more birds with longer legs in the higher order rivers (4th – 7th). These birds were large raptors (e.g. African Fish-Eagle) and wading water birds (e.g. Goliath Heron), and their presence should increase the overall structural diversity measured in these higher order rivers.

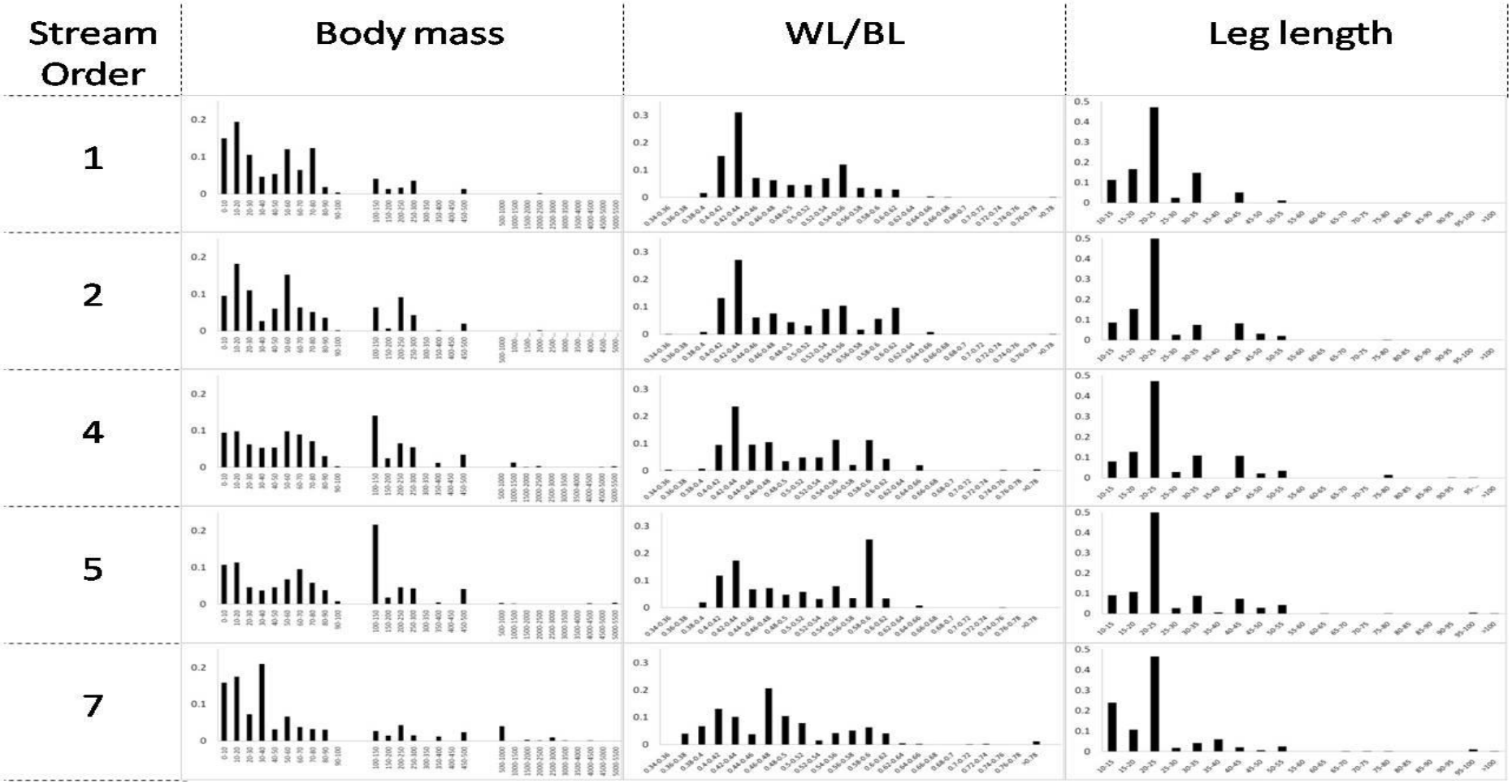

Figure 4.4: Profiles showing the distribution of body mass, WL/BL and leg length measurements for all birds encountered within each stream order during the study.

Structural diversity metrics

The same diversity metrics that were presented for woody vegetation will be presented for birds, for the same reasons.

Body mass and WL/BL category richness increased gradually along the stream order sequence, being lowest in the 1st and 2nd order rivers and highest in the 4th, 5th and 7th order rivers, both at the individual site and the *order* level of organization (Fig. 4.5 (A)). Leg length category richness showed a steeper, incremental increase along the stream order sequence from 1st to 7th stream order than any of the other structural attributes (Fig. 4.5 (A)). The increases in category richness along the stream order sequence for all three attributes was attributable to the presence of large raptors and waterbirds in the higher order rivers.

Simpson's evenness showed a different pattern along the stream order sequence for each of the attributes. Evenness of body mass measurements was highest in the 4th order rivers and lowest in the 7th order river (Fig. 4.5 (B)). Wing length/Body length evenness gradually increased along the stream order sequence from 1st to 7th order. At the *order* level of organization leg length evenness decreased gradually along the stream order sequence from 1st to 5th order, before increasing substantially in the 7th order river. This pattern was however not matched at the individual site level of organization; there were similar levels of evenness in leg length measurements in all five stream orders show.

Differences in evenness between the stream orders tended to be more important in producing differences in overall diversity, and the patterns of Simpson's diversity along the stream order sequence were similar to that observed for evenness. Overall body mass diversity was significantly different and highest in the 4th order river ($F_{(4,10)} = 8.92$, $p<0.01$; Fisher's LSD, $p<0.05$), and lowest in the 1st and the 7th order rivers (Fig. 4.5 (C)). The diversity of WL/BL measurements increased gradually along the stream order sequence at both the order and individual site level of organization, but there were no significant differences between any of the stream orders (Fisher's LSD, $p<0.05$). At the order level of organization leg length diversity was relatively similar in the 1st to 5th order rivers, before increasing substantially in the 7th order river. This pattern was however far less pronounced at

the individual site level of organization and thus the differences in leg length diversity between the stream orders are not significant ($F_{(4,10)} = 0.66$, $p>0.1$).

Structural composition of the bird species assemblage (Similarity indices)

Similarity indices are used to consider the *disparity* aspect of bird assemblage structural diversity.

The structural composition of the bird species assemblage in the 7th order river was distinct from all other stream orders for all three attributes at both the individual site (Fig. 4.6) and order level of organization. Overall sites within the same stream order were more similar to one another than to sites within other stream orders (Body mass: $R_{ANOSIM} = 0.45$, $p<0.001$; WL/BL: $R_{ANOSIM} = 0.48$, $p<0.001$; Leg length: $R_{ANOSIM} = 0.25$, $p<0.001$), and the pairwise comparisons showed the bird assemblage structural composition of the 7th order sites were always significantly more similar to one another than to sites in any of the other stream orders. There was further distinction in bird assemblage structural composition between stream orders as body mass structural composition in the 4th and 5th order rivers was different from that in the 1st and 2nd order rivers (Fig 4.6).

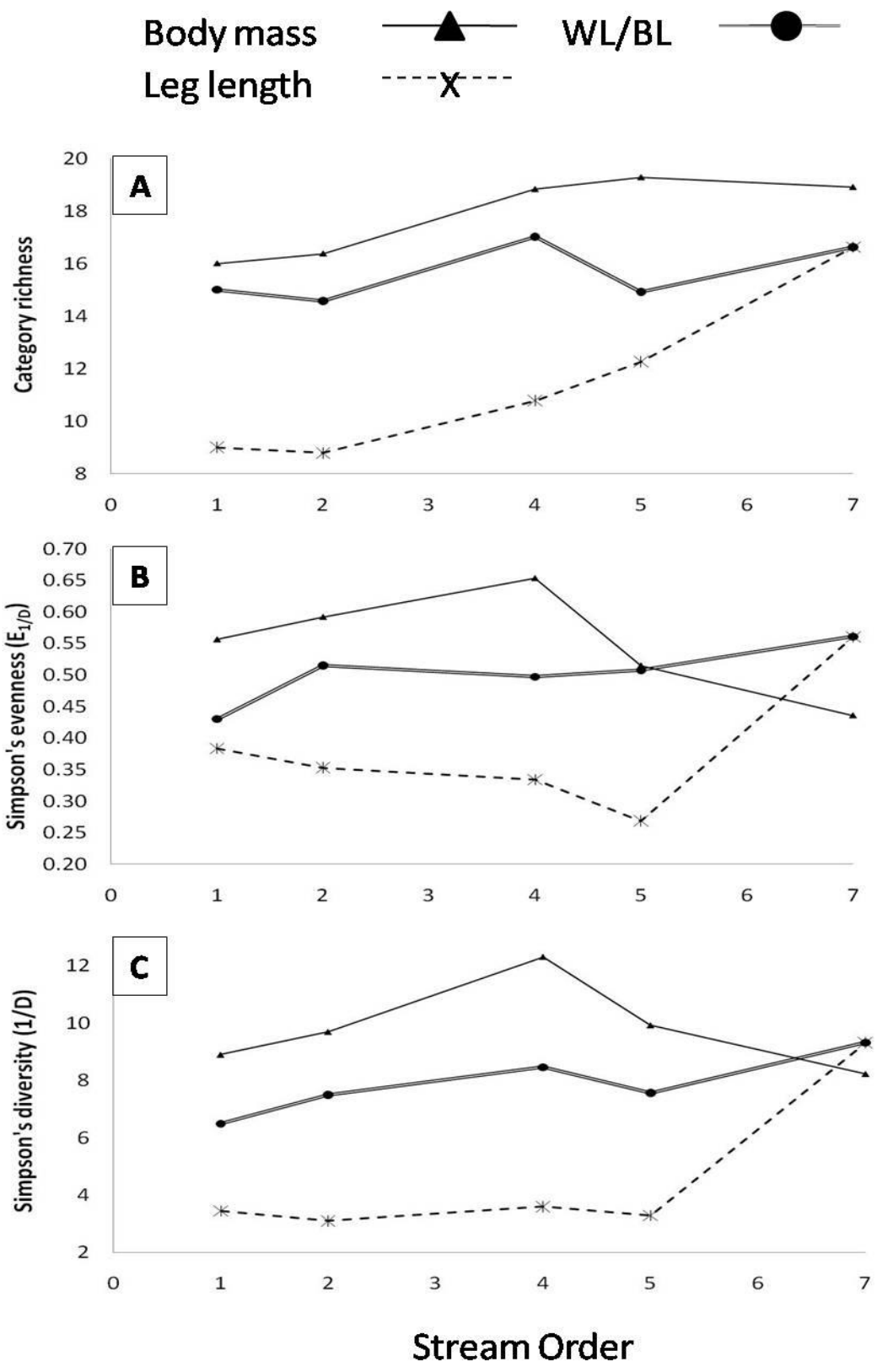

Figure 4.5: Measures of bird assemblage structural diversity across a stream order sequence, showing category richness (A), Simpson's evenness (B) and Simpson's diversity (C) for three separate structural attributes; body mass, WL/BL and leg length. The values are obtained from the "order" datasets.

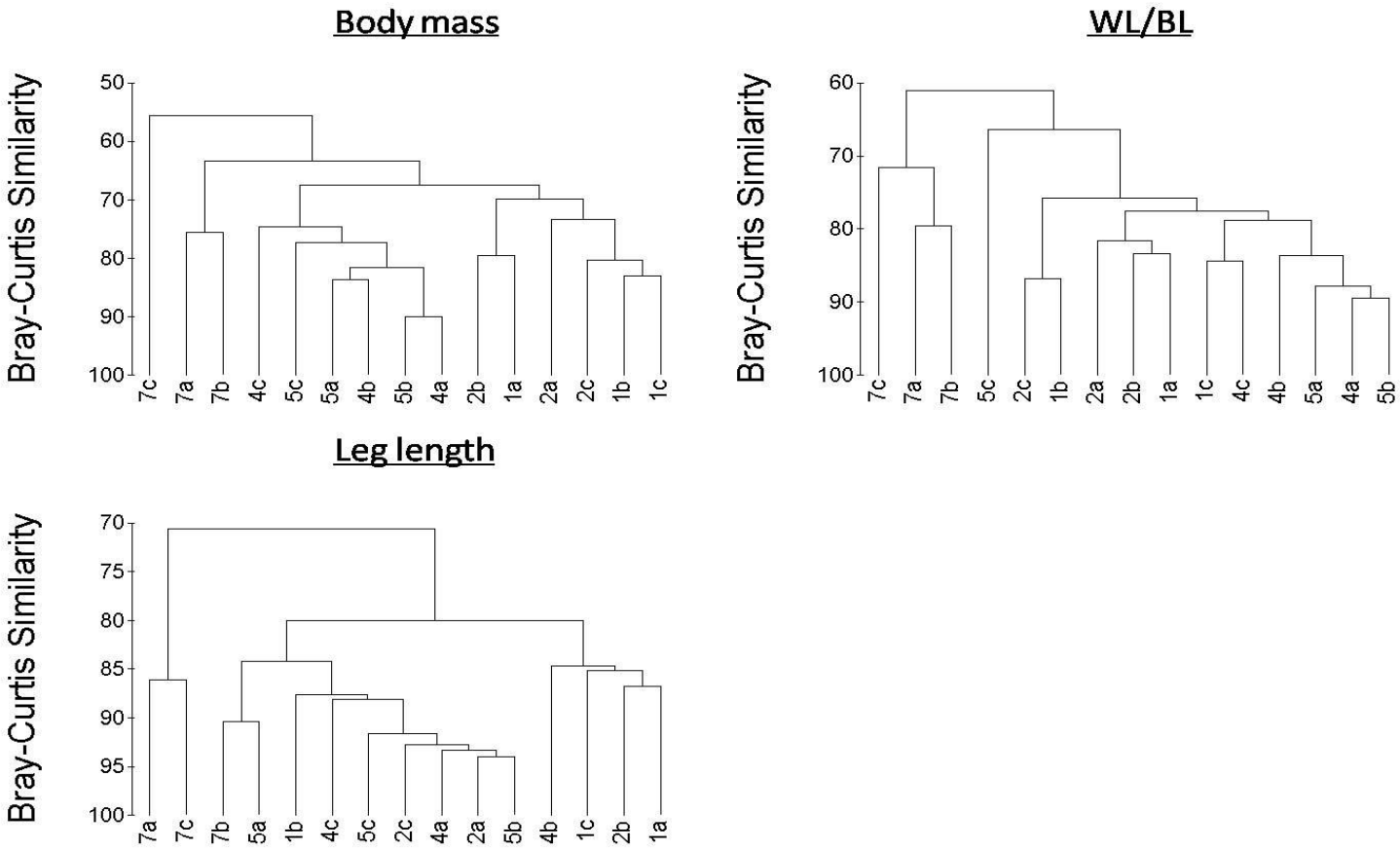

Figure 4.6: Similarity in bird structural composition between sites for three different attributes; body mass, WL/BL and leg length. The figures depict average-linkage hierarchical cluster dendrograms based upon Bray-Curtis similarity matrices.

4.4 Discussion

There is no general pattern describing how structural diversity varied along the stream order sequence. Each attribute, as well as different measures of the same attribute, showed a different trend. In some instances structural diversity was similar in all five stream orders (e.g. woody vegetation height diversity), in some instances it decreased along the sequence from 1st to 7th order rivers (e.g. woody vegetation NoS diversity), and in other instances structural diversity increased along the stream order gradient from 1st to 7th order rivers (e.g. bird leg length diversity). These results lead me to question my initial expectations regarding the pattern of change in structural diversity along the stream order sequence, and to consider structural diversity as a separate component of overall landscape biodiversity.

4.4.1 Structural diversity as a separate and important component of biodiversity

One of the aims of this study was to investigate biodiversity as an ecological concept, rather than simply as a measureable entity. In line with this, each of the structural attributes measured during this study was chosen as it correlated with one or more ecological functions (MacArthur & MacArthur 1961; Norberg & Rayner 1987; Didham & Lawton 1999; Jansen & Robertson 2001; Loon & Loon 2005; Dial *et al.* 2008). The explicit link with ecological functioning, and thus also with the ecological concept of biodiversity, means that knowledge of how the diversity of each attribute individually varies along the stream order sequence is important. Considering that I found no general pattern of change along the stream order sequence for all attributes and that therefore each stream order held its own unique combination of structural diversity, the value of rivers of each stream order in contributing to overall structural diversity in the landscape is highlighted in this study. Structural diversity is often considered to correlate strongly with compositional diversity (Roth 1976; Noss 1990; Oosterhoorn & Kappelle 2000), and thus areas that are highly compositionally diverse are assumed to be highly structurally diverse. In this study there was little similarity between the patterns of change in compositional diversity along the stream order sequence and the patterns of change in structural diversity along the stream order sequence. These findings

emphasize the need to consider and measure structural diversity as an individual and important component of biodiversity.

4.4.2 The role of instream and broader landscape heterogeneity in influencing the observed pattern of change in structural diversity along the stream order sequence

It was expected that structural diversity would increase along the stream order sequence from 1st to 7th order as heterogeneity of the underlying physical template increased. Overall this was not observed. Instead patterns of change in structural diversity of each woody plant structural attribute could be explained by variation in flooding and fire along the stream order sequence.

Generally, as stream order increases so does catchment area and water flow (Gregory *et al.* 1991) and this means that higher order rivers are more susceptible to extremely large floods capable of altering the structure and composition of riparian vegetation. In February 2000 such an extreme flood occurred on the Sabie River. The flood peaked at 3000 $m^3.sec^{-1}$ where the river enters the KNP and at 7000 $m^3.sec^{-1}$ where the river exits KNP (Heritage *et al.* 2001). These discharges compare with typical wet season base flows of 15-20 $m^3.sec^{-1}$. The effect of a flood of this magnitude was to alter the geomorphic channel types of the river as well as to strip away riparian vegetation and expose the underlying physical template (Parsons *et al.* 2006). The woody vegetation stripped away was mostly small or medium sized trees and shrubs; large trees were able to withstand the flood. Since the flood much of the lost woody vegetation has been replaced, but these new recruits have not had sufficient time to grow large. Thus the flood can explain the lack of medium sized trees within the Sabie River, and the associated decrease in height, canopy width and DBH diversity.

Fire is widely regarded as being a fundamental driver of savanna vegetation structure (Higgins *et al.* 2000; van Wilgen *et al.* 2003; Higgins *et al.* 2007). Fire mostly affects vegetation in the 0-3m height interval, a zone often referred to as the "fire trap" (Bond & Keeley 2005), and can reduce seedling establishment and prevent sapling from emerging from this height class. Fire can therefore result in a greater dominance of small trees (<2m) in areas burnt than in areas protected from fire (Higgins *et al.* 2007). Fire can also increase stem densities in burnt areas due to

the capacity of most savanna tree species to resprout after fire from root stocks (Higgins *et al.* 2000). Fire however does not affect the riparian zones of rivers of different stream order uniformly. The riparian zones of lower order rivers are generally narrower and less dense than higher order rivers, and considering that less dense forest edges are more permeable to fire (Didham & Lawton 1999), are thus more likely to be burnt than the wider, denser riparian zones of higher stream order rivers. The more frequent burning of lower stream order riparian zones may thus contribute to the lack of large trees in these rivers. Additionally the observed pattern of NoS diversity decreasing along the stream order sequence can be explained by the diminishing occurrence of fire along this same sequence; more fire in lower stream order rivers creates more multi-stemmed trees and in doing so increases NoS diversity.

The finding that flooding and fire can explain some of the patterns of woody vegetation structural diversity along the stream order sequence indicates that in savannas broad scale heterogeneity (e.g. differences in fire regime, flooding, herbivory), rather than local river scale heterogeneity, may be more important in creating the observed patterns of structural diversity.

4.4.3 The relationship between bird species assemblage structural diversity and perenniality/ephemerality of rivers

Bird assemblage structural diversity was expected to increase along the stream order sequence as woody vegetation structural diversity increased. However, the results of this study showed neither a general increase in woody vegetation structural diversity along the stream order sequence, nor a clear association between woody vegetation structural diversity and bird assemblage structural diversity. Thus these expectations were not met. So what may have influenced the pattern of bird assemblage structural diversity along the stream order sequence?

As was the case in the previous chapter, the switch from an ephemeral to a perennial river seems to have been important to the observed patterns of change in bird assemblage structural diversity along the stream order sequence. The year-round presence of water in the Sabie River attracts a variety of waterbirds, not found in the lower order rivers, whose structural characteristics differed from most other species. Waterbirds observed were usually large (>300g) and had long legs adapted

for either wading or swimming in water (Hockey *et al.* 2005), and thus increased body mass and leg length structural diversity within the 7th order river. Additionally, certain waterbird species recorded solely in the 7th order river had WL/BL measurements different to other species. White-breasted and Reed cormorants, which forage by diving underwater, have short wings which offer less resistance to their movement underwater (Cooper 1986). These species were observed in relatively high abundances solely in the 7th order river, and contributed to the elevated WL/BL diversity observed within in this river. The bird assemblage structural diversity results once again show that in the semi-arid KNP the switch from an ephemeral to a perennial river, rather than simply an increase in stream order, is highly important to the observed patterns of change in biodiversity along the stream order sequence.

4.4.4 Critical evaluation of methods

Unlike the measurement of plant structural diversity, there are no standard methods to measure bird assemblage structural diversity. Many studies examine bird community structure (e.g. Lock & Naiman 1998; Fairbanks *et al.* 2002; Gutzwiller & Barrow Jr 2002; Martensen *et al.* 2008; Wells *et al.* 2009), others determine the distribution of birds among feeding guilds (Wiens 1992; Sekercioglu 2006), and some observe the diversity of birds with different nesting strategies (Wiens 1992; Sandström *et al.* 2006). While all of these approaches can be regarded as measuring aspects of bird assemblage structural diversity, they differ from the approach used to examine plant structural diversity in that none measure diversity in the morphology of birds. The same approach that is commonly used to measure plant structural diversity was used to measure bird assemblage structural diversity during this study. However, unlike woody vegetation where I was able to physically measure each individual plant, for birds I was forced to use average measurements of morphology for each species. This approach was relevant as birds have determinant rather than indeterminant growth, but could be considered flawed because by linking the measurement of each structural attribute to a species, pure structural diversity was not measured, but rather a combination of compositional and structural diversity. However, the patterns of diversity observed for each of the bird structural attributes did not closely correspond with either the bird compositional diversity results or with each other. Considering the links between each of the bird structural attributes

measured and ecological functioning (Loon & Loon 2005; Sekercioglu 2006; Dial *et al.* 2008), I feel that that this approach to the measurement of bird assemblage structural diversity adds valuable information to this, and potentially any other, study.

Chapter 5

Discussion

The aim of this study was to quantify compositional and structural riparian biodiversity in rivers of different stream order within the Kruger National Park. The work of other authors (Harrel *et al.* 1967; Whiteside & McNatt 1972; Barila *et al.* 1981; Beecher *et al.* 1988; Nilsson *et al.* 1994; Lock & Naiman 1998; Spoonseller & Fisher 2006), mainly in the temperate northern hemisphere, as well as an expectation that underlying physical heterogeneity would increase with stream order, meant that an overall increase in biodiversity was expected along the stream order sequence from 1st to 7th stream order rivers. These expectations were not met, and new, broader insights emerged. The combined compositional and structural diversity results of this study have implications for our understanding of biodiversity in general, implications for our understanding of biodiversity within riparian areas, and allow recognition of the heterogeneous nature of biodiversity itself.

5.1 Implications of this study for the understanding of biodiversity in general

Biodiversity, as an ecological concept, is connected to the functioning and organisation of communities (Sugihara 1982). Increases in biodiversity have been linked with increases in community stability, productivity, resistance to invasion, and nutrient cycling (Naeem *et al.* 1994; Tilman 1999), and also with increases in ecological resilience (Peterson *et al.* 1998). When viewing biodiversity from this perspective it is easy to see why areas that are highly biodiverse are considered of

high conservation value (Myers *et al.* 2000), and why the KNP strives to conserve biodiversity in all its facets and fluxes (Du Toit *et al.* 2003). However, the measurement of biodiversity as an ecological concept is difficult, as the concept of biodiversity includes compositional, structural and functional components at multiple levels of organization. While a wide range of possible measures for each of these components exists (Magurran 2004), certain of the more readily measureable and more easily understandable estimates of biodiversity have come to the fore, with species richness and indices of species diversity being the most common. Thus ecologists can often find themselves equating the ecological concept of biodiversity with the quite specific measures of species richness and species diversity; a problem which lead Pielou (1980 pg 742) to write "I was distressed to find that so many people treat 'diversity' and 'diversity index' as synonyms". This study attempted to avoid this common problem by measuring the three different properties of biodiversity (variety, balance and disparity) of both compositional and structural components of biodiversity. By doing this I came closer to measuring biodiversity as an ecological concept.

The approach taken in this study has shown that species richness and/or species diversity are in themselves inadequate measures of biodiversity as a whole, as different measures of both compositional and structural diversity showed different patterns of change along the stream order sequence. For example, bird species richness differed little between stream orders, but the bird community of the 7th order river was distinct from the rest, and while plant species richness placed the 7th order river as the most diverse it ranked lower according to the several of the plant structural diversity measures. Thus, in order to fully understand the biodiversity present within a specific area, it is necessary to measure all three properties of diversity for each of the components thereof, species richness and species diversity do not always encapsulate the biodiversity present.

This is not to say that species richness and species diversity are not useful measures of biodiversity, they are, but rather to point out that they measure specific properties of biodiversity, and thus it is dangerous to equate them with biodiversity as an ecological concept. The crucial message is that scientists/researchers need to be more specific about which aspect of biodiversity they are aiming to

conserve/study, and managers need to broaden their perception of what biodiversity is. Equating biodiversity as a whole with any one specific attribute thereof does not tell the full story. It is difficult to judge which aspect of biodiversity is "best", but if well thought through decisions are made about which aspect of biodiversity is aimed to be conserved/measured, and why, and this is made explicit, it will be far easier to deal with than simply referring to biodiversity in its entirety. I expect that this approach will do better at evaluating biodiversity as an ecological concept, rather than simply as a measureable entity.

5.2 Implications of this study for the understanding of biodiversity in riparian areas

The majority of the research in riparian systems has taken place along large perennial rivers, and they are considered highly important and biodiverse constituents of a landscape (Naiman *et al.* 1993). This study quantified compositional and structural diversity in a large perennial 7th order river, but also in smaller lower order rivers. The results showed that rivers of each stream order held their own unique combination of compositional and structural biodiversity. Unique species and unique structural attributes were observed in each stream order; differentiation in community composition and structural composition was observed between stream orders; and a distinct combination of all the separately quantified compositional and structural diversity measures was observed in each stream order. These findings broaden our understanding of drainage networks in a savanna landscape, illustrating that lower stream order, ephemeral rivers are also important components of the regional biodiversity.

Changes in stream order produce exponential changes in the total number and total length of rivers (Hansen 2001), with 1st order rivers being by far and away the most abundant. Lower order rivers thus have the potential to be highly significant constituents of a landscape. The importance of lower order rivers is not unknown (Meyer *et al.* 2007), yet they rarely feature in conservation or management plans which tend to treat the landscape as a mosaic of terrestrial elements. Based upon the results of this study I think that this needs to change. While recognizing that the large perennial river (Sabie River) is highly diverse and so an important component of the landscape, the unique combination of biodiversity found in each of the other stream orders illustrates their important contribution to overall regional

biodiversity, and thus the need to consider the role of entire drainage networks in the landscape, rather than simply focusing on perennial rivers. A similar conclusion was reached by Stromberg *et al.* (2009) who, after finding year-round plant species richness to be greater at ephemeral river sites than at perennial river sites in Arizona, also suggests that ephemeral reaches are of high conservation value and that there is a need for a landscape-scale approach to river conservation.

5.3 A heterogeneity perspective of biodiversity

The past two decades has seen a shift in the science of ecology, from an equilibrium, homogenous view of nature to a recognition that ecosystems are complex, dynamic and heterogeneous (Levin 1999). Acknowledging that ecosystems are complex adaptive systems (Levin 1998), and thus heterogeneous, means that they exhibit a number of attributes not observed in simple systems, including non-linearity, uncertainty, emergence, scale and self-organization (Gunderson & Holling 2002). These attributes compel scientists to adopt a heterogeneity perspective when designing and interpreting research.

The KNP, as a typical semi-arid savanna that displays wide levels of variability, is recognized as a complex ecosystem (Van Wilgen & Biggs *In Press*). It was thus necessary that this study should view biodiversity from a heterogeneity point of view, recognizing the inherent variability of the system, being conscious of the multiple levels of organization, and explicit of scale. Biodiversity was therefore recognized as encompassing compositional and structural components (measuring the variability) that were measured in rivers of different stream order (explicit levels of organizations with explicit scales). Additionally the variety, balance and disparity properties of diversity were measured, differing from the more common approach of using only richness and diversity indices, which tend to average out much of the underlying variability.

Adopting this heterogeneity approach has furthered our understanding of riparian biodiversity in this landscape. Knowledge has progressed from information regarding biodiversity in the KNP as a single homogenous area (e.g. game counts for the entire park) to data on the biodiversity present in different, smaller scale patches. As an example, where before a study may have been satisfied with generating a bird species list for the south-western area of the KNP (Fig. 5.1 (A)),

with perhaps only a recognition of which species occurred along the main rivers and which species were “terrestrial” (Fig. 5.1 (B)), this study has now provided detailed explanations of the number of bird species as well as community composition in each of the different stream order rivers (Fig. 5.1 (C)). This allows a much better understanding of the heterogeneity that we know is present in this system.

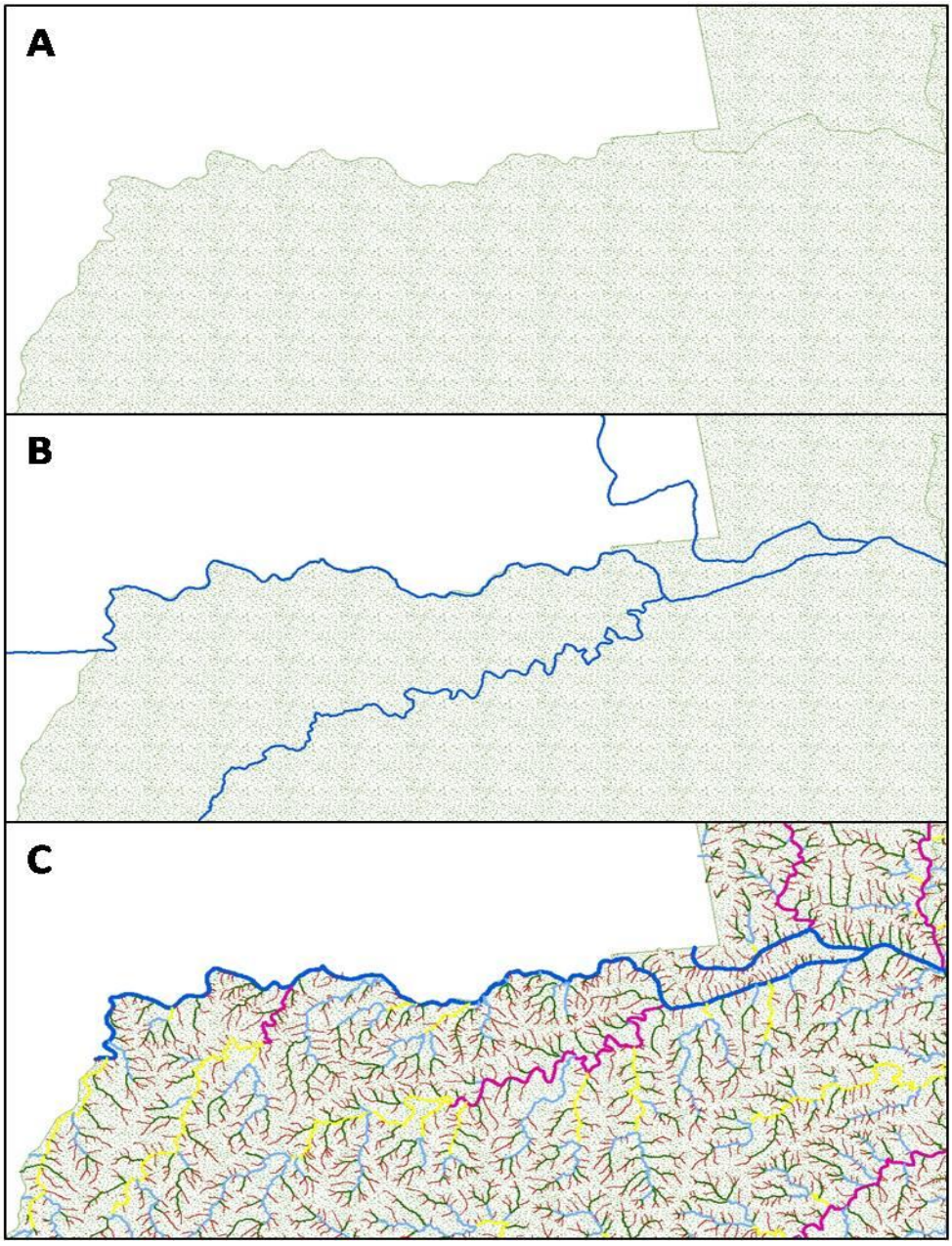

Figure 5.1: Representations of how an increasing awareness of heterogeneity can change the way the south-western KNP is viewed. (A) represents a situation where the entire park is viewed as a single unit, (B) represents a situation where only large rivers are viewed as components separate to the terrestrial mosaic, and (C) represents a situation where all rivers of different stream orders are recognized.

The hypothesis that levels of biodiversity would increase along the stream order sequence from 1st to 7th stream order recognized heterogeneity in the underlying physical template of riverine systems. However, this hypothesis was inadequate, as different components of biodiversity showed different patterns of change along the stream order sequence. These findings led to the realization of the need to consider the heterogeneity inherent in biodiversity itself. Given all the feedback, contingency and non-linearity that we accept from a heterogeneity perspective, why should biodiversity be a simple univariate concept? From this perspective it should be expected that each of the different aspects of biodiversity should behave differently. Having considered the results of this study in this way, I think that the diversity of biodiversity measured in each of the different stream orders in the south-western Kruger National Park is likely a phenomenon common to many systems.

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