Adopting a heterogeneity paradigm for understanding and managing elephants for biodiversity: a case study in riparian woodlands in Kruger National Park

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I declare that this thesis is my own, unaided work. It is being submitted for the Degree of Doctor of Philosophy at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other university.

28th day of October 2015 at Brenton on Sea

Abstract

Decades of study devoted to solving the “elephant problem” have generally concurred that increasing elephant populations inevitably reduce biodiversity. However, recent evidence suggests that such reductions can be accompanied by increases in other components of biodiversity, and that ultimately elephant effects are scale-dependent. Although this new perspective now underpins elephant management strategies in savannas such as the Kruger National Park (KNP), South Africa, few empirical studies in support of this strategy have incorporated the contribution of spatial context, or allowed for the emergence of relevant scales, in their interpretations of heterogeneity. Moreover, use of traditional modes of scientific enquiry and statistical approaches for investigating heterogeneity in complex systems have been challenged. Recent advances in spatial statistics, together with an alternative mode of science that draws upon multiple lines of converging evidence rather than testing narrowly-focused hypotheses, have the potential to address these challenges. However, their practical application for understanding elephants as agents of change remains lacking. Riparian zones along the ephemeral rivers in northern KNP provided an ideal landscape to explore the spatial and temporal parameters of elephant effects in response to surface water, as a critical resource, and hence to develop a framework for a heterogeneity approach for understanding and managing elephants as agents of change in savannas.

Spatially explicit analyses of surface water heterogeneity, elephant responses to this resource heterogeneity, and the subsequent patterns of elephant impact across the riparian landscape, provided the basis for this framework. The resultant scaled, contextual perspective was then advanced by incorporating a local regression technique to explore the underlying causal factors of this heterogeneity. The predictive capacity of the local regression technique also made it possible to explore how the removal of artificial water provision may alter patterns of elephant impact. The final component of the proposed framework involved the use of adaptive inference as an alternative mode of science, to disentangle the role of elephants from other drivers of riparian woody diversity.

Spatially explicit, multi-scaled analyses of the surface water resource provided novel insights into patterns of surface water heterogeneity in this savanna. Traditional distance-to-water approaches underestimated changes in surface water heterogeneity under varying rainfall conditions, as well as the extent to which artificial water supplies dampened this heterogeneity. Moreover, the spatially explicit approach revealed the previously unrecognised contribution of artificial water supplies to waterpoint spatial configurations. However, the scales of this surface

water heterogeneity were still well within the maximum daily foraging ranges of elephants, suggesting that this contextual perspective may not have functional significance in this landscape.

Nevertheless, elephants responded not only to surface water proximity, but also to the patch context provided by neighbouring waterpoints, preferring riparian patches in the vicinity of clustered waterpoints at relatively fine (1500 m) spatial scales. Furthermore, the scale and patchiness of elephant impacts matched the patterns of elephant spatial response to surface water heterogeneity, facilitating understanding of the necessary conditions and underlying mechanisms for generating refuges from elephant disturbances beyond simple distance-to-water patterns. In so doing, these findings provided the first empirical evidence that surface water heterogeneity can generate or maintain spatial and temporal heterogeneity of elephant impacts, even in a landscape where sources of water are relatively abundant. By failing to expose the contribution of artificial water sources to waterpoint spatial configurations, as well as elephant preferences for particular waterpoint configurations, previous studies have therefore underestimated the remaining scope of water provisioning for manipulating elephant disturbance regimes in these landscapes.

Counterintuitively, however, reverting to a natural pattern of surface water heterogeneity was predicted to produce an unintended homogenising effect on the levels of elephant disturbance across the landscape, through the removal of preferred clusters of waterpoints. This emphasized the importance of artificial water sources in generating patterns of waterpoint spatial configuration. By drawing upon the suite of tests of different kinds from the preceding chapters, a heterogeneity interpretation of the Intermediate Disturbance Hypothesis (IDH) indicated that the study area in northern KNP was at the low end of an elephant-mediated trajectory of biodiversity change. There was little evidence to suggest that the patterns and scales of riparian woody species richness and structural diversity had been driven by elephant disturbances, although riparian woody species diversity exhibited early signs of elephant-mediated declines. However, these declines were confined to patches of high elephant disturbance and therefore did not reduce species diversity at the landscape level.

Though confined to elephant disturbances in a particular riparian landscape in northern KNP, the understanding developed here has wider implications for studying how organisms respond to, and hence generate, heterogeneity in complex systems. Specifically, the study (i) exposed the importance of spatially explicit analyses for understanding patterns and scales of spatial and temporal heterogeneity; (ii) demonstrated how the presence of spatial

autocorrelation and non-stationarity common to complex heterogeneous systems can be maximized through the use of spatial statistics, rather than having to be eliminated to satisfy the requirements of traditional parametric approaches; and (iii) demonstrated how adaptive inference can provide an alternative, pluralistic scientific method to overcomes the pitfalls of the traditional narrowly-focused reductionist method, for understanding causation in complex systems.

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1.1 Introduction

African elephants *Loxodonta africana* are agents of change in savannas (Laws, 1970). Their impacts can change the structural complexity of woodlands or even drive plant species locally extinct (Buechner and Dawkins, 1961, Barnes, 1985, Barnes et al., 1994, O'Connor et al., 2007, Kerley et al., 2008, Landman et al., 2008). Previous evaluations of elephant impacts underpinned by equilibrium concepts under a Balance of Nature paradigm (Botkin, 1990, Wu and Loucks, 1995) promoted the idea that diversity loss could be prevented by maintaining moderate levels of elephant impact (Pienaar, 1969, Van Wyk and Fairall, 1969). However, in the Kruger National Park (KNP) attempts to do so through elephant population control did not slow the loss of tall trees (Trollope et al., 1998, Eckhardt et al., 2001), suggesting the involvement of factors other than elephant in the decline. Spreading elephants evenly across KNP through widespread water provision (Pienaar, 1985) maintained moderate levels of impact but led to unintended consequences for other important components of diversity (Walker et al., 1987, Harrington et al., 1999). Such ecological "surprises" and multi-factor cause-and-effect relationships are features of complex systems rather than of systems at equilibrium (Holling, 1973, Kay and Schneider, 1995, Levin, 1998, Ascher, 2001).

A key feature of such complex systems is ecological heterogeneity (Pickett and Cadenasso, 1995, Pickett et al., 1997), which promotes biodiversity by enabling species co-existence over a spatially and temporally differentiated patch mosaic (Bormann and Likens, 1979, Pickett et al., 1997). Maintenance of heterogeneity has therefore become the fundamental concept underlying KNP's revised elephant management plan that now focuses on managing the patchiness of elephant impacts rather than on managing elephant population size (Whyte et al., Whyte, 2004). Nevertheless, empirical studies of elephant-vegetation interactions underpinned by heterogeneity remain scarce (Scholes and Mennell, 2008) and largely based on

reductionist methods of enquiry and narrowly focused hypothesis testing (Holling and Allen, 2002), which may not be suitable for investigating complex systems (Kay and Schneider, 1995, Ravetz, 1999, Nowotny et al., 2001, Holling and Allen, 2002). In view of these shortcomings, I will investigate the role of elephants in shaping savanna biodiversity by exploring how elephants both respond to and generate patterns of heterogeneity (Pickett et al., 2000). My aim is to investigate the underlying processes that lead to elephant-induced biodiversity change by developing a heterogeneity approach (Rogers, 2003) that explicitly accounts for common features of complex systems not considered by reductionist approaches (Cadenasso et al., 2006, Zellmer et al., 2006, Rogers et al., 2013). By exposing these patterns and the underlying processes of vegetation change, I seek not only to improve our predictive understanding of elephant-vegetation interactions, but also to assess more broadly the importance and value of taking such a heterogeneity approach for understanding and managing the interactions and feedbacks between organisms and their environments in complex systems.

In this chapter, I outline the implications of the ecological paradigm shift from Balance of Nature to Heterogeneity, for managing biodiversity in complex systems. Within this context, I review what we know about elephants as agents of biodiversity change, and how the underlying philosophies governing elephant management policies have shifted along with the changing paradigm. Finally, I propose a framework for linking elephant science and management under a heterogeneity paradigm, and outline the broad objectives for my study.

1.2 A paradigm shift from Balance of Nature to Heterogeneity

The notion of a "balance of nature" underpinned ecological theory and practice for centuries (Wu and Loucks, 1995, Wiens, 2000). It implied that nature was ordered and harmonious, that ecological systems were normally in a close, deterministic balance with environmental controls (Fiedler et al., 1997), that ecological systems were closed and homogenous (Wiens, 2000), and that they returned to a previous equilibrium after disturbances (Wu and Loucks, 1995). Consequently, conservation efforts underpinned by this Balance of Nature paradigm were aimed at preserving this "equilibrium" (Wiens, 2000), and any disturbances that disrupted the system were considered undesirable. In KNP, for example, three primary management interventions were designed to prevent change from the status quo. First, a water provisioning programme supplied the park with numerous dams and over 300 boreholes, with the aim of

providing game with a consistent supply of drinking water through seasonal and interannual droughts (Pienaar, 1970, Pienaar, 1985). Second, a prescribed burning regime aimed to create fixed endpoints of desired vegetation structure and composition (Biggs and Potgieter, 1999) . Third, herbivore numbers, notably those of elephants, were kept at a constant population ceiling (Pienaar, 1969). This upper limit on elephant population size was believed to represent an ecological carrying capacity (Peel et al., 1998), or the population level at which animals would be in equilibrium with their food source. Management under a classical equilibrium or Balance of Nature paradigm therefore emphasized the maintenance of spatial and temporal homogeneity (Pickett and Rogers, 1997) and had a strong species focus, both in terms of "problem" species that could disrupt the status quo, as well as by emphasizing species preservation (Rogers, 1997a).

From a theoretical point of view, the assumptions of homogeneity and equilibrium provided the required simplicity for developing unifying generalisations (Pickett and Cadenasso, 1995, Wiens, 2000). However, the latter part of the twentieth century marked an increasing awareness of the complexity of ecosystems (Kay and Schneider, 1995), emphasizing that equilibrium conditions are highly dependent on the scale of observation and are rare in nature over large scales or long time periods (Wiens, 2000). Instead, it was demonstrated that, depending on the combination of environmental factors and the system's particular history (termed "contingency"), different pathways exist that can lead to several possible alternative endpoints within a single system (Fiedler et al., 1997). As a result of these ecological contingencies and multiple causal factors, ecological patterns are therefore seldom the outcome of predictable processes of linear cause-and-effect. In fact, we now know that ecosystem pattern or *heterogeneity* results from the interaction of ecological disturbances (Pickett and White, 1985, Pickett, 1985, Pickett et al., 1989), physical processes, the geophysical template (Venter et al., 2003), and the activities of organisms (Jones et al., 1994, Pickett et al., 2000, Wiens, 2000, Pickett et al., 2003). The interplay between these ecological patterns and processes produces a mosaic of landscape patches across a variety of scales and levels of ecological organization (Bormann and Likens, 1979, Forman and Godron, 1981, Forman, 1995, Pickett and Rogers, 1997). Patch theory can be used to evaluate complexity in ecological systems, and understanding complexity in spatial structure is a powerful approach to exploring structure-function relationships (Cadenasso et al., 2006)

Patches are recognisable areas within a landscape that contrast with adjacent areas and have definable boundaries (Kotliar and Wiens, 1990) at particular scales or levels of organisation. Scale refers to the spatial or temporal dimensions of an object or dataset, and is

characterised by grain (the finest level of resolution within a given dataset) and extent (the size of the study area or duration of time under consideration) (Milne, 1989, Kotliar and Wiens, 1990). The concept of scale should not be confused with that of levels of organisation, which represent a range of functionally distinct ecological units from genes to landscapes, each of which may occur over a range of spatial dimensions. Patches at one scale may be composed of smaller patches that influence how the original patch functions, or they can be parts of larger scale assemblages of patches (Forman and Godron, 1981, Kotliar and Wiens, 1990). Consequently, landscape patches can be arranged in a nested hierarchy of scale or level of organisation. Such ecological hierarchies are limited by the behaviours of their components, as well as by the constraints imposed by higher levels in the hierarchy (O'Neill et al., 1988) The structure of landscape mosaics is defined not only by patch composition, but also by patch configuration or context (Forman and Godron, 1981, Forman, 1995) across this hierarchy. Context refers to the patch's location, adjacency (the elements in contact with the *patch)* and neighbourhood. Together these characteristics determine the value of a particular patch as an environmental resource for organisms. Although understanding patch characteristics is therefore crucial for understanding how organisms make use of different parts of the landscape, patch location is the only element of patch context that has been explored in savanna systems (Levick, 2008).

Succession and other ecosystem dynamics take place within these patches as organisms interact, influence one another and the physical environment, and new organisms take their place over time (Wiens et al., 1976, Pickett, 1985, Caswell and Cohem, 1991). Hence an important consideration about patches is that they change over time, termed "patch dynamics" (Pickett and White, 1985, Pickett, 1985, Pickett and Rogers, 1997, Wright et al., 2004). Landscapes can contain a variety of patch types in different stages of development at any one time. The origin of these patches differs according to the patch's disturbance regime, disturbance in the surrounding matrix and the natural distribution of environmental resources over time (Forman and Godron, 1981, Forman, 1995). These differences in patch origin determine the species dynamics, and the stability and turnover of patches over time (Forman, 1995). Hence patch dynamics is important not only because of the changes occurring in individual patches, but also because the entire mosaic of patches may be shifting (Bormann and Likens, 1979). Whether this shifting mosaic is in a steady state is scale dependent, since local changes to vegetation can be incorporated at larger scales if averaged over sufficiently long time or large areas (Turner et al., 1993). Although the spatial and temporal heterogeneity of

patches are inextricably linked (Turner, 1989, Turner et al., 1993), issues of spatial heterogeneity have received more empirical attention to date.

The hierarchical patch dynamics paradigm (Wu and Loucks, 1995) brings together the spatial and temporal considerations of heterogeneity, providing a framework for tackling the problem of scale across patch mosaics (Levin, 1992). Five main principles underpinning the hierarchical patch dynamics paradigm provide guidance for the investigation of heterogeneous systems: (i) the definition of patches is ***scale dependent***; (ii) constituent patches produce emergent properties at higher levels in the hierarchy (the sum is greater than the whole), and hence better understanding is gained by considering ***adjacent levels in addition to the focal level*** in the patch hierarchy; (iii) ecological ***processes and*** environmental ***controls shift with scale*** along a patch hierarchy; (iv) spatio-temporal ***scale influences*** which processes are ***perceived*** as non-equilibrium, transient or unstable ***dynamics***; (v) non-equilbrium processes at one level may translate to ***metastability*** at a higher level, and variation is likely to decrease with increasing spatial scale as it becomes ***incorporated*** through the levels (Wu and Loucks, 1995).

Rather than being an unnecessary complication in ecosystem studies , heterogeneity has thus been recognized as a key part of the structure and functioning of nature, and is inseparable from the issue of the generation and maintenance of biodiversity (Levin, 1992, Pickett and Cadenasso, 1995). As a result, the classic equilibrium paradigm has failed not only because equilibrium conditions are rare in nature, but because of its inability to account for the effects of spatial and temporal scale and heterogeneity on ecological processes (Wu and Loucks, 1995). The underlying paradigm of contemporary ecology has shifted from one of equilibrium or “Balance of Nature”, towards an emphasis on the frequent occurrence of non-equilibrium states and the importance of stochastic events such as disturbances (Botkin, 1990, Wu and Loucks, 1995, Fiedler et al., 1997, Wiens, 1997). Variously described as the hierarchical patch dynamics paradigm (Wu and Loucks), the non-equilibrium paradigm (Fiedler et al 1997) or the heterogeneity paradigm (Rogers 2003), it does not replace equilibrium theory, but accepts equilibrial and non-equilibrial conditions as being scale-dependent (Fiedler et al., 1997). In the following section, I expand upon the applicability of heterogeneity as the focus for biodiversity management following this new paradigm.

1.3 Heterogeneity as the focus for managing biodiversity in complex systems

Heterogeneity refers not only to the variability among the components of systems, but also to the variability in the processes that create patterns among these components (Pickett and Cadenasso, 1995). Together these heterogeneous patterns and processes are considered to be the ultimate source of ecosystem biodiversity (Pickett et al., 1997). Consequently, the maintenance of biodiversity depends on the preservation of these complex ecological patterns and processes (Pearson et al., 1996), and understanding the scale- and context-dependent consequences of this heterogeneity becomes critical for protecting biodiversity (Pickett and Rogers, 1997). A new thrust to emphasize heterogeneity in the management of ecological systems has therefore emerged (Christensen et al., 1996, Rogers, 1997a, Rogers, 2003), which demands the incorporation of scale and context across mosaic landscapes. This heterogeneity perspective is reconciled with a more comprehensive view of biodiversity than that offered by the previous species focus (Rogers, 2003), by incorporating compositional, structural and functional components that are manifest at multiple levels of organization (Noss, 1990).

Organisms are agents of change that, at any particular time, recognize and respond to this heterogeneity across a range of scales (Jones et al., 1994, Wallace et al., 1995, Pearson et al., 1996, Turner et al., 1997, Pickett et al., 2000, Boyce et al., 2003, Naiman et al., 2003, Owen-Smith, 2004, Grainger et al., 2006, Wright et al., 2006, Chamaillé-Jammes et al., 2007, Feller and Chamberlain, 2007, Ott, 2007, Chamaillé-Jammes et al., 2008, De Beer and Van Aarde, 2008, Cromsigt et al., 2009, Holdo et al., 2009, Fahrig et al., 2011). Individual species require different types of resource patches, and individual patches support different species (Pickett and Rogers, 1997). By focusing their activities in those parts of the landscape that provide their daily resource requirements, the disturbances generated by organisms are confined to these environmental resource patches. In this manner, organisms not only respond to, but also generate heterogeneity (Pickett et al., 2000, Pickett et al., 2003) by creating differential impacts in different parts of the landscape, among organisms with different energy requirements, and over time. Organisms can thus act as ecosystem engineers (Jones et al., 1994, Hastings et al., 2006, Wright and Jones, 2006), and hence the impacts of organisms on the landscape may be viewed as disturbances (Connell, 1979, Pickett, 1985, Pickett and White, 1985). Disturbance theory therefore provides a useful framework for understanding and predicting organism-mediated biodiversity change (Connell, 1979, Pickett et al., 1989, Caswell and Cohem, 1991, Turner et al., 1993, Palmer, 2002). The disturbances created by organisms

can have either positive or negative effects on biodiversity (Jones et al., 1997, Wright et al., 2006, Pringle, 2008), depending on the spatial and temporal parameters of the particular disturbance regime (Turner et al., 1993). Hence, in order to manage biodiversity in variable environments in the presence of ecosystem engineers, it is necessary to understand the scales at which organisms respond to and create heterogeneity. Moreover, management interventions must be undertaken in relation to the scales at which heterogeneity is required for the regeneration or persistence of biodiversity (Jones et al., 1994). In the section that follows, I review the literature to assess the extent to which the imperatives of a heterogeneity paradigm, outlined above, have been accounted for in our current understanding of elephants as agents of biodiversity change.

1.4 Elephants as agents of biodiversity change

Elephants have been described as ecosystem engineers because of their ability to transform landscape composition and structure (Buechner and Dawkins, 1961, Laws, 1970, Anderson and Walker, 1974, Barnes, 1985, Barnes et al., 1994, O'Connor, 1994, Holdo, 2007, O'Connor et al., 2007, Holdo et al., 2009, Lagendijk et al., 2011, Asner et al., 2009, Levick et al., 2009, Asner and Levick, 2012, Levick and Asner, 2013), and ultimately to alter ecosystem function (Huntly, 1995, Gaylard et al., 2003, Skarpe et al., 2004, Kerley et al., 2008, du Toit et al., 2014a, Rutina and Moe, 2014). It is therefore well recognized that elephants are a significant source of ecological disturbance (Pickett, 1985), altering landscapes primarily through the impacts of their feeding on vegetation, but also through trampling and digging.

However, such elephant "impacts" are not necessarily detrimental at the level of individual plants (and hence the use of the word "impact" should not be interpreted as such in the remainder of this thesis), and the mechanism of elephant feeding at this level is well known. Elephants are mixed feeders preferring grasses during the wet (growing) season when food quality and abundance is highest due to the prevalence of new leaves and shoots, but becoming more dependent on browse during the dry (dormant) season when grasses senesce and quality declines (Owen-Smith, 1988, O'Connor et al., 2007, Owen-Smith and Chafota, 2012, Skarpe et al., 2014c). Browsing elephants can damage trees by pushing them over (also known as pollarding) or removing biomass by stripping off leaves, breaking branches or the main tree trunk, bark stripping or tusk marking (O'Connor et al., 2007). Particular species and size classes of tree are more susceptible to the consequences of elephant feeding, or to particular types of elephant impact. For example, elephants feed on the soft, pithy stems of

trees such as baobabs, figs (*Ficus* spp) and chestnut (*Sterculia* spp) species when pressed for food (Owen-Smith, 1988). The most severe form of impact, uprooting of trees, can instantly kill the plant. Shallow-rooted tree species such as *Acacia* and *Commiphora* species are particularly vulnerable to being pushed over, while the main stems of deeper-rooted trees such as *Diospyros mespiliformis* tend to snap when elephants attempt to push them over. Only trees that are able to coppice can survive the main truck being snapped (O'Connor et al., 2007), unless the tree has been uprooted in the process.

In contrast to tree mortality being caused by a single dramatic impact event (e.g. uprooting), less severe impacts accumulated over time can also lead to significant biomass removal or eventual tree mortality. For example, though single branch breaking events only remove a small proportion of the tree's biomass, repeated branch breaking events preclude opportunities for compensatory regrowth, eventually knocking the tree back into a smaller size class without the resources required for regeneration, or resulting in the death of the tree if it can no longer acquire sufficient resources for survival (O'Connor et al., 2007). Consequently, apart from altering the structural diversity of plant communities, elephant feeding can skew the demography of plant populations towards the non-reproductive size classes. Thus biomass removal by elephants can eventually reduce the representation of particular plant species in vegetation assemblages, through reduced regeneration, and ultimately lead to local extirpation of these species (O'Connor et al., 2007).

Seemingly moderate elephant disturbances such as bark stripping can also make trees more vulnerable to other drivers of tree mortality, such as fires, by exposing the less fire resistant heartwood (Owen-Smith, 1988). *Acacia* species and baobabs (*Adansonia digitata*) are prone to extensive bark stripping because their bark is easily removed in long strips. By having a significant effect on the tree's survival or reproductive capacity only after repeated disturbance events over a period of time, cumulative impacts may produce lag effects in the relationship between elephant impacts and their biodiversity consequences. However, these lag effects have not been explicitly incorporated into existing models of elephant-vegetation interactions, and hence an understanding of the role of such cumulative elephant impacts in shaping woody diversity remains lacking. Moreover, in complex systems the magnitude and nature of such cumulative effects is likely to be contingent upon the location's prior impact history, but ecological contingencies have yet to be integrated into conceptual models of elephant-biodiversity relationships (Scholes and Mennell, 2008).

Selective feeding by elephants over time results in an accumulation of impacts on trees of preferred dietary species and size classes. Tree species have different tolerances to elephant

impact, and hence some species are able to survive elephant damage better than others (O'Connor et al., 2007). Species that are able to match the rate of biomass removal by elephants with compensatory regrowth ultimately survive these accumulated elephant impacts (O'Connor et al., 2007). However, tree species that are not able to recover before elephants return to feed on them again will accumulate impacts until they eventually kill the plant. This has led to local (e.g. within a habitat or protected area) extirpation of tree species or changes in the size class distributions of trees in some areas (Buechner and Dawkins, 1961, Van Wyk and Fairall, 1969, Laws, 1970, Mueller-Dombois, 1972, Anderson and Walker, 1974, Swanepoel and Swanepoel, 1986, Shahar, 1993, Cowling and Kerley, 2002, Hofmeyr and Eckardt, 2006, O'Connor et al., 2007, Kerley et al., 2008, Landman et al., 2008). Species that have been eliminated or reduced in population size by elephants in savanna and thicket systems include plants of the genera *Aloe* and *Viscum* (Midgley and Joubert, 1991, Landman et al., 2008), *Acacia* (Anderson and Walker, 1974, Pellew, 1983, Owen-Smith, 1988, Teren and Owen-Smith, 2010), *Adansonia* (Laws, 1970, Jachmann and Bell, 1985, Weyerhaeuser, 1985, Swanepoel and Swanepoel, 1986, Swanepoel, 1993, Barnes et al., 1994, Kelly, 2001, Edkins et al., 2008), *Brachystegia (Guy, 1989)*, *Sclerocarya* (Coetzee et al., 1979, Jacobs and Biggs, 2001), *Commiphora* and *Sterculia* (Napier-Bax and Sheldrick, 1963, Barnes, 1983, Kelly, 2001). Elephants can also increase or reduce the structural complexity of plant populations and communities, although in this context their contribution towards the loss of tall trees of species such as such *Sclerocarya birrea* and *Acacia nigrescens* have been the focus of most studies (Owen-Smith, 1988, Trollope et al., 1998, Eckhardt et al., 2001, Teren and Owen-Smith, 2010). However, despite KNP having exceeded its perceived elephant carrying capacity (Van Wyk and Fairall, 1969), no plant species have yet become extinct through elephant impacts in the park, although extensive changes in woody structure have been reported (Eckhardt et al., 2001). The findings summarised here have tended to focus on the biodiversity changes themselves, rather than on the underlying mechanism of elephant impact at levels broader than individual plants, thereby limiting our understanding of the link between the patterns of elephant impact and the process of elephant herbivory.

The consequences of elephant feeding can also extend to forms of biodiversity other than vegetation. For example, although elephants generally do not compete directly with other large herbivores, elephant-mediated vegetation changes may affect other herbivore species (Owen-Smith, 1988, Halley et al., 2014). By opening up thickets, elephants reduce cover for species such as bushbuck but increase browse availability for other species, particularly smaller ungulate herbivores (Owen-Smith, 1988, Moe et al., 2014). The Chobe bushbuck *Tragelaphus*

scriptus ornatus is a local subspecies that has become scarce along the Chobe riverfront in Botswana as a result of habitat modification by extremely high dry season densities of 4 elephants per km^2 (Addy, 1993, Skarpe et al., 2004, Moe et al., 2009, Moe et al., 2014). Species richness of woodland birds and ants has declined in miombo woodland where the diversity of canopy trees has been reduced by elephant impacts (Cumming et al., 1997). Research has tended to focus on *losses* of biodiversity brought about by elephant-mediated habitat alterations. However, in instances where species have been lost, there may also be compensatory *gains* through the occurrence of species that are adapted to intense disturbances, or to the altered habitat type. For example, the relative abundance of fauna associated with shrublands or more open areas tend to increase where elephants have opened up woodlands.

Although the literature outlined above has emphasized the susceptibility of certain species to elephant disturbances, there has been little recognition that the consequences of these disturbances (even on the same species) are likely to vary over space and time and in different landscape contexts. The heterogeneity paradigm predicts that the maintenance of a dynamic patch mosaic through the generation of such variability could ultimately result in metastability of the system (Bormann and Likens, 1979), rather than a loss of biodiversity. Understanding the various sources of variability in elephant disturbance regimes is therefore crucial for interpreting elephant effects on biodiversity.

For example, the removal of vegetation is less severe for plants during the dry season when they are dormant compared to the summer when they are growing (Owen-Smith, 1996). In addition, trees with greater access to nutrients may be more resistant to elephant impacts if they are able to compensate better for damage compared to trees in areas or growing on soils with less nutrients. It is well-known that because elephants are water dependent, their daily foraging ranges are constrained to 20-30 km from water (Western, 1975, Owen-Smith, 1988, Owen-Smith, 1996). Consequently, trees in those parts of the landscape near to surface water accumulate more impacts than those remote from water (Brits et al., 2002, Gaylard et al., 2003, Redfern et al., 2003), particularly during the dry season when surface water has dried up elsewhere. Apart from water and food, shade is also a significant resource for elephants, aiding in thermoregulation particularly during the hot dry season (Owen-Smith, 1988, Kinahan et al., 2007). At this dry time of year elephants spend more time in those parts of the landscape that provide water (Western, 1975, Owen-Smith, 1996, Redfern et al., 2003, Smit et al., 2007c, De Beer and Van Aarde, 2008, Loarie et al., 2009) and shade (Kinahan et al., 2007), for example riparian zones. While it is therefore clear that the distribution of critical resources shapes the location and timing of elephant disturbance regimes, the scales at which elephants respond to

these resources and hence shape ecosystem biodiversity remain poorly understood (Owen-Smith et al., 2006, Scholes and Mennell, 2008).

Elephant gender provides a further source of variability in patterns of elephant herbivory. Since elephants are sexually size dimorphic, the metabolic requirements of the smaller (by up to 50%; (Owen-Smith, 1988)) elephant cows are higher than those of bulls relative to their body size. These energetic demands are exacerbated by the fact that elephant cows are highly social, living in mixed herds that contain breeding adults as well as lactating females and juveniles, whose increased energetic requirements need to be considered by the whole herd (Poole, 1994). Hence, while elephants are compelled by their large body sizes to ingest large amounts of food daily (ca. 200 kg wet weight per adult elephant per day; (Owen-Smith, 1988)), mixed herds tend to feed on higher quality forage, such as shrubs and grasses (Stokke and Toit, 2000, Greyling, 2004). In contrast, the larger adult bulls are able to tolerate a lower quality diet, ingesting a higher proportion of woody material (Stokke and Toit, 2000). Moreover, the combination of the higher energetic demands on mixed herds and the fact that younger elephant calves within these herds restrict daily travel distances, precludes mixed herds from covering the large foraging distances capable by lone bulls (Owen-Smith, 1988). Although these differential energetic requirements have been acknowledged, there has been no attempt to date to incorporate this source of variation into our understanding of the underlying mechanism of elephant impacts, or indeed their consequences.

In addition, an important implication of the complexity of savanna systems is that elephant herbivory is not the only factor driving vegetation dynamics. Rainfall, substrate variation, topography, fire, herbivory, nutrients and competition have all been linked to the heterogeneity of savanna vegetation (Eckhardt et al., 2001, van Wilgen et al., 2003, Venter et al., 2003, Govender et al., 2006, Levick, 2008). Although savanna vegetation dynamics are therefore the outcome of the interaction of these factors, understanding these interactive effects has largely been confined to the interaction of fire and elephant herbivory (Dublin, 1986, Dublin et al., 1990, Trollope et al., 1998). The extent to which vegetation patterns may have been erroneously attributed to elephant disturbances is likely to remain unknown until the relative contributions of these factors are explicitly differentiated. Furthermore, the few studies that have attempted to disentangle the various drivers of vegetation patterns (Levick and Rogers, 2011) have demonstrated that the magnitude and nature of the various determinants of woody vegetation dynamics vary both over space and time, and are often scale-variant. Hence, the extent to which elephant impacts are likely to affect trees (even of the same species)

relative to other ecological processes is likely to be context-dependent, and contingent upon the legacy of past ecological processes (Levick, 2008).

Critically reviewing the elephant literature above from a perspective that demands explicit recognition of (i) heterogeneity over space and time, (ii) scale-variance and context-dependence, and (iii) multiple causal factors and contingencies, has revealed that our current understanding of the role of elephants in shaping savanna vegetation accounts for few of the crucial elements required for the investigation of complex systems. This realisation calls into question the applicability of previous elephant studies beyond their particular study areas, challenging our existing understanding and management of elephants. In the remainder of this chapter, I make the link between the understanding and management of elephants explicit by contextualising the biodiversity concerns faced by protected area managers, and outlining the conceptual principles that underpinned decision-making under the previous Balance of Nature paradigm. I then outline how a review of the empirical basis for elephant management in KNP revealed the implications of ecosystem complexity to the park's decision-makers, resulting in a paradigm shift to heterogeneity. I end the chapter by outlining a framework for providing empirical support for this approach, with the aim of advancing our understanding of elephants as agents of change in complex savanna systems.

1.5 Understanding and managing the "elephant problem"

The potentially destructive and widespread consequences of elephant feeding on savanna vegetation present park managers with a conservation dilemma commonly referred to as the "elephant problem" (Caughley, 1976, Barnes, 1983, Cumming et al., 1997). This dilemma arises from a widespread perception that growing elephant populations are incompatible with successful biodiversity conservation (Van Wyk and Fairall, 1969, Cumming et al., 1997). Although fluctuating elephant populations presumably occurred throughout history, the notion of an "elephant problem" was coined during the 1970's (Caughley, 1976) after conservation efforts had resulted in a marked recovery of elephant populations from their previously low numbers brought about by extensive hunting for ivory, habitat loss through human encroachment, and diseases such as anthrax and the rinderpest in the early 1900's (Scholes and Mennell, 2008). By protecting elephants, signs of alterations in other important components of diversity began to emerge, notably loss of woody vegetation composition and changes in woody structural diversity (Van Wyk and Fairall, 1969, Eckhardt et al., 2001). Protected area managers therefore required a model for decision-making.

1.5.1 The Intermediate Disturbance Hypothesis and carrying capacity as the past focus for managing elephant-mediated biodiversity change

In the era that spawned the "elephant problem", the Intermediate Disturbance Hypothesis (IDH; (Connell, 1979)) was a popular model invoked to predict the effects of elephants or other ecosystem disturbances on biodiversity (Van Wyk and Fairall, 1969). The IDH predicts that maximum diversity is achievable at moderate levels of disturbance – this moderate level of disturbance was assumed to be linearly related to elephant population size and so equated with an ecological carrying capacity, where elephant numbers were expected to be in equilibrium with vegetation dynamics (Pienaar, 1969). Under the IDH, low diversity was predicted to occur at low levels of elephant disturbance due to a predominance of competitively dominant species (Connell, 1979). At the high end of the IDH curve, low diversity was again predicted, but in this instance due to loss of impact intolerant species at high levels of disturbance (Gillson and Lindsay, 2003). Hence elephant management within KNP was aimed at maintaining moderate levels of impact throughout the park, by keeping elephant densities below an ecological carrying capacity of 7000 elephants (or 0.65 elephants per km^2) through culling and (limited) translocations (Pienaar, 1969). Importantly, this figure for an elephant carrying capacity had no scientific basis, but was simply the prevailing number of elephants in KNP after a key publication recommended elephants be held at their current numbers to prevent further destruction of vegetation in the park (Van Wyk and Fairall, 1969).

In addition to keeping elephants below a population ceiling in KNP, managers also tried to stabilise the highly variable supply of surface water (Pienaar, 1970, Gaylard et al., 2003) by providing over 300 permanently open boreholes ubiquitously across the landscape (Pienaar, 1985). Although the primary goal of this water provision programme was to prevent the loss of game species during droughts (Pienaar, 1985), it was also envisaged that abundant and evenly spaced waterholes would spread water-dependent herbivores such as elephants more evenly, inducing moderate levels of impact and hence optimizing diversity across the landscape (Van Wyk and Fairall, 1969), following a scale-neutral (thought spatially implicit) interpretation of the IDH (Connell, 1979). However, neither keeping elephant populations stable at low densities, nor spreading their impacts across the landscape, prevented a loss of tall trees (Trollope et al., 1998, Eckhardt et al., 2001) or reductions in sensitive plant species, most notably marula *S. birrea* and *A. digitata* (Kelly, 2001, Edkins et al., 2008) in KNP.

The KNP case study demonstrates that basing elephant management on an elephant population ceiling provided no guarantee of biodiversity protection, and that the search for carrying capacity was unhelpful in the context of biodiversity management (Owen-Smith et al.,

2006, Scholes and Mennell, 2008). How, then, are conservationists to make decisions about protecting biodiversity in the presence of elephants?

1.5.2 KNP's review of the ecological basis for elephant management – the shift to an underlying heterogeneity paradigm

A moratorium on elephant culling in South Africa in 1994 prompted a major review of the scientific and social basis for elephant management in KNP (Scholes and Mennell, 2008). From a social perspective, the point at which elephant impacts become undesirable to stakeholders is, by definition, based on their value systems. The underlying Balance of Nature paradigm that still pervades western society predisposes stakeholders to expect ecosystems to remain at some optimum or climax state, and that any deviations away from it should be prevented (Botkin, 1990, Wu and Loucks, 1995). The predominance of tall savanna woodlands encountered by Europeans when they first settled the Lowveld in the early 1900's (Mabunda et al., 2003) was perceived as such an optimal state, and consequently became the benchmark for assessing levels of undesirable change by elephants. However, the preponderance of the woodland component of savannas at that time is now known to have been the consequence of a dramatic reduction in herbivory caused by a major die-off of ungulates during a Rinderpest epidemic at the end of the 19th century (Bengis et al., 2003), as well as through massively reduced elephant populations as a consequence of the ivory trade (Gillson and Lindsay, 2003). Now that herbivore populations, including elephants, have recovered, is the preservation of the woodland component of savannas an appropriate management goal? If not, what is the "right" benchmark to aim for?

A review of the ecological basis of elephant management in the latter 1990's exposed KNP scientists and managers to the emergence of complexity theory and non-equilibrium dynamics in ecology, and their relevance to heterogeneous savannas (Whyte et al., 1999, Whyte, 2004). An important implication of this review was the recognition that complex ecosystems have multiple possible stable states, and that historical benchmarks for the maintenance of particular tree species or size classes may thus be inappropriate management goals for KNP. Moreover, the emphasis on flux or variability led to the realization that management interventions aimed at keeping systems stable in fact eroded ecosystem resilience and was therefore counter to maintaining biodiversity (Holling, 1973, Gunderson and Holling, 2001, Folke et al., 2004). Consequently, disturbance regimes such as those produced by fire and elephant impacts were recognized as being crucial ecosystem processes that promote

biodiversity through the creation of dynamic patch mosaics (Pickett and Rogers, 1997) and the maintenance of ecosystem resilience (Folke et al., 2004).

This paradigm shift in management philosophy for the KNP resulted in a significantly revised elephant management plan (Whyte et al., 1999) in which the primary focus shifted from limiting elephant population size, to managing a variable distribution of elephant impacts over space and time (Whyte, 2004). Implicit in this approach is acceptance of the loss of impact intolerant species or size classes from certain patches of the landscape, or under certain conditions even local extinction from the park if the species is protected elsewhere (i.e. the notion of complementarity; (Justus and Sarkar, 2002)). An early favourite for accomplishing such variability was the removal of artificial sources of water (Pienaar et al., 1997), to increase distances between the remaining water sources and cause elephants to focus their activities around these waterpoints (Owen-Smith, 1996). However, desktop studies using Geographic Information Systems indicated that most areas in KNP would still be closer than 10 km from water even if all artificial sources were removed, and that the entire landscape would therefore remain accessible to elephants (Redfern, 2002, Redfern et al., 2005, Smit et al., 2007a, Smit and Grant, 2009)

1.5.3 Lack of empirical support for an elephant management philosophy underpinned by heterogeneity – a mismatch between science and management

The underlying premise of KNP's revised elephant management philosophy is that patchy elephant impacts will prevent widespread biodiversity losses because the intervening areas, referred to as "refuge" areas, will allow for persistence of impact intolerant species (Owen-Smith et al., 2006). This reasoning is reflected by a spatially explicit interpretation of the IDH, in which a range of elephant impact severities in different patches of the landscape mosaic represent different points along the IDH curve. The existence of a range of disturbance levels promotes the co-existence of different suites of species at a landscape level, rather than a single "optimal" suite of species maintained under moderate levels of impact spread evenly across the entire park. This perspective suggests that the key to mitigating elephant-mediated biodiversity loss over large areas is to allow for spatial or temporal refuges from elephant herbivory, by inducing variable space use by elephants (Owen-Smith et al., 2006, O'Connor et al., 2007, Kerley et al., 2008). However, no empirical studies exist that explore the relationship between

elephant disturbances and the generation or maintenance of heterogeneity explicitly, either in KNP or elsewhere (Scholes and Mennell, 2008). At best a developing trend of collecting elephant movement data remotely over large scales through GPS/satellite technology has resulted in demonstrable patterns of heterogeneity in elephant space use (Grainger et al., 2006, Loarie et al., 2009, Young et al., 2009). As a result, there is still poor understanding of which factors would likely produce sufficiently patchy impacts to create refuges from elephant disturbance, and under what conditions.

Manipulation of water distribution through altered water provisioning has been proposed as a means of generating or restoring such heterogeneity (Owen-Smith, 1996, Gaylard et al., 2003, Owen-Smith et al., 2006, Chamaillé-Jammes et al., 2007, O'Connor et al., 2007). However, since the abundance of natural sources of water in KNP leaves few areas remote from water relative to elephant foraging ranges (Redfern et al., 2003), uncertainty remains as to the extent to which elephants express their water dependence in this landscape, and hence whether further borehole closure would generate adequate scales of heterogeneity to provide refuges from severe elephant impacts (Redfern et al., 2005, Smit et al., 2007a, Smit et al., 2007c, Grant et al., 2008). Hence, despite the fact that South African National Parks, a leading conservation agency, now bases its elephant and biodiversity management on a heterogeneity paradigm, there is still no framework for advancing understanding of elephants as agents of change in complex systems (Scholes and Mennell, 2008). Understanding how elephants alter biodiversity is central to making sound elephant management decisions (Owen-Smith et al., 2006, Kerley et al., 2008), but in the absence of empirical support for a heterogeneity approach to managing elephants, there is a mismatch between the current philosophy underpinning elephant management and the science that is meant to serve it. The following section proposes a framework for such a heterogeneity approach, and in this manner contextualises the broad objectives for my study.

1.6 A heterogeneity approach for linking elephant science and management - study aim, location and objectives

Having outlined the important components of heterogeneity and complex systems in the preceding sections of this chapter, as well as their relevance for elephant disturbance regimes, I propose that a heterogeneity approach for linking elephant science and management requires more than the current tacit acknowledgement of the existence of heterogeneity and complexity (Cadenasso et al., 2006, Rogers et al., 2013) in savanna landscapes. It also requires explicit

quantification of the scales and spatial patterns of elephant responses to key resources, and the associated effects on vegetation. Despite the widely accepted paradigm shift to heterogeneity (Rogers, 2003), the review of previous elephant studies earlier in this chapter has illustrated that these studies have failed to account for several of the key features of heterogeneity. In the first instance, quantifications of the patchiness of elephants' key resources (such as surface water) have been limited to spatially implicit measures, despite the fact that spatial configuration, or patch context, is a key contributor to heterogeneity (Kotliar and Wiens, 1990). Can we fully understand patterns of resource heterogeneity without an appreciation of spatial context? Secondly, attempts to incorporate scale into investigations of elephant landscape use have all imposed *a priori* or anthropogenic scales of analysis, rather than allowing the relevant scales to emerge. Can we be sure that these imposed scales comprehensively describe those aspects of elephant resource use that are relevant to their roles as agents of change in savannas?

Thirdly, traditional parametric statistical techniques are unable to deal with certain common features of heterogeneous systems such as spatial autocorrelation , or regional variation (or non-stationarity), and hence these patterns must be eliminated before such tests can be used (Samuels, 1993, Anand et al., 2010, Fortin et al., 2012). Finally, the multiple possible cause-and-effect relationships, ecological feedbacks and emergent properties common in complex systems are difficult, if not impossible, to disentangle using narrowly focused hypothesis-testing. Instead, adaptive inference (Holling and Allen, 2002) has been suggested as a means of minimising both Type I and Type II errors (Mills et al., 2006) when investiging complex systems, using multiple lines of evidence to winnow out hypotheses that have gained little support. How confident can we be of the understanding generated by previous reductionist investigations (Mills et al., 2006, Rogers et al., 2013) of the drivers of elephant-mediated biodiversity change?

Given this context, the main aim of this study is to develop a framework for a heterogeneity approach that (i) can incorporate patch context as a contributor to patterns of resource heterogeneity; (ii) allow the relevant scale(s) of resource heterogeneity, as well as elephant responses to this heterogeneity, to emerge from, rather than being imposed on, the analyses *a priori*; (iii) are able to make use of the presence of spatial autocorrelation in datasets to elucidate important underlying patterns and processes associated with elephant use of the landscape, rather than trying to eliminate it to satisfy the assumptions of traditional statistical approaches; (iv) can account for regional variation, or non-stationarity, when investigating the drivers of elephant space use and the associated distribution of their impacts; and (v) ultimately

make use of multiple lines of reasoning, rather than narrowly focused hypotheses, to infer elephant-mediated trajectories of biodiversity change. By developing this framework through the course of the thesis, I hope not only to advance our understanding of elephants as agents of change in heterogeneous savannas, but also to demonstrate the broader significance of such an approach for studies of heterogeneity in other complex systems.

Because of its large size (2 million ha) and well-documented management history, KNP represents one of the few remaining areas where spatial heterogeneity and ecological response can still operate relatively freely over large spaces and long time frames (Pickett et al., 2003). The park occurs in a semi-arid environment characterised by high levels of surface water heterogeneity (Gaylard et al., 2003), known to shape elephant distributions and feeding activities elsewhere in Africa (Western, 1975, Owen-Smith, 1988, Owen-Smith, 1996). At the time of the study, KNP had relatively high elephant densities of around 1 km^{-2} (Van Wyk and Fairall, 1969), which were a cause for concern to managers mandated with protecting the park's biodiversity (Whyte et al., 1999). For these reasons, and the recent shift from a Balance of Nature approach, KNP provided a unique opportunity for applying the proposed heterogeneity framework. In the sections that follow, I explain my rationale for selecting riparian zones in the northern region of KNP as my study area, and outline the broad objectives for, and structure of, the study.

1.6.1 Riparian zones of ephemeral rivers in northern KNP as an opportunity to explore a heterogeneity approach

Surface water availability in semi-arid savannas such as KNP varies along with winter droughts and summer rains, as well as over 9-year cycles of wet and dry periods (Gertenbach, 1980). In addition, rainfall varies along a North-South rainfall gradient in the park, and as a result of variable underlying geology and evapotranspiration (Gaylard et al 2003). This results in the presence of primarily perennial rivers with variable flow regimes at the high end of the rainfall gradient in the south of the park (O'Keefe and Rogers 2003). In contrast, in the northern low rainfall areas rivers are mainly ephemeral, flowing only if sufficient rains have fallen during the wet season (Gaylard et al., 2003).

As a result, the northern part of KNP has the greatest seasonal contrasts in surface water availability in the park. Having flowed after good rains during the wet season, the larger ephemeral rivers in KNP, such as those found in the north of the park, are left with only pools

of standing water along their lengths as the rivers dry up over the course of the dry season (Gaylard et al., 2003). These essentially point sources of water within the river channels contrast with perennial rivers further south that have a continuous flow of water throughout their lengths and over time. Water in the adjacent interfluve areas is limited to a few natural springs and pans (Gaylard et al., 2003). In addition, northern KNP was the site of experimental boreholes closure in the 3 years prior to the initiation of this study, restoring surface water distribution to more natural patterns (Harrington et al., 1999). The greater contrasts in surface water availability in this part of the park makes northern KNP an ideal site for exploring patterns of surface water heterogeneity.

Finally, riparian zones provide critical resources for elephants and other herbivores during the dry season when sources of food, water and shade have become scarce elsewhere in the landscape (Western, 1975, Owen-Smith, 1988, Owen-Smith, 1996). Accordingly, elephants focus their activities in riparian zones during the dry season. Riparian zones therefore provide an opportunity to investigate elephant responses (including feeding) to sources of resource heterogeneity such as surface water availability, with ephemeral rivers representing the drier end of the park's surface water availability continuum. Moreover, since fire is infrequent in riparian zones, a primary confounding factor involved in savanna vegetation dynamics (and the resulting vegetation patterns) is eliminated by focusing on this part of the landscape.

1.6.2 Study objectives and thesis structure

To develop the heterogeneity approach, I have divided the thesis into six chapters. The chapters sequentially address each of the components of the framework outlined above (section 1.6), each new chapter cumulatively building on the methodology of previous chapters by incorporating additional components. Consequently, there is a degree of unavoidable repetition of the methodologies deemed to be crucial for developing the heterogeneity approach. Nevertheless, the thesis has been structured with the intention of submitting each data chapter as an independent manuscript, with each chapter addressing a different aspect of how I hypothesize elephants will respond to, and in so doing generate, heterogeneity in the landscape. Specifically, I focus my attention on illuminating the scales and patterns of heterogeneity of the surface water resource, investigating the scales at which elephants respond to these patterns of surface water heterogeneity, and assessing the functional heterogeneity of these patterns by determining whether they generate patchiness in elephant disturbance regimes as a result. Finally, using a spatially explicit interpretation of the Intermediate Disturbance Hypothesis (as

described in section 1.5.3), I use multiple lines of evidence gathered in the preceding chapters to place the study area along a trajectory of elephant-mediated biodiversity change, and assess which components of riparian biodiversity may provide an earlier warning signal of impending biodiversity losses.

Chapter 1: Elephants as agents of change in savannas – why do we need a Heterogeneity approach? (i.e. this chapter)

In this introductory chapter I have provided the overall background to the study, reviewing the literature on elephant-vegetation interactions, as well as on changes in elephant management philosophies following an ecological paradigm shift, to emphasize the need for a fresh perspective of elephants as agents of change in savannas. I have outlined the shortcomings of previous elephant studies, including those that have purported to be underpinned by heterogeneity, and proposed a framework for a heterogeneity approach that explicitly accounts for key features of complex systems.

Chapter 2: Understanding surface water heterogeneity as the template for elephant disturbances: a spatially explicit approach

Our current understanding of how elephants respond to patchiness in surface water distribution is based on spatially implicit measures of surface water distribution (distance to water) that cannot account for the patch context, or spatial configuration, of waterpoints. In Chapter 2, I investigate what insights may be gained by examining surface water heterogeneity in a spatially explicit manner that allows for the quantification of patterns of waterpoint spatial configuration emerging at particular scales. By accounting for this patch context, the technique employed to elucidate these patterns represents the first component of the proposed heterogeneity approach. The results have implications for understanding the template for elephant disturbances provided by prevailing patterns of surface water heterogeneity, as well as for how artificial water provisioning may alter this template.

Chapter 3: The role of surface water heterogeneity in elephant patch choice and feeding in a landscape with abundant water sources

Surface water provides a template for patchy elephant disturbances only if it is sufficiently heterogeneous to generate differential movement and foraging responses by elephants over

space and time. In this chapter I explore whether, and at what scales, elephant patch choice and feeding are associated with the spatio-temporal patterns of the surface water resource elucidated in Chapter 2. The heterogeneity approach is developed further by incorporating a Geographicallly Weighted Regression (GWR) method that makes use of spatial autocorrelation in elephant spatial responses to expose underlying drivers and modulators of elephant patch choice and feeding (including energetic requirements based on elephants' sexual size dimorphism and social systems as proxies), and tests how these drivers and responses may vary over time. The results have implications for understanding the conditions underwhich surface water provides a template for patchy elephant disturbances, as well as how this template may be altered through water provisioning in order to manipulate elephants' use of the landscape.

Chapter 4: Can refuges from elephant impact exist in landscapes with abundant surface water?

Understanding elephant patch choices is important because patches that are infrequently visited by elephants may potentially serve as refuges from elephant impact, allowing impact intolerant species to persist in these parts of the landscape. Although surface water heterogeneity has been proposed to generate such refuges (Owen-Smith, 1996, Chamaillé-Jammes et al., 2007, Kerley et al., 2008), there is general consensus that refuges will only be generated where distances to surface water render parts of the landscape inaccessible to elephants (Redfern, 2002, Redfern et al., 2005, Smit et al., 2007a, Smit et al., 2007c, Smit and Grant, 2009). Given the understanding of patterns of elephant response to surface water heterogeneity gained by incorporating patch context in the previous chapter, this chapter asks whether it is possible for refuges to exist in landscapes where distances between water sources are small relative to elephants' maximum daily foraging ranges.

I address this question by assessing where elephant impacts accumulate in the landscape relative to the patterns of surface water heterogeneity that generated elephant patch choice and feeding, and test the hypothesis that by increasing disturbance return intervals, temporal surface water heterogeneity can provide patches of lower elephant impact in which plants can recover between successive bouts of elephant disturbance. The heterogeneity approach is further built upon in this chapter by the additional use of the predictive component of the GWR, to assess how differently impacts may accumulate in the absence of artificial water sources. The results therefore have implications for understanding the role of surface water heterogeneity in the generation of spatial and temporal refuges from elephant

disturbances, as well as for decision-making regarding the use of water provision to manipulate the spatial and temporal parameters of elephant disturbances.

Chapter 5: Elephant-mediated modifications to biodiversity along a trajectory of change in a heterogeneous landscape

Underlying predictions that surface water heterogeneity can prevent elephant-induced biodiversity loss, is the hypothesis that spatial and temporal refuges from elephant impact allow impact intolerant species to persist in landscapes where local reductions in biodiversity occur elsewhere. This represents a heterogeneity interpretation of the Intermediate Disturbance Hypothesis in which, rather than striving for some intermediate level of disturbance across the entire landscape to optimise biodiversity, the goal would be to ensure patches of varying elephant disturbance in different parts of the landscape. Although this heterogeneity interpretation of the IDH underpins contemporary elephant management philosophies in southern African savannas, there is as yet no empirical evidence to support it. Underpinned by the understanding of the role of surface water heterogeneity in elephant patch choice and feeding, and hence in the accumulation of elephant impacts across the landscape, gained in the preceding chapters, I develop the heterogeneity approach further here by evaluating the multiple lines of evidence from the preceding chapters. Together these lines of evidence pinpoint the study area's placement along a trajectory of elephant-mediated biodiversity change. In this way I incorporate the final, adaptive inference component of the heterogeneity approach. The results have implications for the mode of science required to disentangle the relative roles of the multiple drivers of complex systems, as well as for predicting elephant-mediated biodiversity changes under increasing elephant populations.

Chapter 6: How has the heterogeneity approach advanced our understanding of elephants as agents of change in complex systems?

In this final, concluding chapter, I evaluate how the insights gained by using a heterogeneity approach in Chapters 2 – 5 have advanced our understanding of elephants as agents of change in heterogeneous landscapes. Specifically, I summarise the implications of using approaches that account for key attributes of complex heterogeneous systems, such as patch context and scale, spatial autocorrelation, non-stationarity and multiple drivers of ecosystem pattern. I then

summarise the advances my study has made towards empirical understanding of how elephants respond to surface water heterogeneity beyond simple distance-to-water measures. Given this nuanced understanding of the role of surface water heterogeneity in generating spatial and temporal refuges from elephant impact, I outline the future scope for strategic water provisioning policies to minimise biodiversity loss in the face of increasing elephant populations, and provide recommendations for monitoring trajectories of elephant-induced biodiversity change. Finally, I identify knowledge gaps emanating from this work, and consider its implications for a broader understanding of how organisms respond to, and thereby generate, ecological heterogeneity in complex systems. More broadly, I consider what lessons can be learnt for the approach to investigating complex systems.

Chapter Two - Understanding surface water heterogeneity as the template for elephant disturbances: a spatially explicit approach

2.1. Introduction

The spatial arrangement of resources affects the location, movement patterns, foraging dynamics and persistence of organisms (Turner et al., 1993). Organisms, in turn, create natural disturbances (Pickett and White, 1985), which are among the most important generators of pattern in the landscape (Turner et al., 1993). In this way, organisms both respond to, and create, heterogeneity (Pickett et al., 2000, Kerby et al., 2007). As a result, resource heterogeneity can be functionally stablising by localising consumption to certain patches, or by spreading consumption away from patches of preferred resources before these become critically depleted (Owen-Smith, 2004). These dynamics play an important role in determining whether shifting patch mosaics are created by such localised ecosystem disturbances and maintained in a long-term steady state (Bormann and Likens, 1979), or whether ecosystems shift to an alternative state through extensive over-utilisation instead.

Elephants, for example, are water-dependent (Owen-Smith, 1988), focusing their dry season activities in the vicinity of surface water in semi-arid savannas (Western, 1975, Western and Lindsay, 1984). As the dry season progresses, surface water sources become depleted, constraining elephants to areas that are accessible from permanent sources of drinking water, regardless of the abundance of food elsewhere (Illius and O'Connor, 2000). In this way vegetation in the areas remote from permanent water is relieved of severe herbivory during the dry season. Similarly, the presence of temporary water sources during the rainy season alleviates pressure on vegetation near permanent water, by reducing the period of elephant concentration in these areas (Owen-Smith, 1996). Hence, the distribution of surface water provides a template for elephant disturbances by determining where vegetation impacts occur, as well as the seasonal duration of these impacts (Owen-Smith, 1996). Within this context, surface water heterogeneity can generate spatial or temporal refuges from elephant

disturbances (Illius and O'Connor, 2000, Owen-Smith et al., 2006, Kerley et al., 2008). Gaining an understanding of surface water heterogeneity is therefore a crucial first step towards advancing our understanding of elephants as disturbance agents in heterogeneous systems such as semi-arid savannas.

Current understanding of savanna surface water heterogeneity is based on studies that have focused on the distances that herbivores must travel to reach water, and how this varies over time, commonly referred to surface water availability (Owen-Smith, 1996, Redfern, 2002, Gaylard et al., 2003, Redfern et al., 2005, Chamaillé-Jammes et al., 2007a, Chamaillé-Jammes et al., 2007b, Smit et al., 2007c, Chamaillé-Jammes et al., 2008, Smit and Grant, 2009, Smit and Ferreira, 2010, Smit, 2011). Herbivores in semi-arid savannas are faced with highly variable surface water availability associated with seasonal rainfall fluctuations. Most water sources are confined to riparian zones, with only isolated springs or ephemeral pans in the intervening interfluves (Gaylard et al., 2003). Perennial rivers in higher rainfall areas (>500 mm per annum) represent permanent, linear sources of water that animals can visit at any point along the river course to obtain drinking water. In contrast, the rivers in lower rainfall areas (<500 mm per annum) only flow during the wet season (Jacobson, 1997) . At some points along these ephemeral river courses, notably those with underlying bedrock, water is retained in the same location year after year, providing a reliable source of surface water for elephants and other herbivores (Gaylard et al., 2003). The locations of persistent natural waterpoints along these ephemeral river courses can change after a large flood event, as sediment is scoured away and transported downstream, exposing bedrock that prevents water from seeping beneath the surface into the water table (Jacobson, 1997). In addition to seasonal fluctuations in rainfall, southern African savannas also experience 9-year wet and dry cycles, with additional interannual variability superimposed by El Nino events (Gertenbach, 1980), generating surface water heterogeneity across multiple temporal scales.

Artificial water sources have been used to augment natural sources in savanna systems, in an attempt to dampen this variability and provide a more reliable source of water for game (Pienaar, 1985, Pienaar et al., 1997). Such water provisioning generally involves establishing a large number of boreholes that supply cement troughs, and that are kept open year-round, year after year. Large (up to 5 ha) earthen impoundments (dams) are provided in smaller numbers but, in contrast to the perennial boreholes, these tend to dry up during drought conditions (Gaylard et al., 2003). Hence evenly-spaced water provisioning can dampen the spatial and temporal heterogeneity of surface water in savanna systems (Chamaillé-Jammes et al., 2007b)

by reducing or evening the range of distances between sources of surface water, and by maintaining the location and abundance of water sources even during drought conditions (Pienaar, 1985). Therefore, provision of artificial water sources potentially reduces the amount of landscape that is inaccessible to elephants (Smit, 2011) and reduces the intervals between bouts of elephant disturbance in the vicinity of surface water, by increasing the persistence of surface water through the dry season.

To date quantifying surface water heterogeneity as the template for elephant disturbances has been based on the relative proportions of a landscape that are accessible to elephants within their maximum daily foraging ranges (20-30 km; (Owen-Smith, 1988)). For example, landscapes with few areas inaccessible to elephants even during drier conditions have been deemed to have spatially homogenous surface water, precluding the possibility of providing refuges from elephant disturbances (Owen-Smith, 1996, Smit et al., 2007a). In contrast, landscapes have been deemed to have heterogeneous surface water if substantial portions of the landscape are further than 25-30 km from water, at least towards the end of the dry season (Owen-Smith, 1996). Based on this distance-to-water (DtW) understanding, surface water in KNP was thought to provide an homogenous template for elephant disturbances (Redfern et al., 2005, Smit et al., 2007a), since the relatively abundant sources of natural water in this landscape leave few areas further than 5 km from water (Gaylard et al., 2003, Redfern et al., 2003). Moreover, even if all artificial waterpoints were to be removed, this would not significantly increase the proportion of the landscape >15 km from water, except during extreme drought years (Redfern et al., 2005, Smit et al., 2007a, Smit and Grant, 2009). As a result, most studies agree that surface water does not constrain elephant foraging in landscapes such as KNP, where the abundance and distribution of water sources leaves few parts of the landscape beyond the daily maximum foraging ranges of elephants (Redfern et al., 2005, Smit and Grant, 2009). Consequently, further closure of artificial waterpoints to generate refuges from elephant impacts has largely been dismissed in such landscapes (Grant et al., 2008).

Although DtW studies have been used to quantify surface water heterogeneity, they provide only a spatially implicit measure. Spatially implicit measures quantify the simplest expressions of heterogeneity, measuring the aggregate variation among points in a given area (Wiens, 2000). In contrast, a key principle of the heterogeneity paradigm is that patch context, or the spatial configuration of patches, is an important determinant of spatial heterogeneity that can only be quantified using spatially explicit approaches (Forman and Godron, 1981, Kotliar and Wiens, 1990, Wiens, 1995). Accordingly, more recent empirical and modelling studies of

ecological dynamics have emphasized the need for spatially explicit approaches (Grünbaum, 2002). Importantly, understanding spatial heterogeneity is dependent on the scale of observation (Turner, 1989, Fortin et al., 2012) and its quantification should therefore be computed at multiple scales, rather than at scales imposed by the researcher (Li and Wu, 2004, Fortin et al., 2006). Since spatially implicit analyses do not explicitly account for scale, the understanding that we have gained from broad-scale DtW patterns of surface water heterogeneity to date may not apply at finer scales.

Identifying these potential gaps in our understanding raises key questions that may have important implications for understanding the role of surface water heterogeneity in modulating elephant use of the landscape. For example, would a spatially explicit quantification of surface water heterogeneity provide new insights into the template of surface water available to elephants, and if so, at what scales are these patterns manifest? Waterpoints that are clustered together may experience less severe impacts than those that are further apart, but the impacts may extend across the intervening areas leaving no spatial refuges from elephant disturbance between them. In contrast, local impacts in the vicinity of more isolated waterpoints may be more severe due to aggregation of elephants (Chamaillé-Jammes et al., 2008), but the intervening areas may remain relatively free from elephant disturbance. Secondly, might a spatially explicit analysis of the changes in surface water distribution under varying rainfall conditions provide a more nuanced understanding of temporal surface water heterogeneity than that provided by DtW analyses? If the spatial configuration of waterpoints changes along with varying rainfall over time, patches less frequently visited by elephants (i.e. with large disturbance return intervals) may receive temporal refuge from severe impacts. Finally, might an understanding of the spatial configuration of waterpoints advance our understanding of how artificial water provisioning could be manipulated to enhance spatial or temporal surface water heterogeneity?

In this chapter, I address these questions by comparing the templates of surface water heterogeneity exposed by patterns of DtW versus waterpoint spatial configuration for the same area. In so doing, I develop the first component of the framework for a heterogeneity approach, evaluating the spatially explicit approach by testing the following predictions emanating from the current DtW perspective:

i) the spatial variability of surface water in a landscape where elephants are not constrained by maximum daily distances to water provides an homogenous surface water template for elephants;

ii) as such, surface water only varies over time in this landscape when the distances between waterpoints becomes greater during drier periods; and therefore

iii) artificial water provision only has a dampening effect on spatio-temporal surface water heterogeneity in these landscapes when distances between water sources increases during such extreme drought conditions

Ephemeral rivers provide an ideal opportunity for testing these predictions, since they represent point sources of water with particular spatial arrangements, rather than linear sources of water such as perennial rivers. Moreover, the location and abundance of these point water sources, as well as the distances between them, are not static over time. Rather, they shift in response to the amount and timing of rainfall events, introducing a source of temporal variability not present in perennial river systems (Jacobson, 1997). Riparian zones also represent important areas of criticial resources for elephants during bottleneck periods towards the end of the dry season and during drier years. Hence these riparian zones are the most likely areas in which to find elephants responding to dry season surface water distribution.

2.2 Study area

I selected a study area of 390 000 ha between the Shingwedzi and Mphongolo Rivers in the far northern region of KNP, at the dry end of the park's north-south rainfall gradient (<500 mm rainfall per annum; Figure 2.1). Surface water was available along four ephemeral rivers traversing the study area (the Shingwedzi, Phugwane, Bububu and Mphongolo rivers), as well as in a small number of ephemeral springs (8% of total water) and pans (6% of total water) in the upland areas away from these rivers (Gaylard et al. (2003); Figure 2.1). Distances between these ephemeral rivers ranged between three and 16 km, compared with 10 – 40 km between the perennial rivers in the wetter southern areas of the park. In addition to these natural sources of water, the water provisioning programme initiated in KNP during the 1960's (Pienaar, 1985) provided man-made sources of water in the form of boreholes and dams.

Permanently pumped boreholes (35% of the total water supply) had been placed wherever natural water was expected to have occurred in the past in both the riparian and upland sections of the landscape, while earth dams (14% of total water) occurred only along the ephemeral rivers of the riparian zone. As a result, 68% of the area's dry season surface water was concentrated within the riparian zone, which constituted only 2% of the study area. The density of waterpoints in the riparian zone was as much as two orders of magnitude higher

(134 waterpoints/10 000 ha) than that in the adjacent interfluves (1.2/10 000 ha). Hence surface water in this landscape resembled a natural situation in as much as the riparian zones maintained most of the surface water and thus represented critical dry season resources for herbivores. However, within the riparian zone only half of the water sources were natural (48%) while the other half was artificially supplied (52%).

Three years of highly variable rainfall (measured from July – June) occurred over the course of the study period (1997 – 1999). The Shingwedzi weather station recorded 455 mm of rain during the first year (July 1996 – June 1997), approximating the long-term mean annual rainfall for the area (Gertenbach, 1980). The second year (1998) was very dry, receiving just over half the long-term mean annual rainfall (250 mm between July 1997 – June 1998). During the final year (1999), the study area received more than twice the long-term mean annual rainfall (950 mm July 1998 – June 1999). Henceforth, I refer to these years as average (July 1996 – June 1997), dry (July 1997 – June 1998) and wet (July 1998 – June 1999) years.

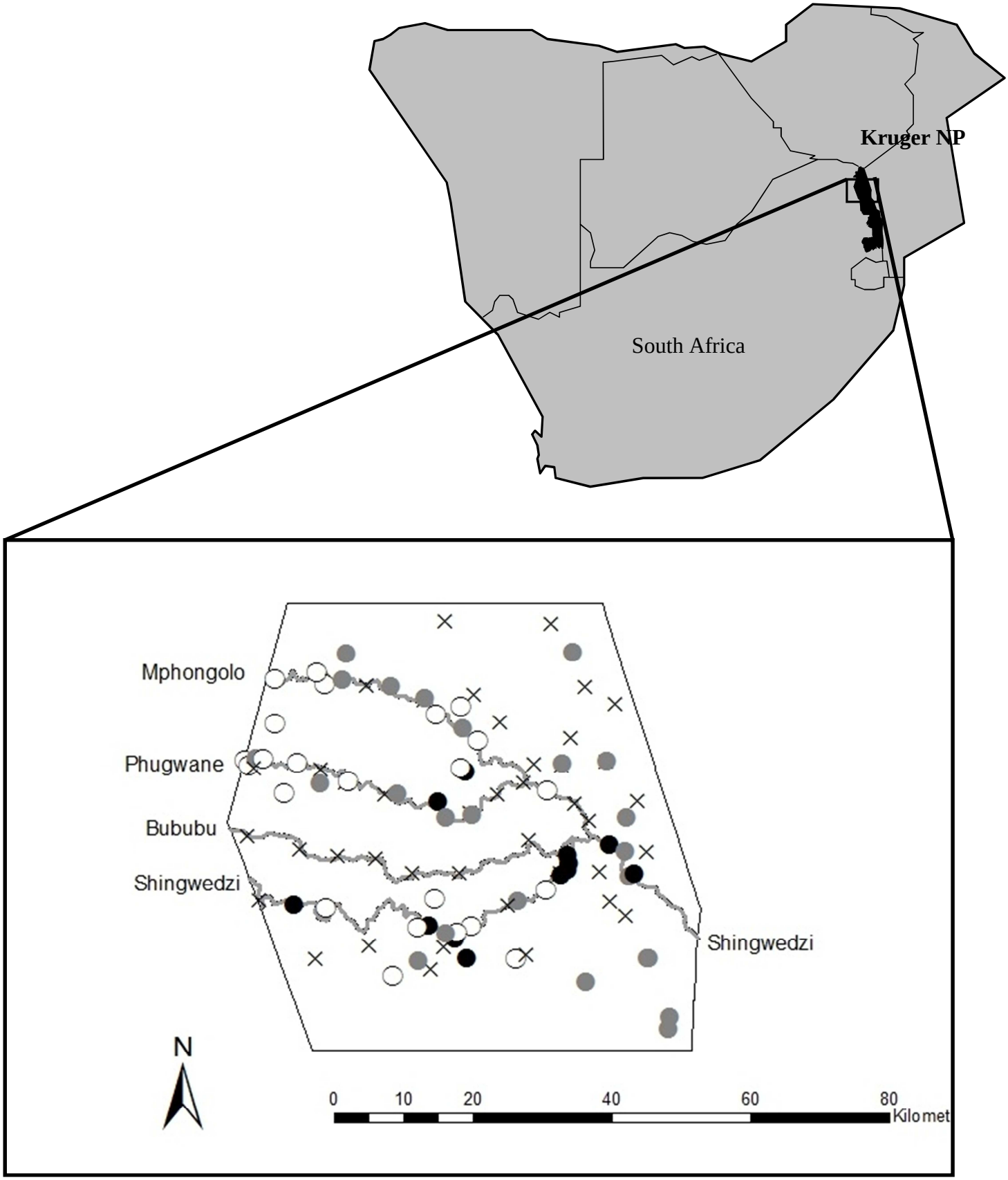


Figure 2.1 Map of perennial surface water in the study area in the drier northern region of Kruger National Park (black dots represent waterpoints that persisted through even the driest year of the study period, grey dots are waterpoints that retained only small volumes of water during the driest year, and white dots are waterpoints that only persisted through the dry seasons of the average and wet years; x's represent artificial water supplies)

2.3 Methods

My approach centered around a comparison of spatially implicit versus spatially explicit methodologies to expose patterns of surface water heterogeneity in the northern ephemeral rivers in KNP. This required the compilation of a spatio-temporal database of all the surface water in the study area before traditional DtW analyses, followed by analyses of waterpoint spatial configurations, could be undertaken. The patterns revealed using these techniques were also compared over time in relation to varying rainfall over the course of the dry season, as well as among years during the study period. Lastly, all of these analyses were repeated using a scenario that included only natural sources of surface water, in order to compare how artificial water provision had influenced patterns of DtW versus waterpoint spatial configuration in the study area. The analyses were restricted to dry season surface water heterogeneity as this represents the water resource bottleneck period when herbivores are expected to be most constrained by surface water availability (Western and Lindsay, 1984).

2.3.1 Compilation of a surface water database

I mapped the locations of all sources of surface water (natural waterholes, springs and pans, and artificially provided boreholes and dams) along the four major rivers (the Shingwedzi, Phugwane, Bububu and Mphongolo rivers) traversing the study area, during an aerial survey at the onset of the first dry season of the study period (May 1997). Although the analyses were restricted to the riparian zone, I included upland water sources because of the spatial context they provided to riparian water sources. The locations of perennial water sources in the intervening upland areas were obtained from 1:50 000 topographical maps from the Land Surveyor General, and from a water database collected as part of the annual aerial survey of large mammals conducted by the Scientific Services Division in KNP. The persistence of all the surface water across the study area was then tracked on a monthly basis through the three dry seasons of the study period, by means of ground visits and through accounts in ranger diaries. These records were then used to create a spatio-temporal database of how long each waterpoint persisted through the dry seasons experiencing varying rainfall between 1997-1999, using ArcMap 10.1 (ESRI, 2001).

2.3.2 Spatial analyses of surface water heterogeneity

Distance to water

I quantified distance-to-water (DtW) as the relative proportions of the landscape at different distances from surface water, in order to compare patterns of surface water heterogeneity in the study area with those of previous DtW studies. To do this, I needed to differentiate the landscape into different distance categories from water in an objective manner. I determined these distance categories by calculating the frequency distribution of distances from all waterpoints in the study area using 1-km increments in the Buffer function of ArcMap v10 (ESRI, 2001). I then used this distribution to determine the upper and lower limits for the distance classes. Firstly, since a negligible proportion of the landscape was further than 16 km from perennial water, I assigned all areas further than 16 km into one distance class. At the opposite end of the DtW range, a number of areas were closer than 1 km from water. I therefore halved the first 1-km increment and assigned areas into distance classes of either <0.5 km or 0.5 – 1 km from water. Distance classes between the smallest (<0.5 km) and largest (>16 km) were assigned by sequentially doubling each distance class until the value reached the largest distance (16 km), to minimise the number of distance classes for ease of interpretation. The resulting distance categories were therefore <0.5, 0.5 – 1 km, 1 – 2 km, 4 – 8 km, 8 – 16 km, and >16 km.

Waterpoint spatial configuration

Quantifying the spatial configuration of waterpoints involved two key steps (Figure 2.2). Firstly, since the detection of spatial configuration is scale-dependent (Turner, 1989), I tested for the scale(s) at which waterpoints were significantly more clustered or dispersed than a random spatial distribution (Legendre and Fortin, 1989, Legendre, 1993) using ArcMap 10.1's Multi-Distance Spatial Cluster Analysis tool (ESRI, 2001). This tool summarizes how the spatial clustering or dispersion of waterpoints changes as the neighbourhood size (or scale of analysis) changes (Scott and Janikas, 2010). This allowed for the emergence of all of the scales at which waterpoint spatial configuration was significantly different from random, as required by the proposed heterogeneity approach, rather than selecting a scale for the analysis *a priori* (Chapter 1, section 1.6).

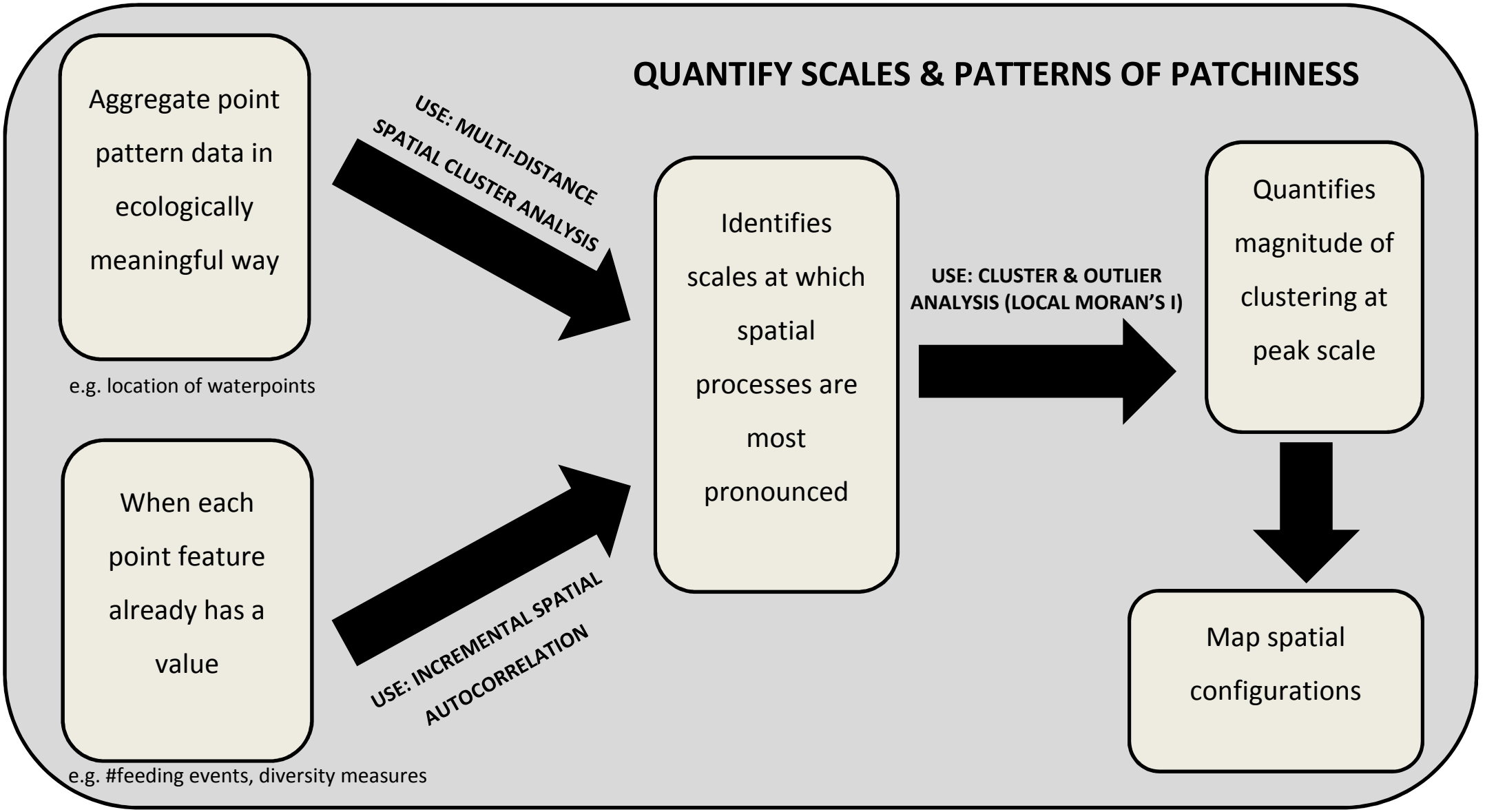


Figure 2.2 Diagrammatic representation of the first step in the heterogeneity approach - quantifying the scale(s) and patterns of spatial heterogeneity of features using spatially explicit analysis tools in ArcMap 10.1 (ESRI, 2000).

Secondly, I used the scale with the most pronounced patchiness in waterpoint configuration, identified in the previous step, to quantify the spatial configuration of each waterpoint in the study area, since this is the scale at which underlying spatial processes are most pronounced (Fortin et al., 2012). For this I made use of a local test for spatial autocorrelation known as the Cluster and Outlier Analysis tool (Scott and Janikas, 2010) in ArcMap 10.1 (ESRI, 2001).

During the first step, identifying scale(s) of patchiness in waterpoint distributions involved a pair-wise comparison of each waterpoint with each neighbouring waterpoint in the landscape (Fahrig and Paloheimo, 1988). The Multi-Distance Spatial Cluster Analysis computes the average number of neighbouring features (in this case waterpoints) associated with each feature (K), neighbouring features being those that are closer than the particular distance being evaluated. As the evaluation distance increases, each feature will typically have more neighbours. The procedure makes use of a common transformation of the Ripley's K-function (Haase, 1995, Fortin et al., 2006), referred to as L(d), that takes the form:

$$L(d) = \frac{\sqrt{A \sum_{i=1}^{N} \sum_{j=1, j \neq i}^{N} k(i,j)}}{\pi N(N-1)}$$

where *A* is area, *N* is the number of points, d is the distance and *k*(*i, j*) is the weight, which (if there is no edge correction) is 1 when the distance between *i* and $j \leq d$, and 0 when the distance between *i* and $j > d$.

If the average number of neighbours for a particular evaluation distance is larger than the average concentration of features throughout the study area, the distribution is considered clustered at that distance (or scale of analysis).When the observed K-value is larger than the expected K-value for a particular distance, the distribution is more clustered than a Complete Random Distribution (CRD) at that scale. When the observed K-value is smaller than the expected K, the distribution is more dispersed than a CRD at that scale (Scott and Janikas, 2010). Observed K-values larger than the upper confidence interval value (i.e. a clustered spatial configuration), or smaller than the lower confidence interval value (i.e. a dispersed spatial configuration), signify statistically significant clustering or dispersion at that scale (

Figure 2.3). Where multiple scales of patchiness (either clumped, dispersed, or both) exist, peaks in significant K-values represent scales at which the spatial processes creating these configurations are most pronounced (Scott and Janikas, 2010). The existence of non-random point patterns can then be used to infer processes that might have led to the observed spatial structure (Legendre and Fortin, 1989, Legendre, 1993).

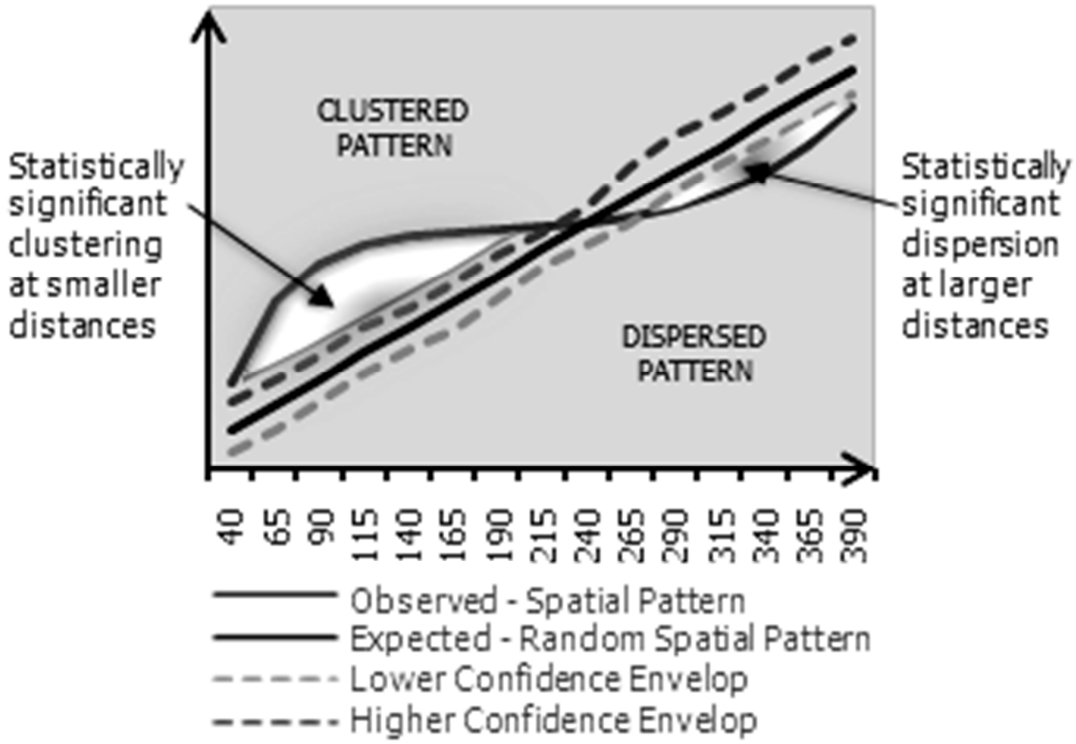


Figure 2.3 Graphical representation of the interpretation of the Multi-Distance Spatial Cluster Analysis (ESRI, 2001) output (from ESRI support documentation at www.esri.com), showing how observed K-values larger than the Confidence Intervals are significantly more clustered than a Complete Random Distribution, whereas K-values below the Confidence Intervals are significantly more dispersed at those scales

The second part of the analysis involved quantifying the spatial configuration of each waterpoint, based on the emergent scale(s) of clustering or dispersion identified above (Figure 2.2). To do so, I selected a form of point pattern analysis (Legendre, 1993, Takahashi, 2006) that identifies statistically significant hotspots, coldspots and spatial outliers by calculating the Anselin's Local Moran's I statistic of spatial autocorrelation among features (Anselin et al., 2006, Cromsigt et al., 2009, Fortin et al., 2012). Given a set of weighted features, the Cluster and Outlier Analysis tool in ArcMap 10.1 (ESRI, 2001) calculates a z-score, based on a randomization null hypothesis computation, while p-values indicate whether the apparent similarity (a spatial clustering of either high or low values) or dissimilarity (a spatial outlier) is

more pronounced than one would expect from a CRD. A high positive z-score for a feature indicates that the surrounding features have similar values (either high values or low values). A low negative z-score (for example, < -1.96) indicates a statistically significant ($p < 0.05$) spatial outlier. A positive value for *I* indicates that a feature has neighbouring features with similarly high or low attribute values, and that this feature is therefore part of a cluster. In contrast, a negative value for *I* indicates that a feature has neighbouring features with dissimilar values, and this feature is therefore an outlier, such as a isolated (or dispersed) waterpoint (Scott and Janikas, 2010).

This tool cannot be utilized on point incident data such as the location of waterpoints, but instead requires a value for each feature. Consequently, the waterpoint incident data had to be aggregated in an ecologically meaningful way that captured the patch context surrounding each waterpoint (Scott and Janikas, 2010). I used the Buffer tool (ESRI, 2001) to construct neighbourhoods for each waterpoint based on the maximum scale of surface water patchiness identified by the Multi-Distance Spatial Analysis, since this is the scale at which underlying process are expected to be most pronounced (Legendre and Fortin, 1989, Scott and Janikas, 2010). I then used the Spatial Join tool (ESRI, 2001) to count the number of waterpoints falling within each waterpoint's neighbourhood. The resultant field containing the number of waterpoints in each neighbourhood served as the value field required for the cluster analysis (Scott and Janikas, 2010), and the spatial configuration was therefore quantified at the peak scale of surface water patchiness.

Since ArcMap's (ESRI, 2001) spatial statistics integrate space and spatial relationships directly into their mathematics, many of the tools in the spatial statistics toolbox require the user to select a conceptualization of the particular spatial relationship in question prior to analysis (Scott and Janikas, 2010, Fortin et al., 2012). Selection of the spatial relationship conceptualisation depends on what is being measured, and should reflect inherent relationships among the features being analyzed. Common conceptualizations include inverse distance, travel time, fixed distance, nearest neighbours and contiguity (ESRI, 2001). I made use of the inverse distance method, which is one of impedance, or distance decay, where all features influence all other features, but the further away something is, the smaller the influence (Legendre, 1993). I made use of this method since the algorithms for inverse distance are based on the assumption that waterpoints further away are less likely to contribute to a focal waterpoint's neighbourhood than waterpoints closer by. The derivation of the Local Moran's I statistic of spatial autocorrelation is provided in Box 2.1.

The Local Moran's I statistic of spatial association is given as:

$$I_i = \frac{x_i - \bar{X}}{S_i^2} \sum_{j=1, j \neq i}^{n} w_{i,j}(x_i - \bar{X}) \quad (1)$$

where x_i is an attribute for feature i, $\bar{X}$ is the mean of the corresponding attribute, $w_{i,j}$ is the spatial weight between feature i and j, and:

$$S_i^2 = \frac{\sum_{j=1, j \neq i}^{n} w_{ij}}{n-1} - \bar{X}^2 \quad (2)$$

with n equating to the total number of features.

The z_{I_i}-score for the statistics are computed as:

$$z_{I_i} = \frac{I_i - \mathrm{E}[I_i]}{\sqrt{\mathrm{V}[I_i]}} \quad (3)$$

where:

$$\mathrm{E}[I_i] = -\frac{\sum_{j=1, j \neq i}^{n}}{n-1} \quad (4)$$

$$\mathrm{V}[I_i] = \mathrm{E}[I_i^2] - \mathrm{E}[I_i]^2 \quad (5)$$

Box 2.1 Derivation of the Local Moran's I statistic of spatial autocorrelation (Anselin and Cho, 2002)

2.3.3 Analyses of temporal surface water heterogeneity

In order to test the DtW prediction that surface water in KNP is so homogenous that it is only temporally distinct from other periods during drier conditions, I performed identical DtW, Multi-distance Cluster Analyses, and Cluster and Outlier Analyses as those described in section 2.3.2, but over time at two different temporal scales. Firstly, I tested whether temporal variations in DtW, in the scales of waterpoint spatial configuration, or indeed in the cluster/dispersion configurations themselves, could be differentiated among the average, dry

and wet years of the study period. Secondly, I compared whether either the spatially implicit or explicit analyses could reveal changes in the patterns of surface water heterogeneity over the course of the dry season, rather than only at the onset of the late dry season as exhibited by previously demonstrated DtW patterns over the broader KNP (Smit and Grant, 2009). In order to do this, I categorized the dry season into three roughly equal categories on a purely exploratory basis, reasoning that the first month into the dry season (May) was unlikely to exhibit significantly different patterns from the preceding wet season that had just come to an end, and dividing the remaining months into two equal 2-month periods. This resulted in three dry season components over which to explore changes in DtW and surface water configuration associated with the progression of the dry season, i.e. early (May), mid (June – July) and late (August – September) dry season.

2.3.4 Assessing the effect of artificial water provision on surface water heterogeneity

To test the DtW prediction that artificial water provision only has a dampening effect on spatio-temporal surface water heterogeneity during extreme drought conditions, I repeated the spatial analyses described in sections 2.3.2 and 2.3.3 for a scenario with only natural sources of surface water present in the study area. I first determined the peak scale of patchiness of natural surface water distribution, and then quantified the pattern of natural waterpoint spatial configuration at this peak scale. I then compared the patterns of natural waterpoint configuration to the full water dataset that included artificial sources of water, to assess how water provision had altered the spatial configuration of natural waterpoints.

2.4 Results

2.4.1 Spatial patterns of surface water heterogeneity in a landscape with abundant water sources

DtW patterns in this drier part of KNP concurred with previous studies of water availability in KNP (Redfern et al., 2003, Redfern et al., 2005, Smit et al., 2007a, Smit et al., 2007b, Smit et al., 2007c, Grant et al., 2008, Smit, 2011) that suggested an homogenous spatial distribution of waterpoints relative to the maximum daily foraging ranges of elephants. Less

than 40% of the study area was beyond 4 km from surface water and up to 20% was as close as 2 km, even during the driest period of the study in late 1998 (Figure 2.4). Very few parts of the landscape (<5%) were 8-16 km from water, with nowhere >16 km (Figure 2.4). Nevertheless, the spatial configuration of surface water in the study area was significantly patchy over a range of scales (500 – 18 000 m;

Figure 2.5). Despite 60-90% of waterpoints being randomly configured (depending on the scale and period under investigation), the broader scales of patchiness reflected the concentration of surface water in the riparian component of the landscape, while finer scales of patchiness indicated heterogeneous spatial configurations of surface water within the riparian zone itself (Figure 2.6).

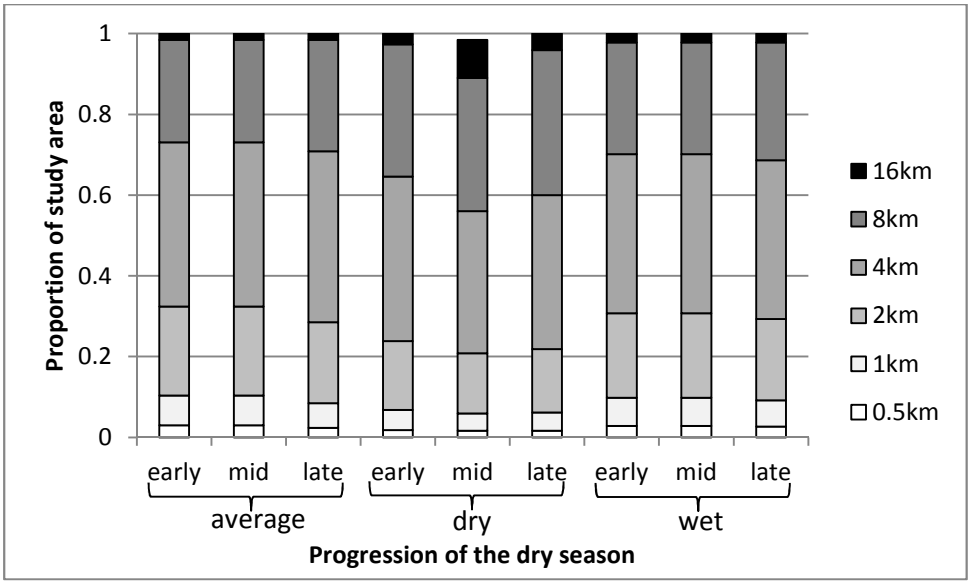
2.4.2 Temporal patterns of surface water heterogeneity over the course of the dry season and among years with varying rainfall

Distances to water changed little in any of the distance categories as water dried up over the course of the dry season, with negligible increases even in the areas furthest from water (8-16 km; Figure 2.4). Instead, temporal heterogeneity in DtW patterns was higher among years with varying rainfall than over the course of the dry season. These changes in patterns of DtW were primarily through considerable reductions (up to 50%) in the areas closest to water (<500 m), but only small increases (from 2 - 5%) in the areas most remote from water (8-16 km), as natural water sources dried up during the driest year (Figure 2.4). However, despite a two-fold difference in annual rainfall (450 mm vs 950 mm), no differences in dry season DtW patterns could be detected between the average and wet years of the study period (Figure 2.4). Again, these results concur with prior studies conducted over the entire KNP. DtW simply reverted to pre-dry year patterns after good rain was received, suggesting a simple linear relationship between rainfall and DtW patterns. However, it should be remembered that the wet year was preceded by a very dry year (950 mm vs 250 mm), suggesting that the depleted water table would first have had to be replenished before it would have been possible for water to persist on the surface and hence reduce DtW.

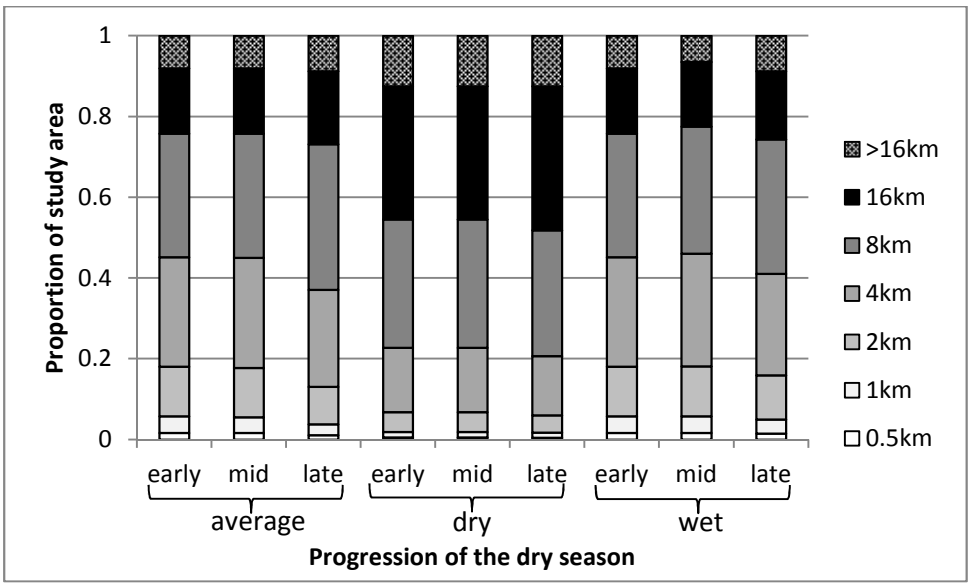
Waterpoint spatial configurations also varied over time. Patchiness in waterpoint spatial configuration was highest (at a scale of 10 km) during the driest part of the study period (mid- to late dry season of the driest year;

Figure 2.5). Even this highest level of patchiness in waterpoint spatial configuration, however, was well within the maximum daily foraging ranges of elephants, making it difficult to assess the functional heterogeneity of these patterns. Nevertheless, in contrast to the small amount of temporal variation in DtW patterns, the spatial configuration of individual waterpoints varied markedly over time at this peak scale, both over the course of each dry season, as well as among the average, dry and wet years of the study period (Figure 2.6). This reflected the difference between the spatially implicit and explicit analysis techniques. Whereas the DtW (spatially implicit) technique treated several clustered waterpoints or a single waterpoint in one distance category equally, the spatially explicit technique was able to detect changes in these spatial arrangements. Unexpectedly, however, the detected temporal changes in surface water heterogeneity were not due to an increase in the number of isolated/dispersed waterpoints associated with increased DtW during drier conditions, nor through a concommitant increase in clustered waterpoints during wetter conditions. Instead, the spatially explicit analyses revealed a more complex pattern of temporal surface water heterogeneity that was non-linearly associated with varying rainfall.

Specifically, the analyses illuminated the primary role played by the persistence of key waterpoints in determining changes in surface water configurations. For example, drier conditions led to an increase in *randomly spaced* waterpoints, as natural waterpoints that had previously played a key role in the formation of waterpoint clusters, dried up (Figure 2.6). The dispersed/isolated waterpoints also decreased in number as the drying up of key natural waterpoints left the remaining water with a random distribution (Figure 2.6).

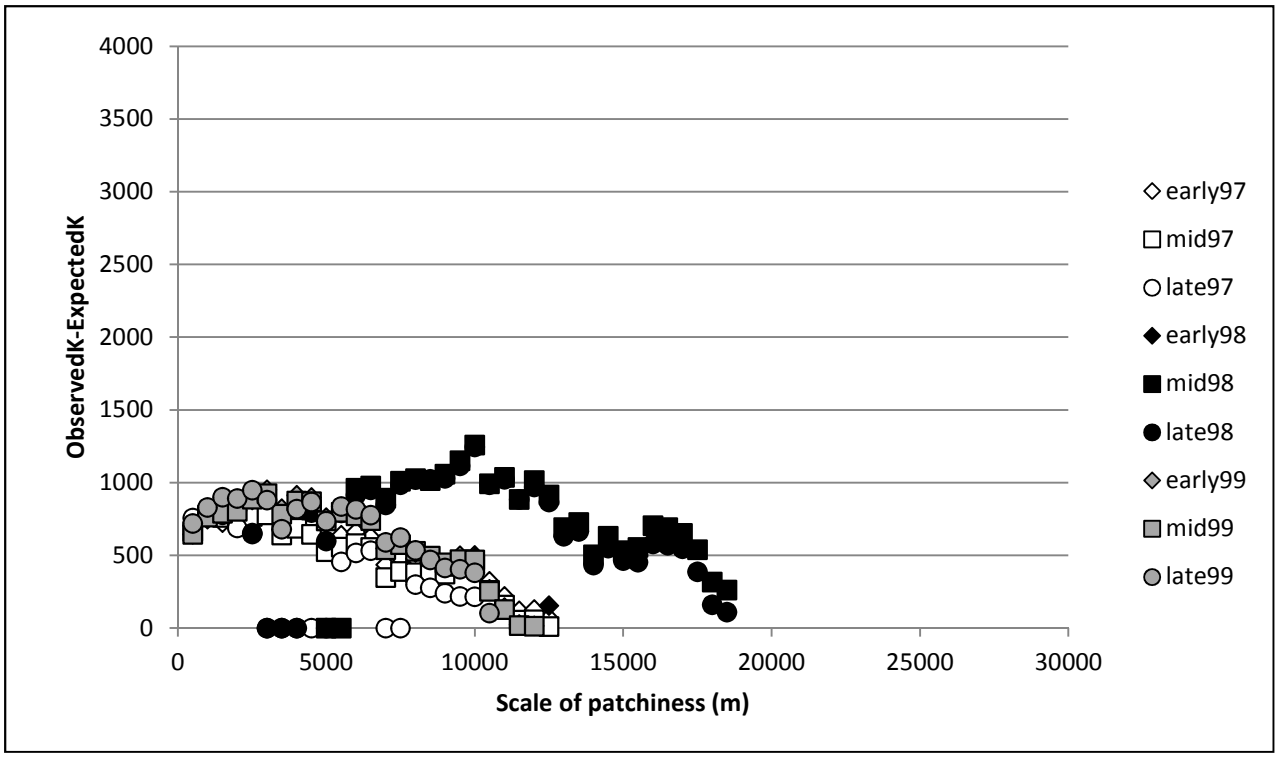


(i)

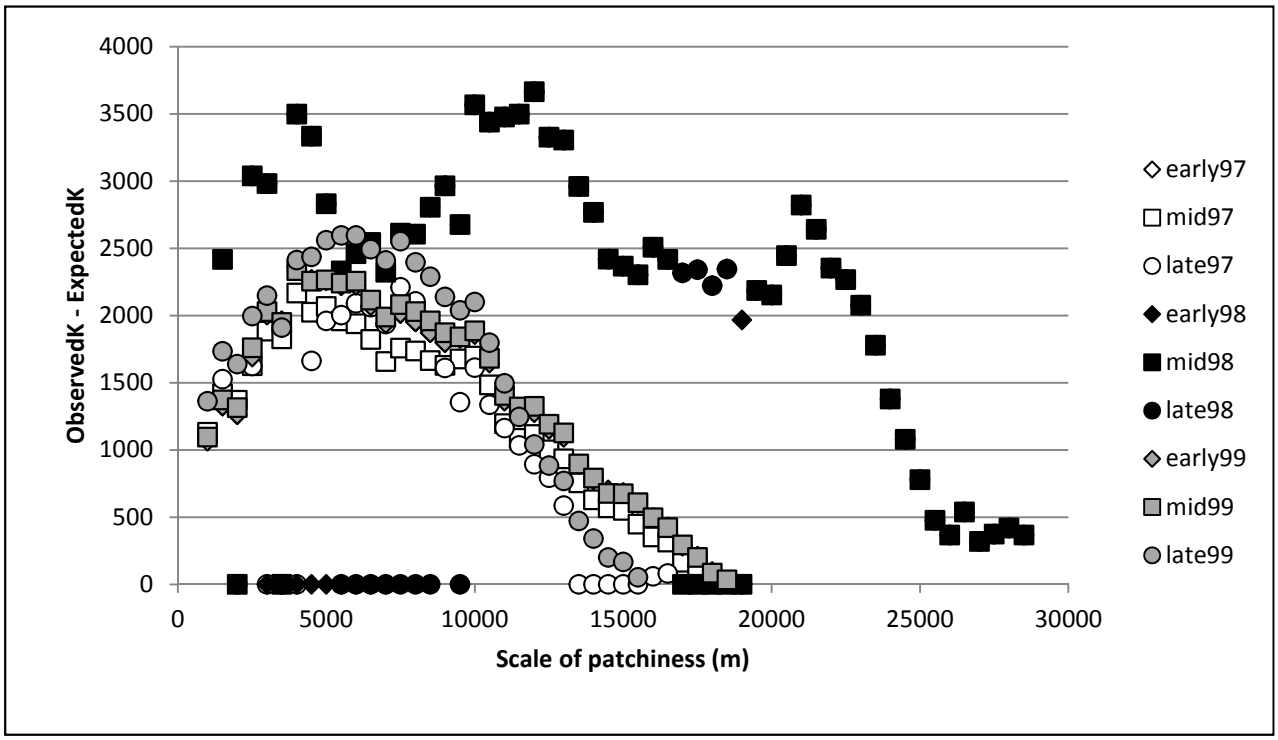


(ii)

Figure 2.4 Patterns of distance to (i) all sources and (ii) natural source of surface water in the northern region of Kruger National Park, over the course of three dry seasons of varying rainfall (average, dry and wet, in relation to mean annual rainfall). Distances in the graphs' legends are the upper limits of each distance class



(i)



(ii)

Figure 2.5 Scales of surface water heterogeneity (as measured by `Multi-Distance Spatial Cluster Analysis (ESRI, 2001)), over three dry seasons (1997-1999) in the far northern region of KNP, (i) with and (ii) without artificial water supplies. Only spatial patterns that differ significantly from a random distribution have been plotted. Larger differences between observed and expected K-values signify a greater magnitude of patchiness at that scale

Furthermore, at this peak scale of patchiness (10 km) the drier conditions changed the spatial configuration of a small number of otherwise randomly distributed waterpoints, into clustered waterpoints (notably the Joao-Spiriwori waterpoint complex near the confluence of the Bububu and Shingwedzi rivers; Figure 2.6). Although, some clustered and randomly distributed waterpoints did become isolated or dispersed during drier conditions, these were mostly along the western border of the park, where the presence of the boundary fence precluded any water outside of the park from functionally contributing to their spatial configuration (Figure 2.6).

Changes in waterpoint spatial configuration during the dry year were not simply reversed at the onset of rains in the subsequent wet year (Figure 2.6), indicating a more complex relationship with rainfall than suggested by DtW patterns. For example, even though the number of clustered waterpoints increased again along the Shingwedzi River during the wet year, none of the previously clustered waterpoints elsewhere in the study area reverted back from their shift to a random distribution during the dry year (Figure 2.6).

2.4.3 Influence of artificial water provision on patterns of distance to water and waterpoint spatial configuration

Removal of artificial water sources from the analyses halved the proportion of the landscape in the smallest distance classes (<0.5 km and 0.5 – 1 km), while increasing the larger distance classes (8 – 16 km and >16 km) by up to five times (Figure 2.4). However, in accordance with the previous DtW studies, even after all artificial water sources were removed from the analysis, only a small portion of the landscape (5 - 15%) was >16 km from surface water (Figure 2.4). Hence the low levels of spatial and temporal surface water heterogeneity revealed by the DtW patterns above (section 2.3.1 and 2.3.2) could not be solely attributed to the widespread provision of artificial water sources in the study area. This supports the contention of the previous studies that further borehole closures, even in this driest part of the park, would do little to increase parts of the landscape inaccessible to elephants. Furthermore, water provision did not change the fact that DtW patterns only differed (with increased proportions of the landscape further away from water) during the driest year, with few differences in DtW between average and wet years (Figure 2.4).

In contrast, the spatially explicit analyses revealed several notable differences in surface water heterogeneity associated with water provision in the study area. Firstly, under a natural

surface water scenario, water configuration was significantly patchy over a larger range of scales (500 – 29000 m) than in the presence of artificial water sources (500 – 18000 m; Figure 2.5). Moreover, the peak scale of surface water patchiness increased from 10-km to 12-km for natural surface water, while the magnitude of spatial patchiness was up to three times higher (Figure 2.5). In addition, the three peaks in natural surface water heterogeneity (Figure 2.5) were reduced to a single peak in the presence of augmented water supplies (Figure 2.5). Finally, while clusters of natural waterpoints only occurred along the Shingwedzi River (Figure 2.7), the addition of artificial water sources created clusters of waterpoints along the Bububu and lower reaches of the Mphongolo rivers as well (Figure 2.8).

Water provision also had a dampening effect on temporal variations in the scales and spatial arrangements of waterpoints. In the first instance, artificial water sources reduced the difference in magnitude of patchiness between dry and wetter years by up to four times (Figure 2.5). The dampening effect of water provision was also apparent by means of fewer changes in the spatial configurations of waterpoints associated with varying rainfall conditions (Figure 2.7). Notably, certain natural waterpoints that were only clustered during the driest year (for example, the Joao-Spirowiri waterpoint complex along the Shingwedzi River; Figure 2.7) remained consistently clustered over time as a result of water provision (Figure 2.8).

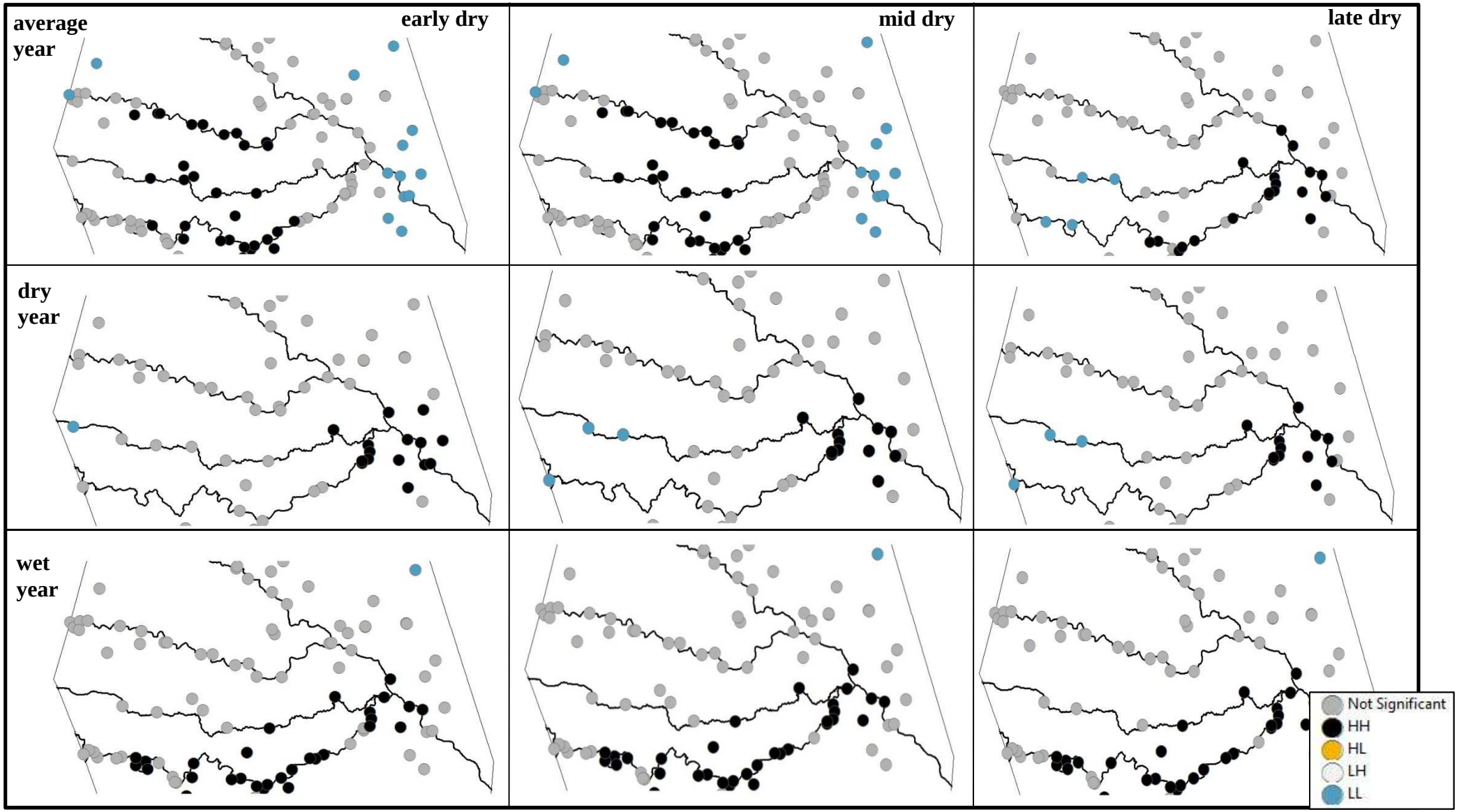


Figure 2.6 Patterns of waterpoint spatial configuration over the course of three dry seasons, quantified at the peak scale of patchiness (10 km) by the Anselin's Local Moran's I index of local spatial autocorrelation (HH = clustered waterpoint in a clustered waterpoint context; HL = clustered waterpoint in a randomly distributed or dispersed waterpoint context; LH = dispersed waterpoint in a randomly distributed or clustered waterpoint context; LL = dispersed waterpoint in a randomly distributed or dispersed waterpoint context)

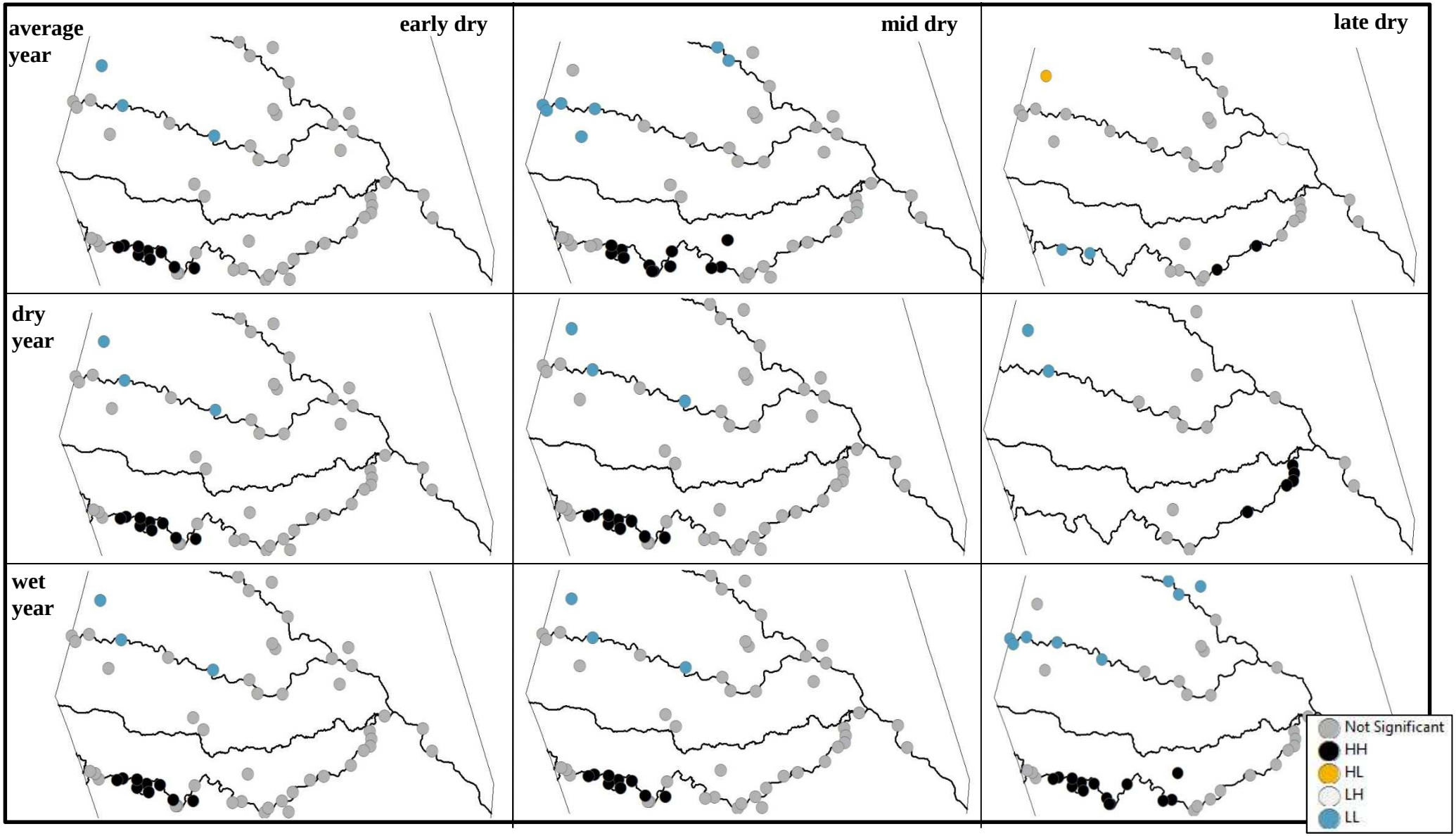


Figure 2.7 Patterns of natural waterpoint spatial configuration over the course of three dry seasons, quantified at the peak scale of patchiness (12 km) by the Anselin's Local Moran's I index of local spatial autocorrelation (HH = clustered waterpoint in a clustered waterpoint context; HL = clustered waterpoint in a randomly distributed or dispersed waterpoint context; LH = dispersed waterpoint in a randomly distributed or clustered waterpoint context; LL = dispersed waterpoint in a randomly distributed or dispersed waterpoint context)

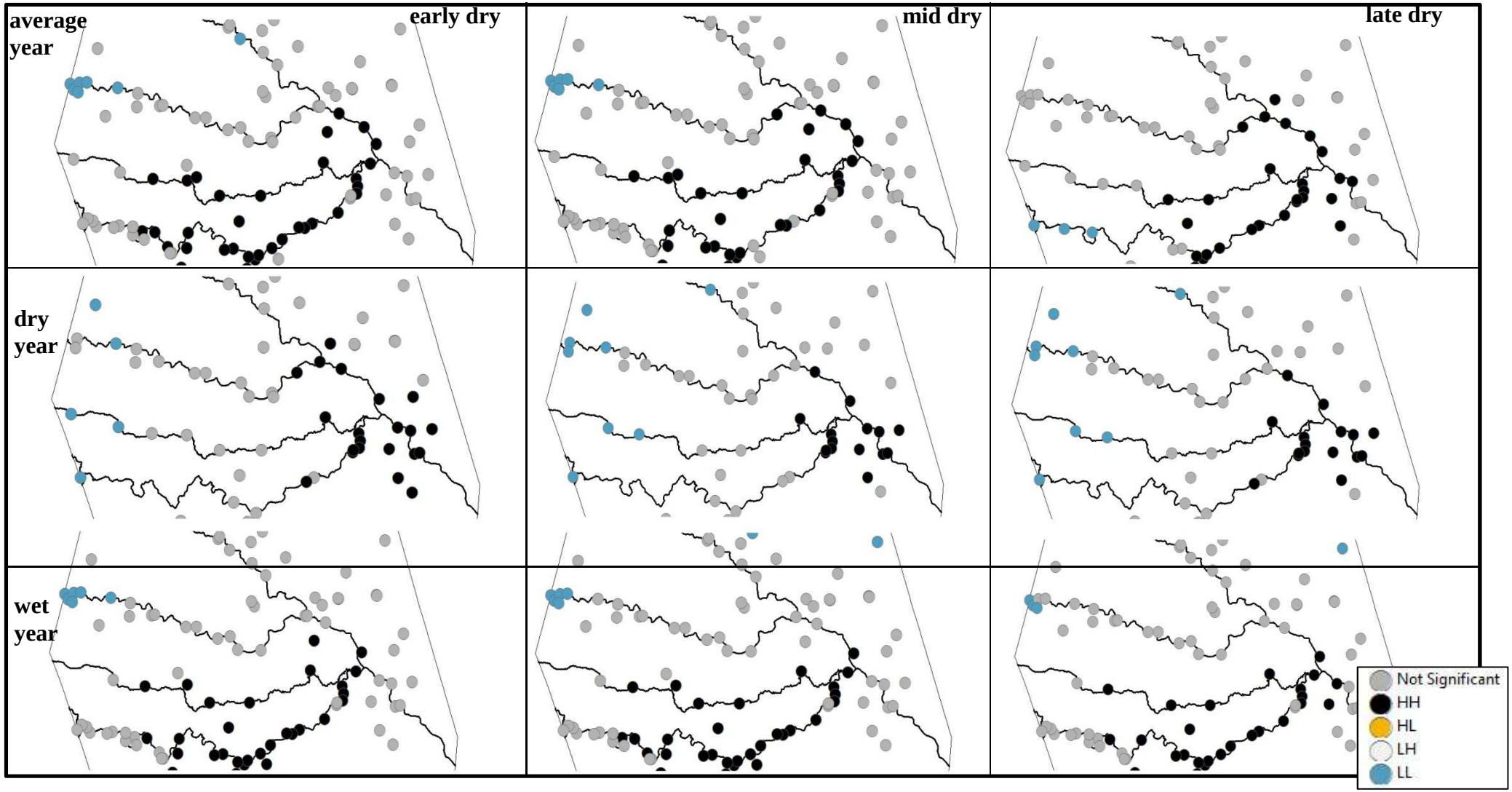


Figure 2.8 Patterns of waterpoint spatial configuration for all sources of surface water over the course of three dry seasons, quantified at the peak scale of natural water patchiness (12 km) by the Anselin's Local Moran's I index of local spatial autocorrelation (HH = clustered waterpoint in a clustered waterpoint context; HL = clustered waterpoint in a randomly distributed or dispersed waterpoint context; LH = dispersed waterpoint in a randomly distributed or clustered waterpoint context; LL = dispersed waterpoint in a randomly distributed or dispersed waterpoint context)

2.5. Discussion

This study compared the traditional spatially implicit means of analysing surface water heterogeneity, with a spatially explicit method that incorporated a scaled and contextual perspective of waterpoint spatial configuration. The spatially explicit approach exposed spatial and temporal variability of the surface water template available to elephants in this semi-arid savanna, that were not apparent using previous DtW analyses. Even though DtW measures suggested homogenous surface water distribution, the spatial configuration of waterpoints was patchy across a wide range of scales (500 – 18 000 m), reflecting variation in the proportion of clustered, dispersed and randomly configured waterpoints. Recognising waterpoints' patch context in this way revealed changes in spatial configuration not only during the driest periods (as with DtW) but also between average and wet years. These changes in spatial configuration were not linearly related to rainfall as with DtW patterns, but rather depended on the persistence or drying up of key waterpoints that contributed to waterpoint configuration patterns. As a result, this work also illustrated that simple, spatially implicit DtW measures have underestimated the extent to which artificial water supplies have dampened surface water heterogeneity in this landscape. These findings emphasize the importance of a scaled, contextual perspective for quantifying resource heterogeneity, to form the basis of a heterogeneity approach.

2.5.1 Understanding the surface water template for elephant disturbances

Comparing spatially implicit and explicit measures of surface water heterogeneity along the ephemeral rivers in northern KNP revealed several key differences in the resultant surface water patterns. By treating all waterpoints within a single buffer distance from a focal point as one (Moilanen and Nieminen, 2002), the spatially implicit DtW approach provides an aggregate measure for each distance band in the analysis of surface water heterogeneity. Previous studies of DtW have rested on the assumption that such an aggregate measure is an adequate descriptor of surface water heterogeneity.

In contrast, the findings documented here provide supporting evidence for one of the key principles of the Hierarchical Patch Dynamics Paradigm (Kotliar and Wiens, 1990) – that understanding spatial heterogeneity requires the explicit recognition of both scale and context. Specifically, this principle was illustrated by the fact that DtW analyses underestimated temporal changes in patterns of surface water heterogeneity that were exposed by the

contextual perspective of waterpoint spatial configuration. By differentiating among waterpoints with clustered, dispersed and random spatial arrangements, the spatially explicit approach illuminated changes in surface water heterogeneity over time that may well represent a dynamically shifting mosaic (Bormann and Likens, 1979, Pickett and White, 1985, Pickett et al., 1989, Wiens, 1996) of surface water distribution, that potentially reduces elephant return times to otherwise well-visited parts of the landscape. Such a mechanism has been proposed as a means to provide landscapes with metastability (Bormann and Likens, 1979, Wu and Loucks, 1995) from disturbances over the longer term. If patches of accumulated elephant impact remain distinct from one another, and elephant return intervals to these patches are long enough relative to vegetation regeneration, manipulating surface water heterogeneity could provide such metastability. However, whether the particular scales of waterpoint configurations in this landscape are adequately differentiated at scales that will generate elephant spatial responses remains unknown.

By quantifying surface water heterogeneity in a spatially explicit fashion, the heterogeneity approach also made it possible to infer the underlying dynamics of waterpoint spatial configurations associated with varying rainfall conditions. The results demonstrated that the particular spatial arrangement of waterpoints was contingent upon the persistence or drying up of key waterpoints in the landscape, rather than on an overall retention or loss of a proportion of the total water source. Moreover, these changes in waterpoint spatial arrangements were not simply reversed when rainfall reverted back to wetter conditions. Hence, rather than being linearly related to the current seasons' rainfall as is the case with DtW (Cronje et al., 2005), these contingencies generated emergent patterns of surface water heterogeneity. Such emergent patterns are a feature of complex systems (Levin, 1998), and stress the importance of using analytical methods that are able to expose ecological contingencies (Kay and Schneider, 1995, Milne, 1998).

2.5.2 Implications for the use of water provision to enhance surface water heterogeneity

A key challenge of preserving biodiversity in any managed landscape is to incorporate natural levels of spatial and temporal heterogeneity into management schemes (Pearson et al., 1996). While complete closure of artificial water sources in KNP held initial promise with respect to confining elephant effects on biodiversity (Owen-Smith, 1996), water availability studies concluded that water provisioning policies had had a negligible dampening effect on surface

water heterogeneity at scales relevant to the generation of elephant disturbances, at least where few portions of the landscape remain inaccessible to elephants (Redfern et al., 2005, Smit et al., 2007a, Smit et al., 2007c, Smit and Grant, 2009, Smit and Ferreira, 2010).

In contrast, this study has revealed that even where maximum distances to water can't be changed substantially through closure of artificial water sources, the scales and spatial configurations of individual waterpoints, as well as the persistence of particularly configured water resource patches (groups of waterpoints), can be strategically manipulated through water provisioning. Specifically, my findings indicate that, rather than simple closure of all artificial water supplies, surface water heterogeneity could be enhanced by changing the spatial configurations of waterpoints through strategic placement or closure of key waterpoints in the landscape. Spatial analysis tools that can optimize a required spatial configuration of features are already in existence for such strategic surface water scenario planning (Legendre and Fortin, 1989, Fortin et al., 2006, Scott and Janikas, 2010, Fortin et al., 2012). Such optimization studies also hold promise to improve our understanding of the strategic use of various water provisioning scenarios, and their outcomes for surface water heterogeneity at various scales.

The current dogma that precludes further scope for water provision was developed on the basis that elephant foraging behaviour is only constrained where distances between water sources are small relative to their maximum daily foraging ranges. However, should the spatial configuration of waterpoints provide a functional template for elephant disturbances, by generating a range of disturbance return intervals to previously well-visited patches, there may well be further scope for water provision to manipulate elephant impacts in semi-arid savannas with relatively abundant water sources. If this proves to be the case, the move away from using water provision to manipulate elephant impacts where large portions of the landscape remain accessible to elephants, will be a good example of the risks of obtaining a Type II error where emergent scales, context and contingency are not incorporated into studies of complex systems (Mills et al., 2006). Understanding the scales of elephant response to surface water configuration is required in order to determine whether the use of water provision was prematurely dismissed in landscapes where foraging is not constrained by large distances between water and forage resources.

2.5.3 Implications for understanding resource heterogeneity in other systems

An inherent feature of complex systems is the key role of scale, context and contigency in producing emergent ecological patterns (Kay and Schneider, 1995). Hence, although the particular scales and spatial configurations of surface water are likely to be different at the higher end of KNPs rainfall gradient, and in other systems, the spatially explicit approach presented here is one that can be used to quantify the heterogeneity of surface water, or other resources, in other systems. Maximum distances to resource patches are likely to underestimate resource heterogeneity where the spatial configurations of these patches vary. Moreover, the locations and spatial configurations of resource patches may well vary over time, even when the scales of resource patchiness do not. Consequently, spatially explicit approaches are favourable over spatially implicit methods, when the goal is to understand the spatial and temporal parameters of resource heterogeneity (Moilanen and Nieminen, 2002).

Nevertheless, the functional implications of any resource heterogeneity revealed will be dependent on the nature and scales of organism responses to these resource patterns (Wiens, 2000), and the tradeoffs that these organisms make to reach foraging and other resources (Dunning et al., 1992). Understanding these underlying behavioural mechanisms would improve our ability to develop new, innovative management practises for modifying patterns of herbivory (Bailey et al., 1996), and hence the associated effects on biodiversity. In the KNP landscape it remains important to assess whether the insights about surface water heterogeneity gained here represent functional heterogeneity for elephants through their spatial responses to the varied distribution of surface water, and the resultant distribution of elephant impacts. These issues will be investigated in the following two chapters.

Chapter Three - The role of surface water heterogeneity in elephant patch choice and feeding in a landscape with abundant water sources

3.1 Introduction

Understanding how heterogeneity affects ecological systems requires an understanding not only of environmental patterns, but also of how organisms respond to different forms of heterogeneity (Wiens et al., 1976, Milne, 1989, Johnson et al., 1992, Wu and Hobbs, 2002). These organismal responses are underpinned by three spatial mechanisms – movement, patch choice and perceptual scale (Wiens, 2000). Organisms move over the landscape to make choices among patches in response to variable resource availability (O'Neill et al., 1988, Owen-Smith and Ogutu, 2012), which they perceive at different scales (Senft et al., 1987, Bailey et al., 1996). As a result, resource heterogeneity is fundamental to variability in the movement of organisms and their patch selection amongst scales (Boyce et al., 2003).

Spatial memory allows herbivores to improve foraging efficiency by selecting among previously visited patches of varying quality (Bailey et al., 1996). These patch choices by herbivores determine how the disturbances created by their activities are distributed across the landscape, as well as how these disturbances vary over time (Kareiva, 1983, Wiens, 2000). The factors and perceptual scales that determine these patch choices are therefore at the heart of whether organismal responses to resource availability produce disturbances that are widespread or localised, potentially allowing for spatial and temporal refuges where impact tolerant species may persist (Pearson et al., 1996). Hence, even where disturbances are locally severe, the generation of dynamic patch mosaics (Bormann and Likens, 1979, Pickett and White, 1985) through heterogeneous disturbance regimes can provide metastability at broader scales (Wu and Loucks, 1995). However, the environmental parameters that are most important for determining organisms' spatial and temporal responses to resource heterogeneity at different scales are not well known (Turner et al., 1997). Elucidating these mechanisms, and the factors that drive them, therefore remains a key challenge for ecology and protected area management.

Elephants are agents of change (Laws, 1970) that are considered to be ecosystem engineers (Jones et al., 1994), since the consequences of their feeding behaviour can span entire landscapes (Van Wyk and Fairall, 1969, Caughley, 1976, Coetzee et al., 1979, Barnes et al., 1994). It is this capacity for widespread ecosystem change that creates concern that elephants could ultimately cause undesirable or even catastrophic regime shifts. However, if elephant feeding is constrained to certain patches in the landscape, or to certain times, the heterogeneity paradigm predicts that the existence of such a patch mosaic of elephant impacts would provide metastability at the landscape level, thereby preventing a regime shift (Scheffer et al., 2001, Folke et al., 2004). This concept provides the basis of KNP's new elephant management philosophy, which focuses on managing a range of elephant disturbance levels in different parts of the landscape, rather than keeping the elephant population at a perceived carrying capacity (Whyte et al., 1999, Whyte, 2004).

Consequently, understanding the conditions that may allow for spatial and temporal refuges from elephant disturbance is important for biodiversity management in savannas (O'Connor et al., 2007), and requires knowledge of the drivers of elephant patch choice, patterns of feeding within these patches, and how these change in response to fluctuations in critical resources. Surface water is a critical resource for elephants, since they require drinking water every 2-3 days. Elephants must therefore make trade-offs between the energetic costs of finding forage and drinking water. Hence, in landscapes where distances between water sources exceed the maximum daily foraging ranges of elephants (ca. 20 – 30 km; Owen-Smith (1996)), it is well known that elephant movements and foraging are confined to patches in the vicinity of surface water, particularly during the dry season (Western, 1975, Western and Lindsay, 1984). This leaves substantial portions of the landscape remote from water with low levels of elephant disturbance. Since elephants are sexually dimorphic, this expression of water dependence may be even more marked for elephant cows, who are 25% smaller than their male counterparts and hence have relatively higher energetic costs associated with movement (Owen-Smith, 1988). In addition, the relatively greater energetic requirements of the smaller individuals present in elephant breeding herds, together with the presence of pregnant or lactating females (Stokke and Toit, 2000), place larger energetic constraints for patch selection on these breeding herds, compared with their generally solitary male counterparts (Owen-Smith, 1988, Stokke and Toit, 2000, Greyling, 2004). As a result, roaming distances of up to 6 km from surface water can have significant impacts on the survival of recently weaned elephant calves (Young and Van Aarde, 2010).

However, where distances between water sources are so small that the entire landscape is effectively accessible to elephants, weaker responses to surface water distribution have been reported (Redfern et al., 2003, Smit et al., 2007c). These findings have led to a general consensus that surface water is not heterogeneous enough in these landscapes at scales relevant to elephant patch choice and feeding (Redfern, 2002, Redfern et al., 2005, Smit et al., 2007a, Grant et al., 2008). Consequently, these studies have challenged whether it is possible for spatial refuges from elephant disturbance to exist there (Smit and Grant, 2009). As a result, manipulation of artificial water provision as a means of inducing patchy elephant impacts in these landscapes is currently considered unfeasible (Smit et al., 2007a, Grant et al., 2008).

In the previous chapter I demonstrated that the preponderance of spatially implicit distance-to-water (DtW) studies has limited our understanding of the heterogeneity of the surface water resource, by ignoring the role of spatial context and scale in generating patterns of surface water heterogeneity (Chapter 2). Specifically, even within landscapes where DtW appears to be homogenous at scales relevant to elephant maximum daily foraging ranges, there is marked variation in the spatial configuration of point water sources over a range of scales (Chapter 2, section 2.3.1). Moreover, the spatial configurations of these waterpoints varies to a much larger extent over time than fluctuations in DtW (Chapter 2, section 2.3.2). However, gaining an understanding of the scales and patterns of surface water heterogeneity to which elephants respond is required in order to evaluate whether variable waterpoint spatial configurations represent functional heterogeneity to elephants.

For example, does surface water heterogeneity play a role in elephant patch choice and feeding, beyond simple considerations of DtW? Specifically, do elephants respond differently to the varied spatial context of patches provided by neighbouring waterpoints, and if so, at what scale(s) are these responses manifest? Furthermore, do the energetic considerations associated with elephant sexual dimorphism modulate the ways in which surface water heterogeneity constrains elephant use of the landscape? The previous chapter demonstrated that the particular placement of artificial water sources altered the spatial configurations of waterpoints. However, in order to assess whether there is still scope for strategic water provisioning in landscapes with relatively small distances between water sources, it is important to understand whether natural water modulates elephant responses to surface water heterogeneity.

In this chapter, I address these questions by investigating:

i) the scale(s) of elephant patch choice and feeding in the drier region of northern KNP;
ii) the roles of DtW and waterpoint spatial configuration in determining elephant patch choices, and how this translates into spatial patterns of elephant feeding;
iii) how these patterns differ for elephant bulls and herds, and over time with varying rainfall conditions; and
iv) how natural or artificial sources of surface water modulate these patterns of patch choice and feeding

By improving our understanding of elephant responses to this more comprehensive quantification of surface water heterogeneity that incorporates scale and patch context, I aim to address an important knowledge gap identified in the preceding chapter – understanding what patterns and scales of surface water heterogeneity produce functional heterogeneity for elephant space use responses. Moreover, I build upon the heterogeneity approach developed in the preceding chapter by adding a spatially explicit regression technique for exploring the drivers and modulators (Pickett et al., 2000, Pickett et al., 2003) of these responses.

The riparian zones of ephemeral rivers in northern KNP provide an ideal opportunity to explore this issue, for a number of reasons. Firstly, since few parts of this landscape exceed 15 km from water (Gaylard et al., 2003), distances between water sources do not impose a constraint on elephant maximum daily foraging ranges (Redfern et al., 2003). Secondly, riparian zones provide critical sources of forage and surface water during resource bottleneck periods, and elephants therefore focus their activities here during the dry season (Western, 1975, Western and Lindsay, 1984, Owen-Smith, 1988). Since elephants must leave the adjacent upland areas to visit the riparian zone, non-random points of movement across the riparian-upland boundary (entry/exit points) represent patch choices (as defined by (Wiens et al., 1993)). Moreover, elephants make use of multiple critical resources in the riparian zone, e.g. water for drinking and bathing (Wackernagel, 1993, Rogers, 1997b, Smit and Ferreira, 2010), evergreen forage (Owen-Smith, 1988, Greyling, 2004), and shade for temperature regulation (Kinahan et al., 2007). Since surface water along ephemeral rivers represents point sources of water along the otherwise dry river courses (Gaylard et al., 2003), it is possible to infer whether the presence of water at these points is associated with where elephants choose to make use of the riparian zone.

3.2. Methods

The heterogeneity framework developed in the previous chapter (Figure 2.2) formed the basis of my approach for this chapter. As such the first requirement was to assess whether elephant movements across the riparian-upland boundary were randomly distributed or patchy, and if so, at what scale(s) this patchiness was exhibited. The methodology for this first step therefore mirrored the way in which I quantified surface water heterogeneity in the first chapter. I inferred riparian patch choice through tests for significantly patchy clusters of elephant movement across the riparian-upland boundary. Advancing our understanding of patterns of elephant spatial response also requires knowledge of the underlying processes or causes of these patterns. In this case, I was interested in evaluating what role the more comprehensive, spatially explicit perspective of surface water heterogeneity might play in determining patterns of elephant space use. As demonstrated in Chapter 2, spatial autocorrelation is a feature of complex, heterogeneous systems that can be used to identify underlying spatial processes. Therefore, apart from identifying the pertinent scales for analyses, spatial autocorrelation can also be used to explore the drivers of these spatial patterns (Legendre, 1993, Fortin et al., 2006, Fortin et al., 2012).

3.2.1. Quantifying elephant patch choice and feeding

Quantifying elephant patch choice and feeding comprised two key steps (Figure 3.9). The first step involved field observations of where elephants entered and left the riparian zone during visits to this part of the landscape, as well as observations of how much feeding took place as they moved through various patches in the riparian zone. The second step involved spatial analyses to determine whether these elephant movements across the riparian-upland boundary were randomly distributed or patchy, and how closely the amounts of feeding matched these movement patterns.

Field observations of elephant movement across the riparian-upland boundary

I recorded the locations of elephant visits to the riparian zone along two dirt roads of approximately 40 km each running parallel to the Shingwedzi and Phugwane rivers in northern KNP (Figure 3.10). A short section of the Mphongolo River also occurred along the Phugwane transect (Figure 3.10), but due to its proximity to the Phugwane River and for ease of interpretation it will be considered together with the portion of the transect along the Phugwane

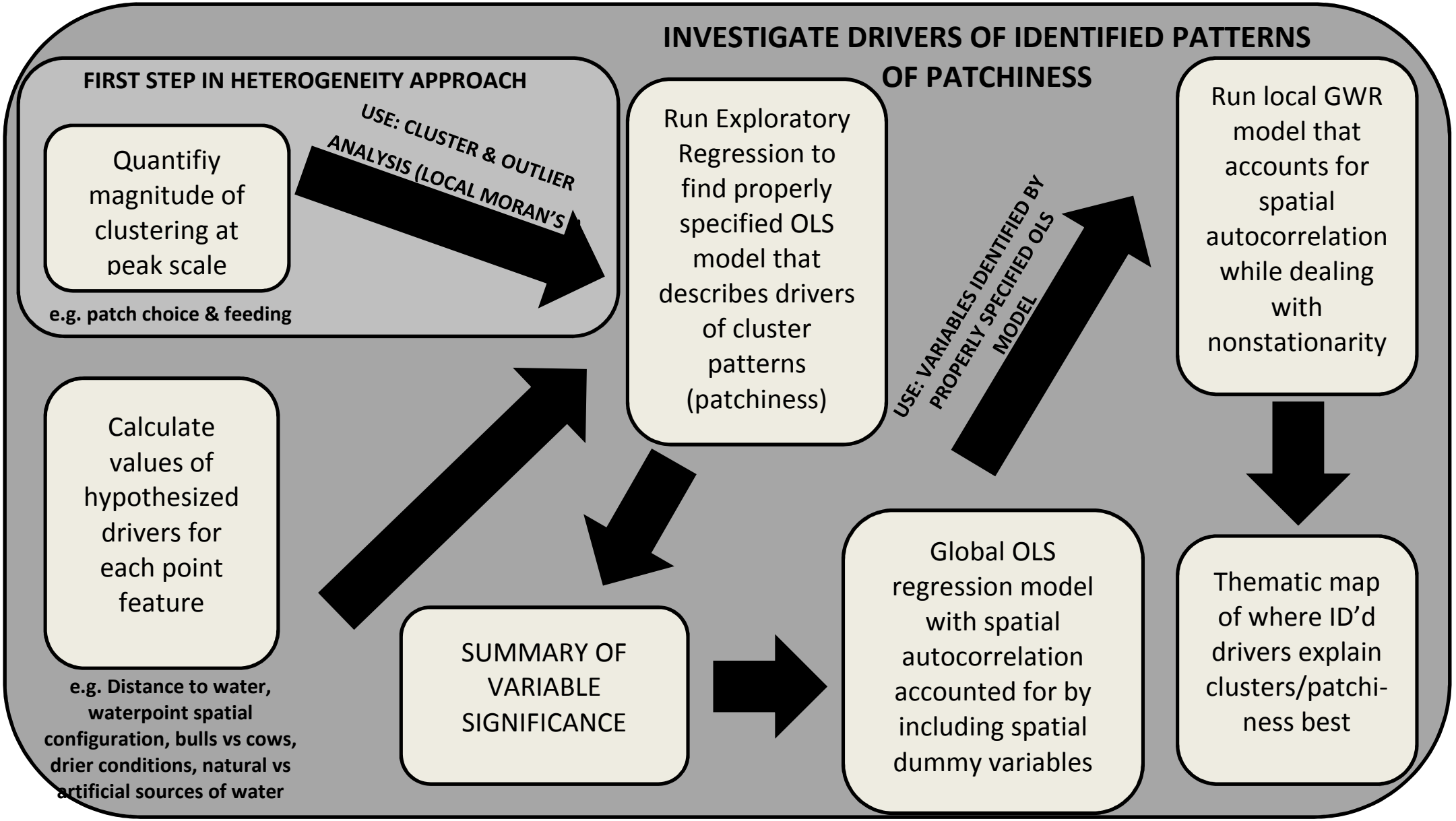


Figure 3.9 - Diagrammatic representation of the second component of the heterogeneity approach - investigating the drivers of heterogeneity through a local spatial regressiontechnique (Geographically Weighted Regression). The steps in the process proceed from left

River. The dirt roads served as transects situated more or less on the boundary between the riparian zone and the adjacent upland areas. The riparian zone was distinguished from the adjacent interfluves as the area from the macrochannel floor, including the adjacent vegetated macrochannel banks, and up to the point where the characteristic riparian woody species such as *Diospyros mespiliformis*, *Philonoptera violacea* and *Croton megalobotrys* were replaced by near monospecific stands of *Colophospermum mopane*, characteristic of the adjacent upland area in KNP's northern region (Venter et al., 2003).

The existence of the dirt roads alongside the river courses made it possible for an expert game tracker to detect elephant tracks, hereafter referred to as spoor, where elephants had moved through the riparian-upland boundary. Together with the expert tracker, I searched for fresh elephant spoor by driving along these spoor transects at least three times a week over the course of three dry seasons (May – October) between 1997 – 1999 (n = 142). Spoor transects were driven at any time of day, but only spoor <24 hours old (as determined by the expert game tracker) were noted to avoid resampling previous days' elephant movements. By examining the sizes and number of spoor located, the expert game tracker was able to identify whether the elephant(s) was solitary (only bulls), part of a bull group (multiple sets of spoor all large in size), or part of a mixed breeding herd (a range of spoor sizes, including the much smaller spoor of juveniles). I assumed that patch choices by different (groups of) elephants recorded on the same day were determined primarily by resource distribution, and that the presence of other elephants played a lesser role. I recorded the location of each set of spoor using a Global Positioning System, along with the gender, group size and direction of movement (where possible).

Amounts of elephant feeding while in the riparian zone

In order to quantify elephant feeding once they had crossed the riparian-upland boundary, I randomly selected a subset of the spoor encountered along the transects. At each of these locations, the expert game tracker located the trail of spoor indicating where elephants had moved through the riparian zone. We followed these trails through the riparian zone from the point at which they had been located along the transect, until they reached the macrochannel floor, noting whether the trail moved towards or away from the macrochannel, or whether it simply wound through the riparian zone parallel to the macrochannel. We searched for any signs of elephant feeding along these trails, including freshly broken branches, uprooted grass tussocks or other plants, pieces of stripped bark, and fresh leaves lying on the ground. The

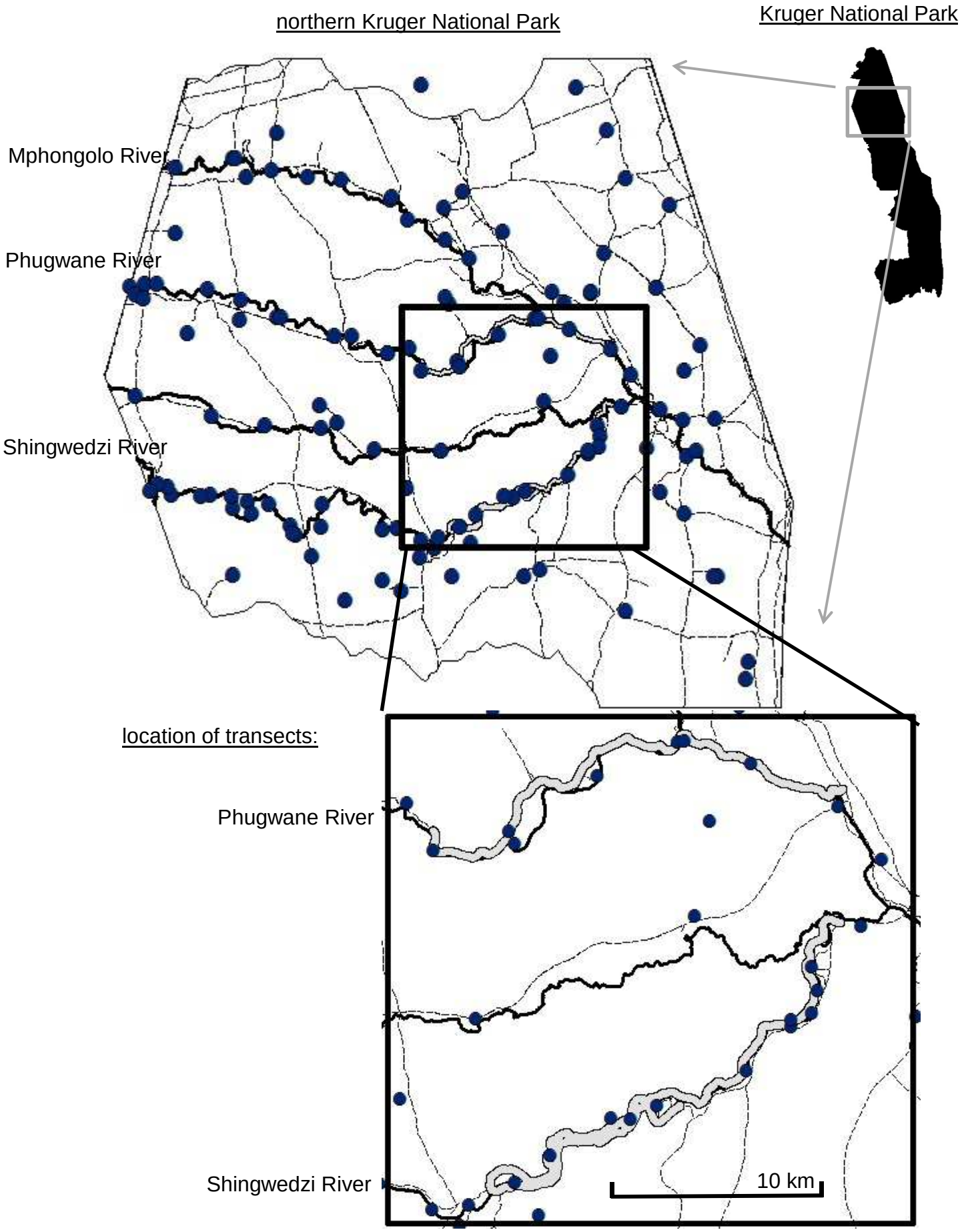


Figure 3.10 Location of the transects undertaken to investigate elephant patch choice and feeding along three ephemeral rivers in northern KNP (solid lines are rivers, stipled lines are roads, dots are all waterpoints, solid grey lines are the transects)

expert game tracker was able to differentiate between feeding by elephants and other herbivores, and could identify the occurrence of elephant feeding through characteristic disturbances to soil even if the entire plant had been removed and consumed.

At each point along the trail at which elephant feeding was identified, a circular "plot" of 5-m radius (approximating the reach of an adult elephant's trunk; (Owen-Smith, 1988)) was searched for additional signs of feeding. In this way, I attempted to reduce the chances of missing elephant feeding that had occurred immediately beyond the trail itself, where elephants reached outward to take in forage with their trunks. Since it was not possible to account for the biomass of vegetation already removed by elephants along the trails through consumption, I simply recorded the number of feeding incidents along each of the feeding trails to serve as an index of the amount of elephant feeding.

Determining the patchiness of elephant movements across the riparian-upland boundary

I inferred that elephants had made patch choices in terms of where to cross the riparian-upland boundary if I could detect non-random clusters of elephant spoor along the transects (Wiens, 2000). I therefore tested whether the points of entry/exit during elephant visits to the riparian zone were randomly distributed or patchy. Firstly, since patchiness is scale-dependent (Turner, 1989, Li and Reynolds, 1995, Pickett and Cadenasso, 1995), and I wished the scales of patch choice to emerge, rather than to impose a particular scale(s) of analysis, I tested the scale(s) at which spoor locations were significantly more clustered or dispersed than a random spatial distribution using the Ripley's K statistic in ArcMap 10.1's Multi-Distance Spatial Cluster Analysis tool (ESRI, 2001). This is the same tool that I had used successfully to identify scales of surface water heterogeneity in the preceding chapter. The tool summarizes how the spatial clustering or dispersion of features changes as the neighbourhood size (or scale of analysis) changes (Scott and Janikas, 2010). In this manner, the tool identifies peaks in the scales of feature patchiness, indicating the presence of underlying spatial processes (Legendre, 1993, Scott and Janikas, 2010), as described in Chapter 2 (section 2.3.3). Since Ripley's K is sensitive to the area of the study region, edge correction factors should be applied or alternative boundary options tested during the analysis (Haase, 1995). Similarly, large-scale heterogeneity of point patterns can bias Ripley's K at small scales. ArcGIS uses Monte Carlo simulations to construct confidence intervals around the null model of CRD, which is particularly useful for study areas with irregular boundaries (Wiegand and A Moloney, 2004), such as the riparian zones in northern KNP.

Having determined whether, and at what scale(s), spoor were clustered, I then quantified the magnitude of clustering of each set of spoor located along the transects, at the peak scale of patchiness that had been determined by the Multi-Distance Spatial Cluster Analysis tool. To do this, I once again made use of the local test for spatial autocorrelation known as Anselin's Local Moran's I statistic (Anselin et al., 2006) using ArcMap 10.1's Cluster and Outlier Analysis tool (ESRI, 2001). Given a set of weighted features, this tool identifies statistically significant hot spots, cold spots, and spatial outliers, also described in Chapter 2 (section 2.2.3). However, this tool cannot be utilized for point incident data such as the location of spoor incidences, since it requires a value for each point feature. Consequently, the spoor incident data had to be aggregated in a manner that captured neighbouring spoor observations in an ecologically meaningful way (Scott and Janikas, 2010). Accordingly, I used ArcMap 10.1's Buffer tool (ESRI, 2001) to construct neighbourhoods for each spoor location based on the maximum scale of spoor patchiness identified by the Multi-Distance Spatial Cluster Analysis. I then used the Spatial Join tool to count the number of spoor incidences falling within each neighbourhood, in the same manner that I had aggregated waterpoint features in Chapter 2 (section 2.2.3). The resultant field containing the number of spoor incidences in the neighbourhood of each focal spoor sample served as the value field required for the cluster analysis. Having identified significant clusters of spoor using the Cluster and Outlier Analysis tool in this manner, it was then possible to map the locations of these non-random clusters of elephant movement across the riparian-upland boundary, and hence explore their patch choices when visiting the riparian zone.

Determining patchiness in the amounts of elephant feeding in the riparian zone

Since the elephant feeding data represented a value for each location (number of feeding incidents), it was not necessary to aggregate the data before testing for clusters of feeding events. Instead, the Incremental Spatial Autocorrelation tool in Arcmap 10.1 (ESRI, 2001) could be used to test for significant clustering of high and low values for elephant feeding at different locations. This tool measures the intensity of spatial clustering by investigating spatial autocorrelation of features over a series of distances (Scott and Janikas, 2010). As with the Ripley's K statistic, the resultant z-scores (rather than K-scores as in the case of Ripley's K) reflect the intensity of spatial clustering at each distance, and statistically significant peaks in the z-scores indicate distances, or spatial scales, at which spatial processes promoting clustering are most pronounced (Scott and Janikas, 2010).

Once the peak scale of clustering had been identified, the local Anselin's test for spatial autocorrelation was used to obtain a z-score, approximating the magnitude of clustering for each observation of feeding. These z-scores were used to map amounts of feeding across the riparian landscape, and the locations and clusters of movement and feeding could then be compared, to assess whether elephants fed equally wherever they moved in the riparian zone.

3.2.2. Assessing the role of surface water heterogeneity as a determinant of riparian patch choice and feeding by elephants

Having quantified elephant patch choice during visits to the riparian zone, I then investigated the role of surface water heterogeneity in determining these patch choices, and assessed how well clusters of elephant feeding matched the locations of these patch choices. I evaluated the role of surface water heterogeneity as a determinant of elephant patch choice by means of the strength of the relationship between spoor clustering and both water proximity and waterpoint spatial configuration. In this manner, a negative relationship with DtW would indicate that greater clustering, or patch choice, was associated with patches closer to riparian surface water, whereas a positive relationship with clusters of waterpoints would signify patch choices based on the spatial configuration of waterpoints. The location of each set of spoor encountered along the transects was used to calculate the Euclidean distance of that patch to the nearest surface water using the Near tool in ArcMap 10.1 (ESRI, 2001). The patch context provided by nearby waterpoints (including those outside of the riparian zone) was calculated by creating a neighbourhood for each set of spoor equal to the maximum scale of spoor clustering identified in section 3.2.1 with the Buffer tool, and then using the Spatial Join tool to count the number of waterpoints within this neighbourhood (ESRI, 2001).

Having quantified patch choice in this manner, the next step was to explore the role of surface water heterogeneity in generating these patterns of elephant patch choice (Figure 3.9). As outlined in the Introuductory chapter (section 1.6), spatial data exhibit at least two properties that make it difficult to meet the assumptions and requirements of traditional statistical methods such as OLS regression. Firstly, geographic features are more often than not spatially autocorrelated (Legendre and Fortin, 1989, Legendre, 1993), creating an overcount bias in traditional (nonspatial) regression methods (Scott and Janikas, 2010). However, since spatial autocorrelation can indicate the presence of important spatial processes at work, we may not wish to discount this spatial autocorrelation. If it is possible to identify the full set of explanatory variables that effectively capture the inherent spatial structure in the

dependent variable (for example by using dummy spatial variables such as geology), this type of overcounting bias can be avoided in OLS models by eliminating spatial autocorrelation (Scott and Janikas, 2010).

Secondly, ecological processes in complex, heterogeneous systems behave differently in different parts of the study area, even where similar environmental factors prevail (Levick and Rogers, 2011). This characteristic of spatial data is referred to as regional variation or nonstationarity (Samuels, 1993, Anand et al., 2010, Wheeler, 2014). Global models, like OLS regression, create equations that best describe the overall data relationships in a study area. When these relationships are consistent across the study area, OLS regression equations model these relationships well. However, when these relationships behave differently in different parts of the study area, the regression equations represent an average of the mix of relationships present (Samuels, 1993). Moreover, where this mix of relationships represents two extremes, the global average will not model either extreme well. This feature of complex systems was already demonstrated mathematically in the mid 20th centry (Simpson, 1951), yet is seldom accounted for in ecological studies. Levick (2008) demonstrated the presence of such nonstationarity between the patterns and underlying processes of woody structure in my study area, underscoring the necessity for using spatial statistical methods that are able to deal with such regional variation (Legendre and Fortin, 1989, Anand et al., 2010).

In order to investigate the spatial processes underlying elephant patch choice while accounting for nonstationarity, I therefore made use of Geographically Weighted Regression (GWR) using Arcmap V10.1 (ESRI, 2001). GWR is a true spatial regression method developed to robustly account for non-stationarity (Brunsdon et al., 1998, Fotheringham et al., 2003) and, when properly specified, is also able to manage spatial autocorrelation (Scott and Janikas, 2010). It is a local form of linear regression used to model spatially varying relationships by fitting a separate regression equation to every feature in the dataset (Brunsdon et al., 1998, Fotheringham et al., 2003). It does so by incorporating the dependent and explanatory variables of features falling within a particular bandwidth of each target feature (Scott and Janikas, 2010).

In order to ensure a properly specified GWR model, the analysis must begin by finding a properly specified OLS model that represents the process under investigation (Scott and Janikas, 2010). Thereafter, the same explanatory variables are used to run GWR, excluding any "dummy" spatial variables that may have been used to eliminate spatial autocorrelation in the OLS model (Figure 3.9). Since GWR already allows explanatory variable coefficients to vary

over space, spatial regime explanatory variables are unnecessary and, if included, may create problems with local multicollinearity (Scott and Janikas, 2010). ArcMap 10.1 has an Exploratory Regression tool to assist in finding a properly specified OLS model in a spatially explicit context. It is a data mining tool that will try all possible combinations of explanatory variables to see which models pass all of the necessary OLS diagnostics. By evaluating all possible combinations of the candidate explanatory variables, the chances of finding the best model are greatly increased. Moreover, by testing all of these combinations before eliminating variables unnecessary for a best fit model, the chances of producing a Type I error are reduced (Mills et al., 2006). While Exploratory Regression is similar to Stepwise Regression, it looks for models that meet all of the requirements and assumptions of the OLS method, rather than only looking for models with high Adjusted R^2 values. A properly specified OLS model has:

- Explanatory variables where all of the coefficients are statistically significant
- Coefficients reflecting the expected, or at least a justifiable, relationship between each explanatory variable and the dependent variable
- Explanatory variables that are not collinear (none are redundant; small Variance Inflation Factor values < 7.5)
- Normally distributed residuals indicating that the model is free from bias (specifically, the Jarque-Bera p-value is not statistically significant)
- Randomly distributed over- and under-predictions indicating model residuals are normally distributed (the spatial autocorrelation p-value is not statistically significant)
- Standardised residuals are not spatially autocorrelated

The Exploratory Regression tool tests for spatial autocorrelation using a spatial weights matrix to analyze spatial structure in the OLS model residuals (ESRI, 2001). I made use of an Inverse Distance weighting method to create the spatial weights matrix, as described in the previous chapter (Chapter 2, section 2.2.3). This spatial weights measure is one of impedance, or distance decay, where all features influence all other features, but the further away something is, the smaller the influence. Accordingly, the algorithms for inverse distance assume that spoor locations further away are less likely to contribute to a focal spoor sample's neighbourhood, than spoor closer by.

An important output of the Exploratory Regression is a Summary of Variable Significance (ESRI, 2001). This provides information about variable relationships, as well as the consistency of these relationships over 999 permutations of all possible models (Figure

3.9). Each candidate explanatory variable is listed along with the proportion of times that it was statistically significant during the various model permutations. This summary output provides an indication of how stable variable relationships are, by revealing what percentage of the time the relationship was negative or positive. Strong predictors are consistently significant and the relationship will be stable (primarily negative or primarily positive). Candidate surface water heterogeneity variables included in the Exploratory Regression to address each of the key questions included: distance to any source of water, distance to natural source of water, and waterpoint spatial configuration (#waterpoints within 1500 m). I used the summary of variable significance to investigate the relative contributions of different variables (and first order interactions of all the variables with the surface water variables, to test for modulating effects; see section 3.2.4, this chapter) towards elephant patch choice. During the Exploratory Regression process, I discarded any variables that were unnecessary for a properly specified, best fit OLS model.

The output of the best fit OLS model provides a measure of nonstationarity using the Koenker (BP) statistic. A statistically significant Koenker (BP) value indicates nonstationarity in the global OLS model, and hence that the GWR should be used to improve predictions and to better understand regional variation inherent in the explanatory variables (Scott and Janikas, 2010). Of the GWR models that meet all the requirements of a properly specified model, the best-fit model is selected on the basis of the highest adjusted r^2 value, and the lowest Akaike Information Criterion (AICc) value (Johnson, 1999). I tested both the fixed (a specified number of neighbours) and adaptive methods (where feature distribution is dense, the spatial context is smaller; where feature distribution is sparse, the spatial context is larger) to define the search radius from or spatial context of each spatial feature.

Finding a properly specified GWR model through the steps described above ensure that earlier criticisms of the technique (Jetz et al., 2005) are addressed. Specifically, these criticisms include (i) that standard GWR models do not adequately address spatial autocorrelation, and that (ii) allowing parameters to vary locally precludes meaningful comparisons of r^2 values between global and local models, which should rather be compared using the Akaike Information Criterion that allows for model complexity, and (iii) that there is often multicollinearity among GWR co-efficients (Páez et al., 2011).

3.2.3 Assessing clusters of elephant feeding relative to patch choices when visiting the riparian zone

I tested whether elephants fed wherever they moved through the riparian zone using an identical exploratory regression procedure as the one explained above. However, in this instance the amount of feeding (number of feeding events) represented the response variable. In addition, I assessed how closely elephant patch choice and feeding coincided by comparing the location and magnitude of clustering (z-scores) of elephant movement across the riparian-upland boundary, against clusters of elephant feeding. Closely matching clusters of patch choice and feeding would support the prediction that elephants fed wherever they chose to move through the riparian zone. In contrast, unmatching cluster patterns would indicate that elephants fed selectively in other parts of the riparian zone. I compared the Cluster and Outlier Analyses (ESRI, 2001) of elephant patch choice and feeding undertaken in section 3.2.1, to evaluate how well the spatial locations of patch choices coincided with patches of higher feeding. This made it possible for me to assess how closely patterns of elephant patch choice matched spatial patterns of feeding during visits to the riparian zone, and hence whether elephants fed equally wherever they moved through the riparian zone.

3.2.4. Exploring how elephant patch choice and feeding may be modulated by temporal changes in resource availability, elephant social structure/sexual size dimorphism, or the type of water source

Since rainfall is a primary driver of forage and water resources in semi-arid savannas (Huntley and Walker, 1982, Pickett et al., 2003, Venter et al., 2003), resource availability for water dependent herbivores such as elephants becomes reduced over the course of the dry season, as well as during years with relatively lower rainfall (Gaylard et al., 2003). I therefore tested whether elephant patch choice or feeding were modulated by temporal changes in resource availability by including the progression of the dry season, and the three years of my study period that had varying annual rainfall (as a proxy for resource availability), as variables (indepedently and as interactions with the surface water variables) in the regression analyses described above. Since I had demonstrated in the previous chapter that surface water heterogeneity did not decline in a predictable linear fashion over the course of the dry season and among years with varying rainfall (Chapter 2, section 2.4.3), I used categorical dummy variables instead of continuous variables (Lynch, 2003) to signify temporal changes in the

water and forage resources. I used identical categories for the temporal changes in surface water heterogeneity as those used in Chapter 2 (early, mid and late dry season; average, dry and wet rainfall years; Chapter 2 section 2.2.3). Similarly, I included elephant gender as a dummy variable in the regression analyses (elephant bulls, elephant herds) to infer whether the energetic differences imposed by elephant sexual dimorphism and social structure modulated elephant patch choice or feeding.

Finally, I assessed the importance of natural sources of surface water relative to artificial sources for determining elephant patch choices and feeding, by including surface water variables (DtW, waterpoint spatial configuration) for both natural water and augmented water scenarios in the exploratory regressions described above. In this way I tested whether a particular type of water source modulated patterns of elephant patch choice and feeding, providing a means to infer the influence of artificial water provision on elephant space use within the riparian landscape.

3.3. Results

3.3.1. Patterns of elephant patch choice inferred from visits to ephemeral riparian zones

When elephants visited the riparian zones along the ephemeral rivers of the study area, the points at which they crossed the riparian-upland boundary were not randomly distributed. Instead these points were significantly clustered at scales between 500 – 4500 m, as indicated by the significant difference between observed and expected K-values (Figure 3.11). A peak in spoor clustering at 1500 m indicated that the spatial processes underpinning elephant patch choice reached a maximum at this scale.

This scale of patchy space use was almost an order of magnitude finer than the maximum scale of surface water heterogeneity observed for this landscape (10 000 m) in the previous chapter (Chapter 2, section 2.4.1). Hence this pattern of elephant space use was clearly not associated with the maximum scale of surface water heterogeneity in the study area. However, in the previous chapter I had found surface water to be heterogeneous over a range of scales (500 – 18 000 m), including at the 1500-m scale at which I found clusters of elephant movements through the riparian zones to be patchy. Therefore, before I explored how surface water heterogeneity may have contributed to the spatial processes underpinning this patchy

space use by elephants, I reanalysed waterpoint spatial configurations at this finer scale (1500 m).

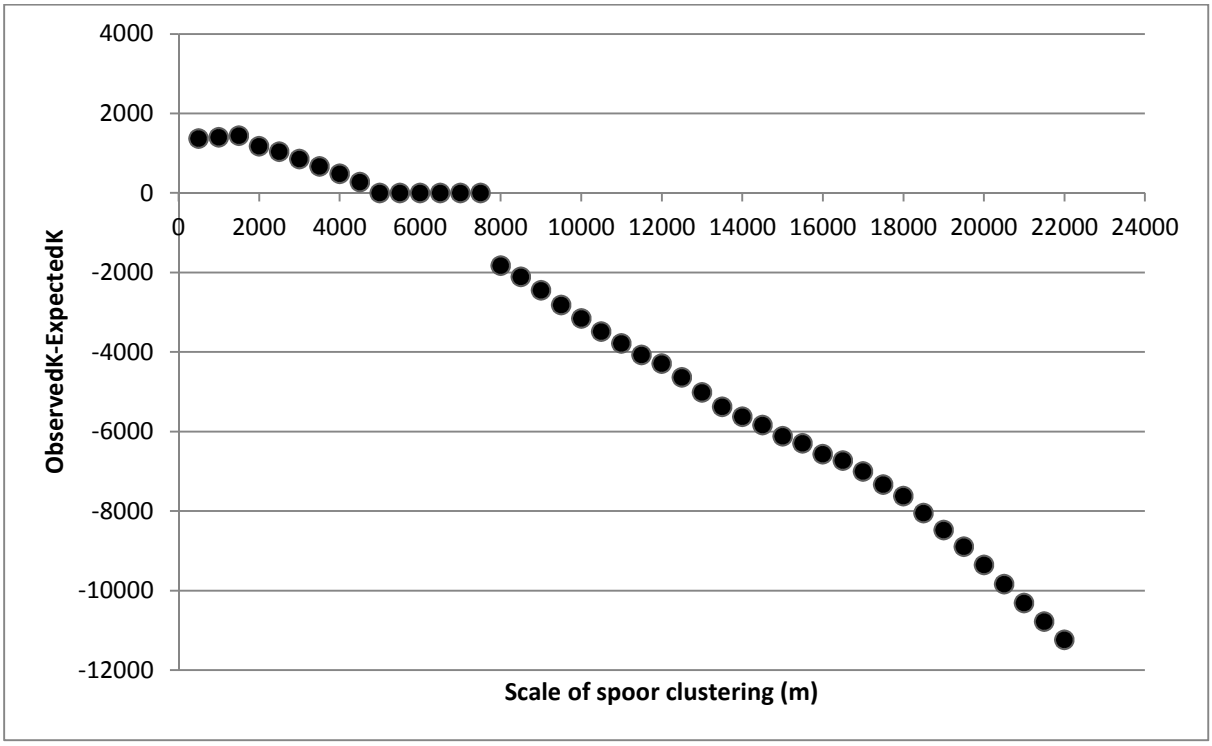


Figure 3.11 Scales of patchiness in the clustering of elephant entry/exit points during visits to the ripatian zone, as measured by the Ripley's K statistic. The point of largest difference between observed and expected K indicates a peak in spoor clustering at neighbourhoods of 1500 m

The spatial configurations of >80% of the waterpoints at this scale were not significantly different from a CRD, regardless of the progression of the dry season or years with varying rainfall (Figure 3.12). Clustered waterpoints at this scale only occurred along the Mphongolo River at one location on the western boundary of the park, outside of the area where I had investigated elephant visits to the riparian zone. Apart from this, only two other groups of clustered waterpoints occurred in the study area at this scale, both of them along the Shingwedzi River (Figure 3.12). Here, one group of waterpoints near the confluence with the Bububu River towards the east of the study area (henceforth referred to as the Joao-Spirowiri waterpoint complex) consistently remained clustered at this scale over time, regardless of the seasonal or annual variations in rainfall (Figure 3.12). The other group of clustered waterpoints, approximately 8 km westwards (henceforth referred to as the Redrocks waterpoint complex), were only clustered when nearby waterpoints dried up during the driest year of the study period (Figure 3.12). By mapping a comparative natural water source scenario at the 1500-m scale, it

became evident that, apart from increasing the overall abundance of waterpoints, artificial water provision caused the Redrocks waterpoint complex to be clustered, rather than randomly distributed, during the driest period of the study (Figure 3.13). Water provision had also changed the spatial configuration of the nearby waterpoint between the Redrocks and Joao/Spirowiri waterpoint complexes into a dispersed waterpoint, embedded in a matrix of clustered waterpoints (Figure 3.13).

Comparing these finer-scale patterns of surface water heterogeneity to a map of spoor clusters at the 1500-m scale revealed that significant clusters of spoor along the Shingwedzi River coincided with these two groups of clustered waterpoints – one at the southern end of the Joao-Spirowiri waterpoint complex, and the other at the Redrocks waterpoint complex (Figure 3.14). Although no clustered waterpoints occurred at this scale along the Phugwane River, significant clusters of spoor were nevertheless identified at one location in the vicinity of the Sandpiper waterpoint at the confluence with the Mphongolo River (Figure 3.14). These results suggested that there may be differences among these two rivers with regards to the role of surface water heterogeneity relative to other resources, in determining elephant responses. The results of the regression analyses (in the following section) provided insights into what these different drivers might be.

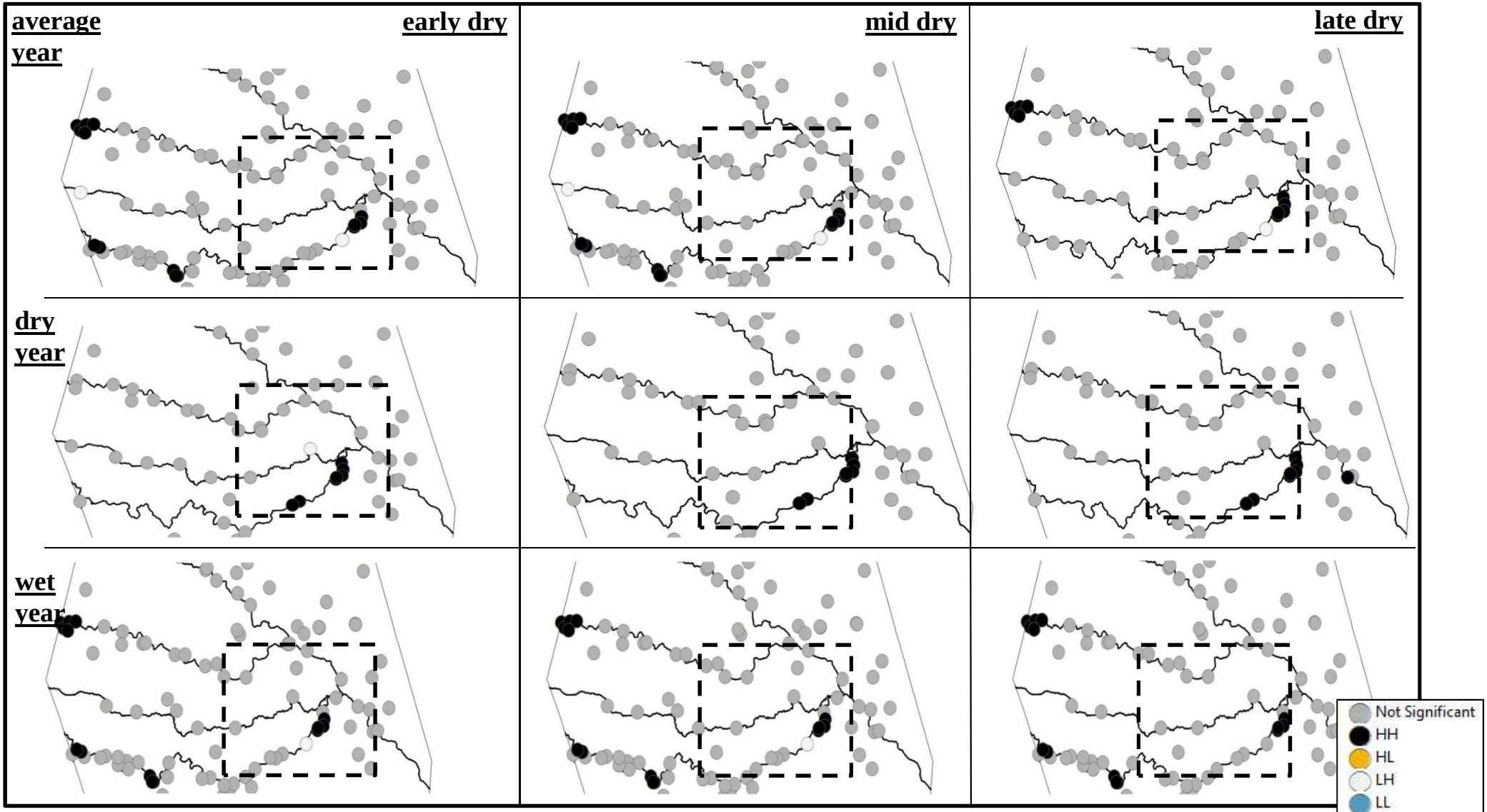


Figure 3.12 Spatial configuration of waterpoints at 1500-m scale (HH = clustered waterpoint in a clustered waterpoint context; HL = clustered waterpoint in a randomly distributed or dispersed waterpoint context; LH = dispersed waterpoint in a randomly distributed or clustered waterpoint context; LL = dispersed waterpoint in a randomly distributed or dispersed waterpoint context; stipled line is transect area)

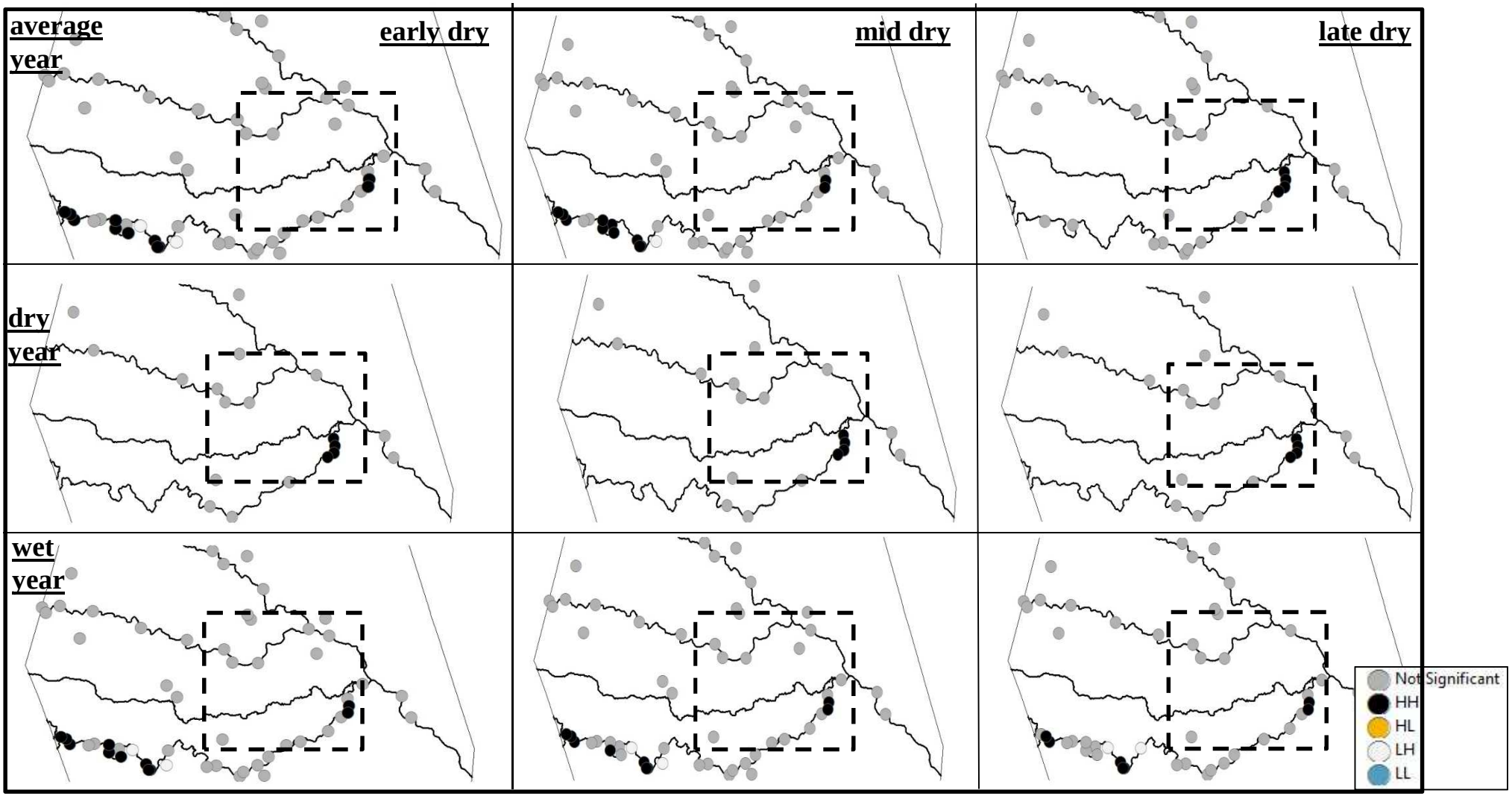


Figure 3.13 Spatial configuration of natural waterpoints at 1500-m scale (HH = clustered waterpoint in a clustered waterpoint context; HL = clustered waterpoint in a randomly distributed or dispersed waterpoint context; LH = dispersed waterpoint in a randomly distributed or clustered waterpoint context; LL = dispersed waterpoint in a randomly distributed or dispersed waterpoint context; stipled line is transect area)

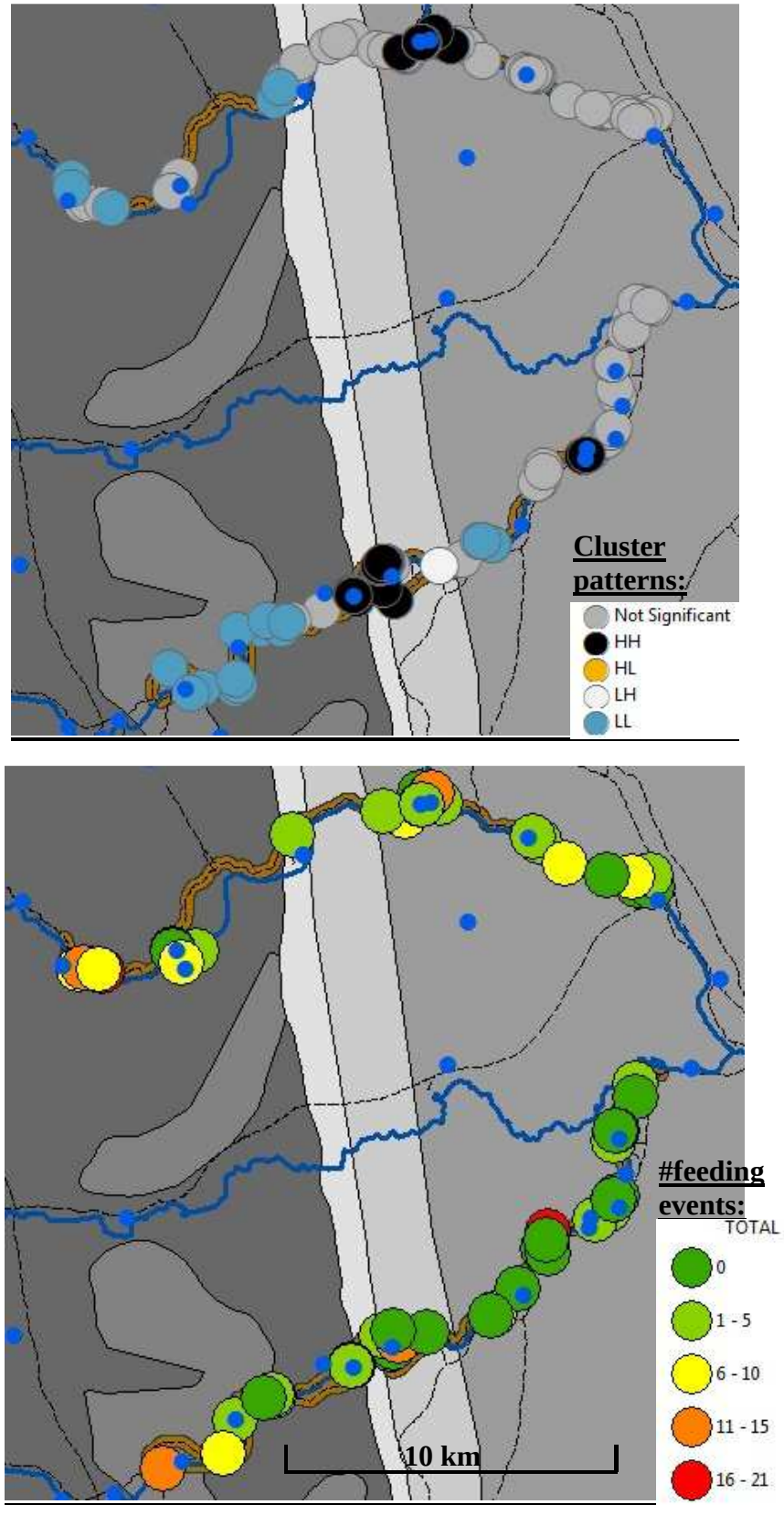


Figure 3.14 Clusters of elephant movement (top: HL = clusters of spoor in a randomly distributed or dispersed spoor context; LH = dispersed spoor in a randomly distributed or clustered context; LL = dispersed spoor in a randomly distributed or dispersed context) and feeding (bottom: total number of feeding events per trail) during visits to the riparian zone. Blue dots signify the presence of surface water. Underlying geology is represented by the different shades of grey, but is not described in detail because it was only included as a dummy variable in the process of finding a properly specified OLS model

3.3.2. Drivers and modulators of elephant patch choice during visits to the riparian zones of ephemeral rivers

Contrary to the findings of previous studies (Redfern et al., 2003, Redfern et al., 2005), exploratory regression revealed that clusters of elephant movement through these riparian zones were consistently well explained (significant in >83% of model permutations) by proximity to surface water, regardless of fluctuations in dry season resource availability (Table 3.1). By differentiating among natural and artificial water sources, the consistency of water proximity as a significant explanatory variable increased from 83% (all sources of water) to nearly 99% (natural sources only) of model permutations (Table 3.1). This finding supports the prediction that elephant patch choice is modulated by the presence of natural sources of riparian surface water. Although elephant patch choice was associated with proximity to natural surface water throughout the dry season, DtW became an even more consistent predictor during drier conditions at the end of the dry season (significant in 75% of models), and during the driest year of the study period (significant in 44% of models ca. 20% during wetter conditions (Table 3.1). Elephant preferences for patches with natural surface water therefore become more marked in this landscape during resource bottle neck periods, even though distances between these water sources were small relative to their maximum daily foraging ranges. In addition, differentiating patch choice by gender revealed that the proximity of natural surface water was a more consistent predictor of the movement of elephant herds (significant in 78% of models) than for bulls (significant in 52% of models), supporting the prediction that elephant herds were more selective about the type of water source.

However, the spatial patch context provided by neighbouring waterpoints (number of waterpoints within 1500 m) provided an even better (significant in 100% of model permutations) explanation of patch choice than DtW, reflecting the concentrations of spoor found near the clustered waterpoints in the study area (Figure 3.14). Elephants of both genders preferred patches in the riparian zone that had a larger number of waterpoints within 1500 m (i.e. clustered waterpoints; Table 3.1) regardless of prevailing rainfall conditions.

Table 3.1 Summary of variable significance in n = 32747 model permutations of the predictors of elephant patch choice (1500-m scale). Underlying geology was included as a spatial dummy variable during the process of trying to eliminate spatial autocorrelation in order to find a properly specified OLS model

Variable	%significant	%negative	%positive
Patch context	100	0	100
Distance to natural waterpoint	98.56	100	0
Underlying geology Granite	96.18	97.98	2.02
Underlying geology Basalt	85.92	0	100
Distance to any waterpoint	83.23	97.34	2.66
Distance to natural water (bulls)	79.51	97.82	2.18
Distance to water x late dry season	75.49	96.7	3.3
Distance to natural water (herds)	54.47	83.73	16.27
Distance to any waterpoint (bulls)	51.56	84.11	15.89
Distance to any waterpoint (herds)	47.13	86.22	13.78
Distance to water x dry year	44.19	87.61	12.39
Distance to artificial waterpoint	39.42	38.53	61.47
Herd	37.59	21.69	78.31
Bull	37.59	78.31	21.69
Distance to artificial water (bulls)	34.05	28.32	71.68
Distance to water x average year	28.66	93.96	6.04
Underlying geology sand/lava	24.74	4.35	95.65
Distance to water x mid dry season	21.83	47.19	52.81
Distance to artificial water (herds)	16.92	58.67	41.33
Distance to water x wet year	14.69	64.74	35.26
Distance to water x early dry season	10.45	72.95	27.05

3.3.3. Best fit models of elephant patch choice during visits to ephemeral rivers

The explanatory power of models exploring the drivers of elephant patch choice were improved by adding spatial variables that accounted for the underlying geology of preferred patches, with lower levels of clustering occurring in the western granitic landscape, and greater clustering in the eastern basaltic areas (Table 3.1). However, even by incorporating these spatial variables, a significant amount of spatial autocorrelation remained, indicating that additional spatial factors were still required to adequately explain elephant patch choices in this riparian landscape. Since I was unable to identify any further significant spatial variables, I strongly suspected the presence of regional variation (spatial non-stationarity) in the factors determining patch choice. To test whether this was the case, I selected the best fit OLS model with the lowest AICc value, from the n = 32747 model permutations run during the exploratory regression.

The best fit OLS model included the variables patch context, proximity to natural surface water, proximity to artificial water for elephant herds, basalt as the underlying geology, and sand/lava as the underlying geology (Table 3.2). Together these variables explained nearly 55% of the variation in patch choice (AICc = 187.42; $p < 0.000005$; Table 3.2). The Jarque-Bera statistic confirmed that the model residuals satisfied the OLS requirement of a normal distribution ($p = 0.156$; d.f. = 2). However, the Koenker (BP) statistic revealed a significant amount of spatial non-stationarity ($p = 0.006$; d.f. = 5; Table 3.2). I therefore used the same variables to run a Geographically Weighted Regression (GWR), which is able to calculate local adjusted r^2 values for each feature (sample) in the model.

By running the local GWR model, spatial autocorrelation was eliminated from the model at the 95% level (Global Moran's I z-score of GWR standardized residuals = 1.870; $p = 0.062$), confirming that non-stationarity had indeed been a significant source of the remaining spatial autocorrelation in the best fit global OLS model. Moreover, by accounting for this non-stationarity, the explanatory power of the model (adjusted r^2) increased from 55% to nearly 83%, and reduced the AICc to by more than half (to 74.68; Table 3.2).

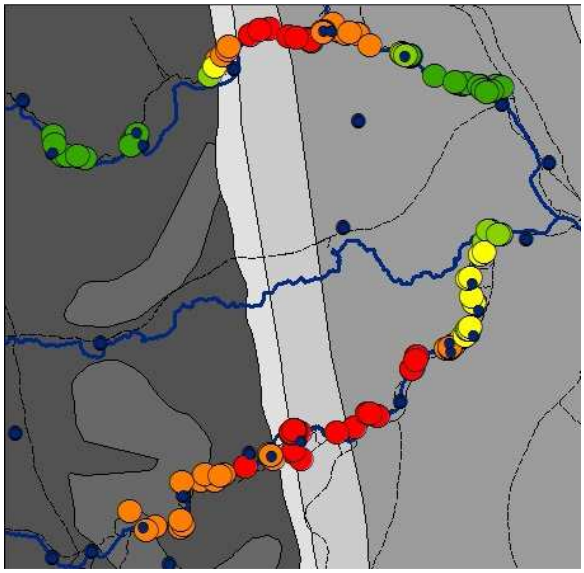
Table 3.2 Comparison of global (Ordinary Least Squares OLS) and local (Geographically Weighted Regression GWR) best fit model summary statistics describing clusters of elephant movement through the riparian zones of three ephemeral rivers in northern KNP. The Jarque-Bera statistic denotes deviation away from a normal distribution, the Koenker (BP) statistic tests for non-stationarity, and the Joint F (for stationary models) or Wald statistic (for non-stationary models) provides a measure of the overall statistical significance of the model

Response variable	**OLS adjusted r^2**	**OLS AICc**	**Jarque-Bera p-value (df)**	**Koenker (BP) p-value (df)**	**Joint F-/Wald p-value$_{df}$**	**factors included**	**t-statistic**	**robust p-value**	**GWR adjusted r^2**	**GWR AICc**
magnitude of spoor clustersing (#neighbouring spoor within 1500 m)	**0.549**	**187.42**	0.156_2	0.006_6	$<0.000005_5$	context provided by neighbouring waterpoints	-0.0005	0.0002	**0.828**	**74.68**
						distance to nearest natural waterpoint	1.86	0.003		
						distance to nearest artificial waterpoint (herds)	-2.28	0.004		
						basalt	-1.60	0.011		
						sand/lava	1.80	<0.00005		

Mapping the local r^2 values calculated by the GWR revealed that patch context and proximity to natural surface water explained up to 92% of the variation in elephant patch choice in the central regions of the spoor transects along both the Shingwedzi and Phugwane rivers (Figure 3.15). In contrast, the model performed relatively poorly (explaining only 14 – 29%) on the western end of the Phugwane transect and along the small section of this transect that occurred along the Mphongolo River (Figure 3.15), indicating that surface water heterogeneity played a lesser role in elephant patch choice in these regions of the study area.

Thematic maps of the local co-efficients for patch context and natural water proximity illuminated where these variables explained elephant patch choice best (Figure 3.15), revealing that although patch choice was generally very well explained nearer to natural surface water, this relationship was reversed in two localised areas along the Shingwedzi and Phugwane Rivers (Figure 3.15). Similarly, in two localised areas along the transects patch context explained elephant patch choice poorly, the relationship even becoming reversed in these areas (Figure 3.15).

(i)



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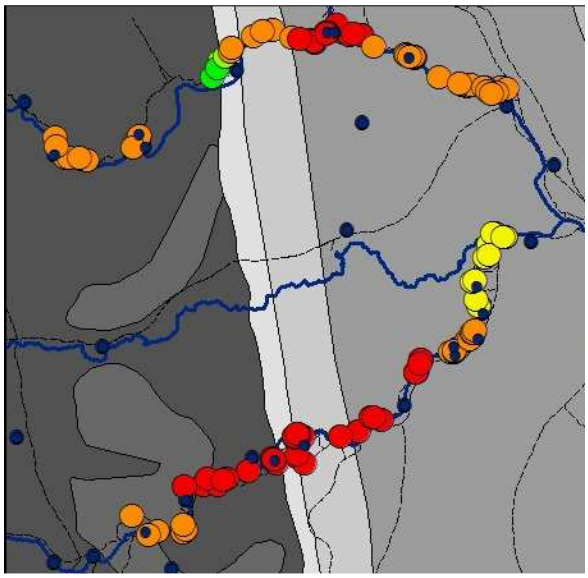

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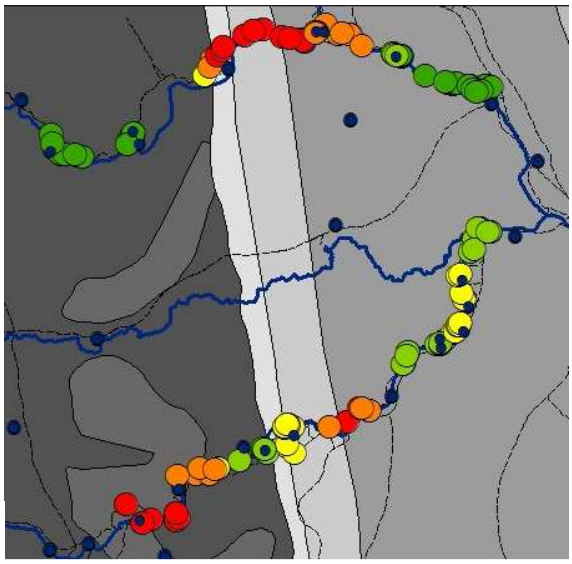

Figure 3.15 Regional variation in the factors explaining elephant patch choice during visits to the riparian zone, as determined by Geographically Weighted Regression. Figures represent (i) local adjusted r^2, and local co-efficient values for (ii) distance to natural surface water, and (iii) patch context provided by neighbouring waterpoints (blue dots represent the presence of surface water)

3.3.4. Patterns and drivers of elephant feeding during visits to the riparian zone

Reflecting the fact that elephants selected particular patches when moving through the riparian zone, the amount of feeding while there differed significantly from a CRD, with peaks in the patchiness of elephant feeding at 2000 m and 7500 m (Figure 3.16). The first peak at 2000 m closely matched the scale of elephant patch choice identified above (1500 m; section 3.3.1), suggesting that elephants fed equally wherever they chose to move through the riparian zone.

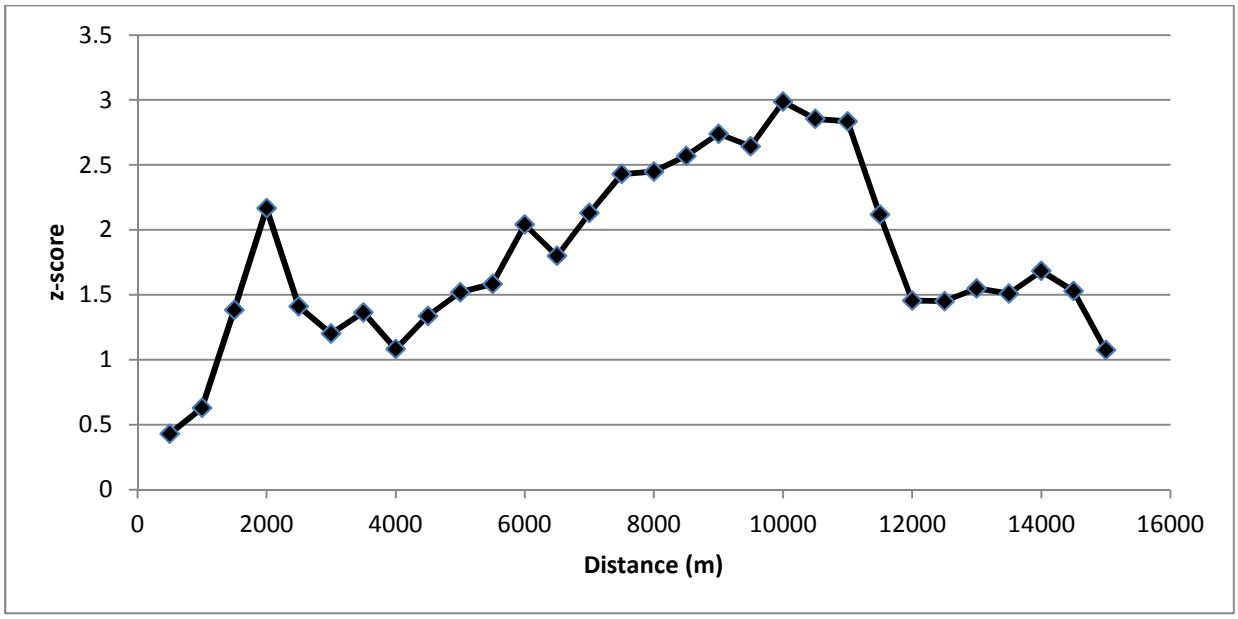

Figure 3.16 Scales of patchiness in the amounts of elephant feeding while in the riparian zones of three ephemeral rivers in the drier northern region of KNP, as measured by incremental tests of spatial autocorrelation (ESRI, 2001)

However, clusters of higher feeding overlapped at only three of the five clusters of spoor (Redrocks and Joao clustered waterpoints, along the Shingwedzi River, and Sandpiper waterpoint at the confluence of the Phugwane and Mphongolo rivers; Figure 3.14 i and ii), refuting this suggestion. Indeed, a large proportion of riparian visits was associated with little or no feeding at all (Figure 3.14). Interestingly, the only other patches of high elephant feeding were at two randomly configured natural waterpoints, but that persisted through even the driest conditions (Zari waterpoint along the Phugwane River, and the Tshange spring along the Shingwedzi River; Figure 3.14), suggesting that factors or other resources not incorporated into my models might be at play here. Accordingly, I was not able to identify any variables

that were consistently significant predictors of the amounts of elephant feeding while in the riparian zone (Table 3.3), and the best fit model had poor explanatory power (adjusted r^2 = 0.09; p = 0.012) despite the absence of spatial autocorrelation (z-score = 0.01; p = 0.99), and non-stationarity (p = 0.86; d.f. = 1).

Table 3.3 Summary of variable significance in 3650 model permutations of the predictors of amounts of feeding (@1500-m scale)

Variable	%significant	%negative	%positive
Distance to water x mid dry season	34.95	0	100
Distance to water x early dry season	5.32	67.19	32.81
Distance to water x late dry season	4.93	87.21	12.79
Distance to water x dry year	4.68	47.2	52.8
Distance to any water source	2.55	29.84	70.16
Distance to water x herd	1.43	17.19	82.81
Distance to water x average year	0.88	82.47	17.53
Distance to natural waterpoint	0.86	54.56	45.44
Distance to artificial waterpoint	0.43	25.96	74.04
Distance to water x bulls	0.07	65.28	34.72
Distance to water x wet year	0	14.15	85.85

Taken together, these findings indicate that while elephant patch choice in this landscape is primarily determined by surface water heterogeneity, choices for feeding, although non-random, are nested within only a subset of these patches. The determinants of this patchy feeding during visits to the riparian zone were not within the group of variables that I tested, and therefore remain to be identified.

3.4 Discussion

Having demonstrated in the preceding chapter that the surface water template available to elephants in the study area had a variety of clustered, random and dispersed spatial configurations over a range of scales (from 500m – 18000m), this chapter explored whether any of these surface water patterns focused elephants' dry season activities in particular patches within the riparian zone, and hence whether these scales of surface water heterogeneity had functional significance for elephant disturbance regimes. The methodological approach used here built upon the spatially explicit perspective developed in

the previous chapter, by adding a local regression modelling technique to explore the relative contributions of both DtW and waterpoint spatial configuration to patterns of elephant space use (**Error! Reference source not found.**). The approach differed from earlier investigations of elephants' expressions of water dependence in that it made use of spatial statistics to allow the scales of elephant movement and feeding to emerge, rather than to be subjectively imposed on the analyses. In addition, a local form of linear regression (GWR) that could account for the spatial autocorrelation and nonstationarity common in complex, heterogeneous systems, was used to evaluate how well not only DtW, but also waterpoint spatial configuration, explained elephant dry season use of the riparian zone under conditions of varying resource availability. This scaled and spatially explicit approach revealed that elephants of both genders consistently chose to visit the riparian zone near patches with clustered natural waterpoints during the dry season, even though distances between waterpoints were small (ca. 4 km) relative to the maximum daily foraging ranges of elephants. However, clusters of higher feeding coincided with only a subset of the preferred clustered waterpoints, indicating that elephants did not feed equally wherever they spent time in the riparian zone. Even though elephants preferred natural waterpoints, the distribution of neighbouring artificial water sources contributed to the patch context that determined whether these natural waterpoints were clustered, dispersed or randomly configured. This suggests that the strategic placement or closure of artificial waterpoints to generate randomly configured or dispersed waterpoints, could draw elephant activity away from patches with previously clustered waterpoints. This is in contrast with the understanding generated by DtW measures of surface water heterogeneity, which have concluded that even complete closure of artificial water sources would do little to alter elephant distributions.

3.4.1. Surface water controls on elephant space use in a landscape with abundant water supplies

By demonstrating that elephants responded to both DtW and waterpoint spatial configuration in this landscape, these findings challenge previous assumptions that surface water in KNP is not sufficiently heterogeneous at scales relevant to elephant space use (Redfern et al., 2005, Smit et al., 2007a, Grant et al., 2008, Smit and Grant, 2009). Elephants must travel large distances away from water in landscapes where forage resources near water have already been depleted (Owen-Smith, 1988). However, travelling such large distances is associated with the costs of travelling, as well as lost feeding opportunities. Large herbivores are able to

modify their foraging behaviour in response to the spatial scale of resource patchiness (Senft et al., 1987, Hewitson et al., 2005). Therefore, where forage resources have not yet been depleted close to water, choosing patches that contain both water and forage resources is a better strategy for meeting metabolic requirements.

Moreover, a host of organisms ranging from insects (Palmer et al., 2000, Silver et al., 2000, Steffan-Dewenter et al., 2002, Lancaster et al., 2003, Thies et al., 2003, Gripenberg and Roslin, 2007), to fish (Le Pichon et al., 2006), birds (Cortes-Avizanda et al., 2011) and large mammals (Wallace et al., 1995, Boyce et al., 2003, O'Brien et al., 2006) have been shown to prefer resource patches with particular spatial configurations, taking advantage of spatial patterning to optimize their utilisation of the resource (Wallace et al., 1995). Such neighbourhood effects of clustered resources cause a particular focal patch to attract individuals because the resources in adjacent patches are usually more accessible than resources in more distant patches (Dunning et al., 1992). Accordingly clustered waterpoints reduce the distances that elephants have to travel to reach alternative water sources.

The peak scale of elephant response (1500 m) did not match the maximum scale of surface water heterogeneity (12 000 m), supporting the view that the scaling of elephant-habitat relationships arises from elephants' scale-dependent responses to habitat, rather than through the spatial structure of the environment itself (De Knegt et al., 2011). This emphasizes the importance of understanding not only the scales of resource heterogeneity, but also the scales of organism response to this heterogeneity (Wiens et al., 1976, O'Neill et al., 1988, Turner, 1989, Johnson et al., 1992, Wiens et al., 1993, Wallace et al., 1995, Pearson et al., 1996, Turner et al., 1997, Boyce et al., 2003). The particular scales and patterns of surface water heterogeneity uncovered here are likely to be context specific, and the energetic trade-offs that elephants must make to acquire various critical resources will therefore differ in other landscapes. Nevertheless, the heterogeneity approach developed here can be used to quantify elephant spatial responses to surface water in elsewhere.

3.4.2 Implications for artificial water provisioning policies

The preference by elephant breeding herds, in particular, for natural sources of surface water reflects elephant distributions near rivers in KNP demonstrated by Smit and Ferreira (2010). This may at first suggest that closure of boreholes would not affect elephant movements

(Smit et al., 2007a, Smit et al., 2007c, Smit and Ferreira, 2010). However, this study showed that the spatial configuration of neighbouring waterpoints played an even greater role in determining elephant patch choices and feeding than did DtW. The distribution of artificial waterpoints contributed towards the generation of these spatial configurations (Chapter 2, section 2.4.3). Hence this work suggests that water provisioning may still have a role to play in manipulating elephant impacts, and that this may be achieved by altering waterpoint spatial configurations through strategic closure, or even opening, of artificial waterpoints in key locations. For example, although water provision did not change the fact that the Joao-Spirowiri waterpoint complex was consistently clustered, it did change the spatial configuration of the nearby Redrocks natural waterpoint into a clustered complex of waterpoints in the driest year of the study period. Strategic closure of only the borehole adjacent to Redrocks natural waterpoint (known as Gubyane) would therefore return Redrocks to a random spatial configuration, suggesting that Redrocks would no longer be a preferred riparian patch for elephants.

3.4.3 Understanding of functional heterogeneity of surface water for elephants

The approach developed in this chapter improved the ability to assess the template that surface water provides for elephant disturbances, by advancing understanding of the role of surface water for generating patchy elephant movements and feeding beyond simple distance to water measures. For example, despite the consistency with which surface water heterogeneity variables explained patterns of elephant patch choice, the overall explanatory power of the linear best-fit model was relatively poor. Instead, comparing clusters of movement and feeding by mapping patterns of spatial autocorrelation highlighted a small number of focal patches or hotspots of elephant activity rather than the gradual attentuations away from water detectable using traditional linear methods of analysis (Boyce et al., 2003). This finding challenges the validity of traditionally-used piosphere models of gradual attenuation of elephant impacts away from sources of surface water (Thrash and Derry, 1999, Derry, 2004), and may explain why other studies have only demonstrated weak expressions of water dependence by elephants in these landscapes (Redfern, 2002, Smit et al., 2007a, Grant et al., 2008, Smit and Grant, 2009, Smit, 2011). Whether elephant responses to surface water heterogeneity will continue to follow the patterns demonstrated in this study when

elephant densities increase remains unknown. Since the time of the study, the elephant population has grown to around 15000 animals. There is therefore an opportunity to re-evaluate how elephants respond to surface water heterogeneity at higher elephant densities.

Similarly, lack of overlap between some clusters of elephant movement and feeding suggested that visits to some of the riparian waterpoints may have been primarily for drinking or bathing, with little or no associated feeding. If this is indeed the case, it calls into question the widespread use of satellite/GPS collars and aerial census data to infer the distribution of elephant impacts - a critical assumption of this methodology is that elephant distributions provide a good proxy for elephant feeding and the associated impacts. However, a shortcoming of this study was that the amounts of elephant feeding in different patches could only be quantified in terms of the number of feeding events observed. Vegetation biomass consumed would have provided a better indicator of how much elephants fed in the riparian zone, and may have painted a different picture of where their feeding was focused. Variations in the local adjusted r^2 value and co-efficients of the GWR model indicated that the particular combination of drivers of elephant patch choice varied in different parts of the landscape. The existence of such non-stationarity in this landscape has been demonstrated before (Levick, 2008), and should serve as a caution in terms of finding trends that are statistically significant but spurious (Simpson, 1951), using non-spatial regression models.

Since the resources contained in patches generally have their own temporal dynamics (Pickett and White, 1985, Pickett et al., 1987, Pickett et al., 1989, Kolasa and Rollo, 1991, Pickett and Rogers, 1997), the quality of a patch for a foraging individual is a time-dependent variable (Wiens et al., 1985). Consequently, temporal heterogeneity of surface water in favoured patches will occassionally result in reduced elephant utilisation (O'Connor et al., 2007, Kerley et al., 2008). However, empirical evidence of patchy accumulation of elephant impacts over the longer term is still lacking (Scholes and Mennell, 2008). Similarly, other sources of variability in elephant patch choice and feeding demonstrated here and in other studies (Stokke and Toit, 2000, Greyling, 2004, Greyling, 2010, Codron et al., 2011, Owen-Smith and Chafota, 2012), may modulate the longer term accumulation of impacts in particular parts of the landscape. Hence it remains important to investigate how these sources of variability in elephant patch choice and feeding produce functional heterogeneity for the patterns of elephant impact over the longer term. This will be addressed in the next chapter (Chapter 4).

Chapter 4 - Can refuges from elephant disturbance exist in landscapes with abundant surface water?

4.1. Introduction

The underlying philosophy for protecting susceptible species from elephant impacts under the previous Balance of Nature paradigm (Wu and Loucks, 1995), was to ensure moderate levels of elephant impact across the entire landscape (Pienaar, 1969, Van Wyk and Fairall, 1969). In contrast, instead of aiming to protect species from elephants, the heterogeneity paradigm advocates the maintenance of a patchy disturbance regime that allows for a range of elephant impacts (see section 1.2, Chapter 1). Through the existence of such a patch mosaic, the management focus has shifted to maintaining a variety of species in different parts of the landscape, rather than on the persistence of all species throughout the landscape (Whyte et al., 1998, Whyte, 2004). Accordingly, localised patches of severe impact are tolerated (or even "sacrificed"), with the understanding that other patches will serve as spatial refugia from elephant disturbance (Owen-Smith et al., 2006). Temporal refuges occur where the intervals between bouts of elephant disturbance are long enough to allow for recovery of patches. The susceptibility of plant species to elephant impact will influence how well these patches can serve as refuge for these species (O'Connor et al., 2007).

The role of spatial refuges in protecting impact intolerant species has been demonstrated by studies that have found cohorts of baobabs *A. digitata* growing in areas too steep for elephants to access (Kelly, 2001, Edkins et al., 2008). Where elephants have been excluded entirely, either by means of exclosures or boundary fences, other studies have demonstrated increased survival and persistence of impact intolerant species such as marula S. *birrea* (Jacobs and Biggs, 2001), knobthorn *A. nigrescens* (Eckhardt et al., 2001) and baobabs (Kelly, 2001, Edkins et al., 2008). Investigating the role of surface water heterogeneity in producing such refuges has been confined to piosphere studies of attenuating elephant effects with distance from water (Thrash et al., 1991, Fruhauf, 1997, Thrash and Derry, 1999, Brits et al., 2002). These studies have demonstrated that woody species are

subject to greater structural changes in areas closer to water, and are more numerous in areas remote from water (Van Wyk and Fairall, 1969). However, they have only inferred the effects of elephant disturbance through observed patterns of biodiversity, rather than by investigating the impacts directly. Moreover, the role of surface water heterogeneity in generating these patterns has been restricted to distance to water (DtW) measures. Hence, although the existence of spatial or temporal refuges from elephant disturbance forms the basis of the heterogeneity approach for managing elephants (Whyte et al., 1998, Whyte et al., 1999, Whyte, 2004, Owen-Smith et al., 2006, O'Connor et al., 2007, Kerley et al., 2008), an understanding of the underlying spatial and temporal mechanisms that generate variable impacts in different parts of the landscape, and thus the potential for refuges, remains lacking (Scholes and Mennell, 2008).

Disturbance theory provides a useful framework for investigating these mechanisms, since elephant impacts through feeding are ecological disturbances (Pickett, 1985, Pickett and White, 1985). The spatial and temporal dynamics of elephant feeding consitutes a disturbance regime, including the size and severity of disturbance patches and their spatial distribution, the disturbance frequency and return interval to a particular patch, and the predictability associated with the disturbance's return intervals (Pickett, 1985, Pickett et al., 1989, Caswell and Cohem, 1991, Turner et al., 1993, Turner, 2010). Disturbances can also generate ecological feedbacks that constrain or enhance other disturbances (Dublin et al., 1990, Kerby et al., 2007). The outcomes of these elephant disturbance regimes are evident in the differential accumulation of their impacts over time in different parts of the landscape.

In this chapter, I use disturbance theory to make predictions about how elephant impacts will accumulate in different parts of the riparian landscape, given the elephant disturbance regimes identified in Chapter 3. Within this context, I evaluate the scale(s) of surface water heterogeneity required to generate a range of elephant impacts across the landscape, and hence how the closure of artificial water sources might change these impact patterns. Previously (Chapter 3, section 3.3.3), I demonstrated that elephant patch choice and feeding in the riparian zone were strongly associated with clustered and/or natural waterpoints during the dry season in this landscape. If these patterns of patch choice and feeding remain consistently associated with surface water heterogeneity, disturbance theory predicts that patches with preferred patterns of surface water heterogeneity will accumulate higher levels of impact because they experience more severe and frequent disturbances (or smaller disturbance return intervals; Figure 4.17). Within this context, I expected to find:

i) severe levels of elephant impact accumulated in patches near to waterpoints with a clustered spatial configuration, since these have been shown to be preferred patches for elephant activity (Chapter 3, section 3.3.2), and therefore have higher elephant disturbance frequencies and less time to recover between consecutive bouts of elephant impact. However, if these clustered waterpoints are so close to one another that even the areas between them are frequently visited by elephants, I expected that even the intervening areas would accumulate high levels of impact over time.

ii) In contrast, I expected that patches in the vicinity of less preferred waterpoints (e.g. dispersed waterpoints or randomly configured waterpoints) would have more time to recover between bouts of elephant feeding, and would therefore have lower levels of accumulated impact, and

iii) the areas between dispersed or random waterpoints would have even lower levels of severe accumulated impacts than the dispersed waterpoints themselves, since they are remote from any source of water and therefore represent the least preferred patches. Moreover, the piospheres around the dispersed waterpoints are far enough apart to remain discrete from one another.

In addition, since I demonstrated in Chapter 3 that surface water heterogeneity, as well as elephant spatial responses to this heterogeneity, vary with rainfall over time in this landscape, I expected that:

iv) patches with less consistent or predictable patterns of preferred surface water heterogeneity (such as ephemeral waterpoints, or waterpoints that are seldom or never clustered) would accumulate fewer severe impacts over the longer term because they have longer disturbance return intervals.

Finally, since the provision of artificial water sources has not only reduced distances between waterpoints in this landscape, but has also contributed to the clustering of certain waterpoints (Chapter 2, section 2.4.3), I expected that closure of these waterpoints would:

i) increase disturbance return intervals around waterpoints that are no longer clustered, thereby reducing levels of accumulated impact around these waterpoints; and

ii) increase disturbance return intervals to previously perennial waterpoints.

The riparian zones of ephemeral rivers provided an ideal opportunity for testing these predictions, for several reasons. Firstly, since elephants focus their activities in the riparian zone during the dry season, their impacts accumulate in this part of the landscape towards the end of each dry season, making it likely to find a large enough sample of impacts to draw inferences about the underlying processes and their relationship to surface water heterogeneity. Elephant impacts on woody vegetation are easily identifiable from those of other herbivores (Anderson and Walker, 1974), due to their distinctive mechanism of snapping the main stem or branches, and stripping leaves or bark. Therefore, it is possible to distinguish elephant impacts from those of other abiotic such as wind and fire, or biotic agents such as impala. Elephant impacts on woody vegetation are also discernible for several years after the feeding event (Anderson and Walker, 1974), making it possible to investigate the long-term patterns of impact that have accumulated over several years with varying rainfall. Furthermore, since ephemeral rivers provide point sources of water, rather than the linear sources provided by perennial rivers, it is possible to relate the spatial patterns of accumulated impact in riparian patches to a variety of waterpoint spatial configurations, as well as proximities, not possible along continuously flowing sources of surface water. Finally, since fire is uncommon in riparian zones, its confounding influence as a disturbance agent for riparian woody vegetation can be discounted.

Understanding how, and under what conditions, elephant impacts accumulate in particular parts of the landscape over time will enhance our understanding of the role of surface water heterogeneity in generating spatial and temporal refuges from elephant disturbance.

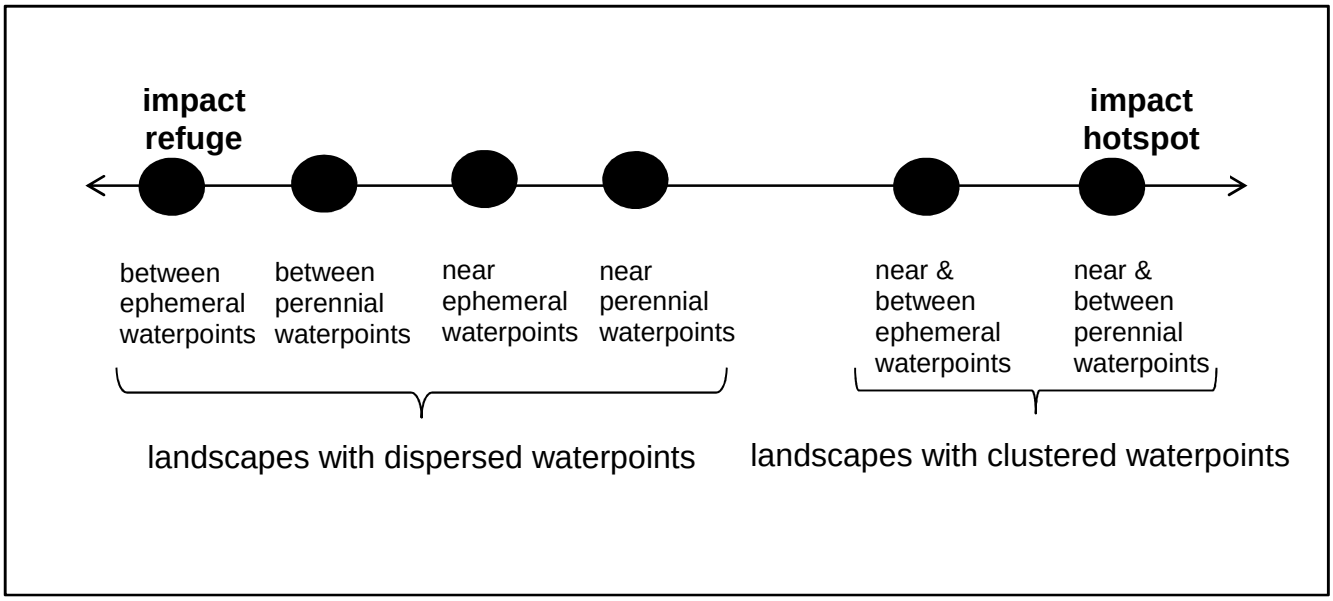

Figure 4.17 Diagrammatic representation of the hypothesized relationship between surface water heterogeneity and the existence of spatial and temporal refuges from elephant impact

4.2. Methods

The methodology for this chapter is built on the heterogeneity approach developed in the preceding two chapters. Specifically, it relies on using the spatially explicit approach developed in Chapter 2 (section 2.3.1) to test for patchiness in the levels of elephant impact accumulated in different parts of the riparian landscape (Figure 2.2), and then using the spatial regression technique incorporated into the approach in Chapter 3 (section 3.2.4), to investigate the contribution of surface water heterogeneity towards generating the observed patterns of impact (Figure 3.9). I advanced the heterogeneity approach further in this chapter by making use of the predictive capabilities of the local spatial regression model, in this case to evaluate how levels of elephant impact might be expected to change should all artificial sources of water be removed (Figure 4.18).

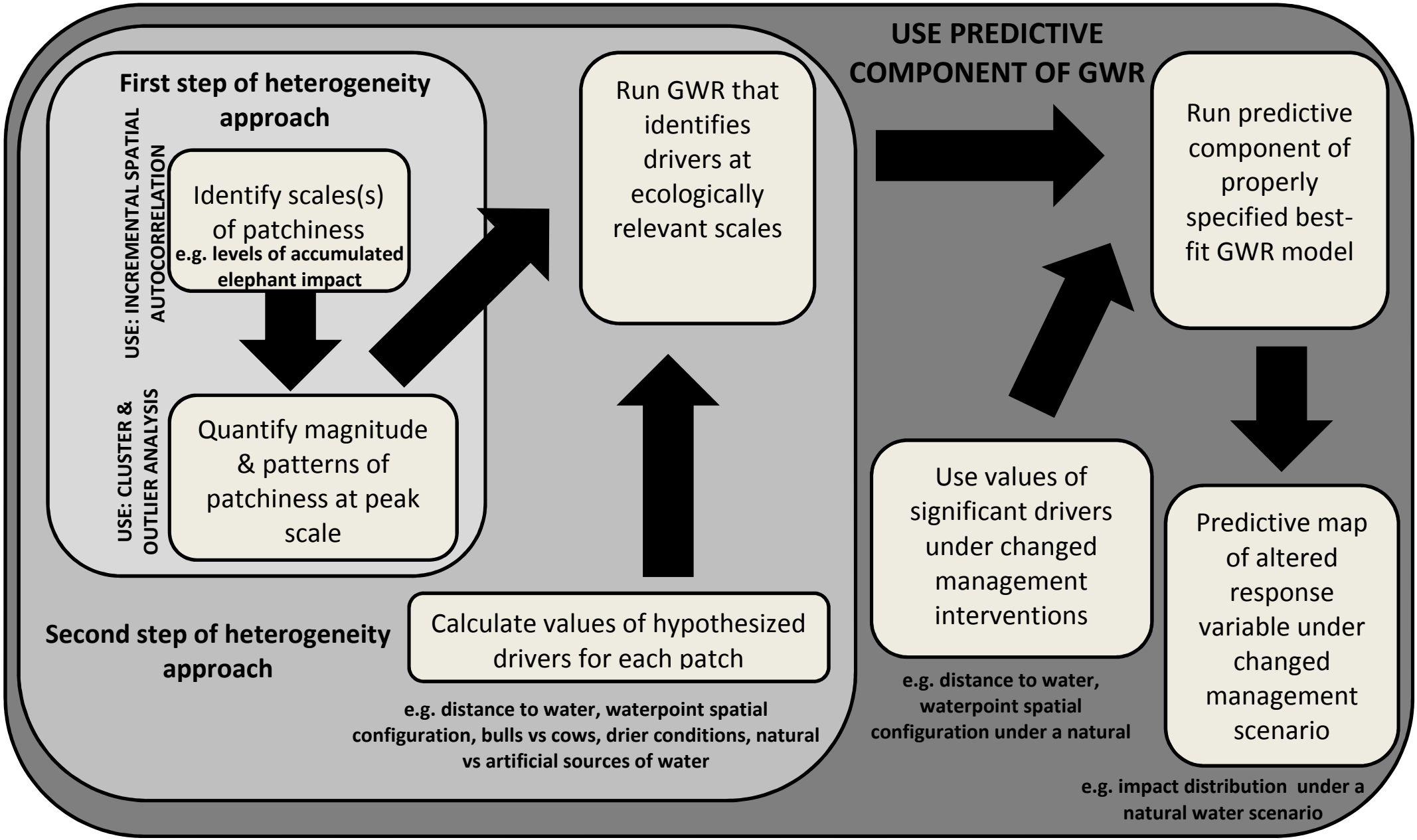

Figure 4.18 Diagrammatic representation of the third component of the heterogeneity approach, which incorporates the predictive component of the GWR.

4.2.1. Vegetation surveys to quantify accumulated elephant impacts

I measured levels of accumulated elephant impact on woody riparian species directly, by means of vegetation surveys in patches at varying distances from waterpoints with different spatial configurations along three ephemeral rivers in the study area. I selected a total of 143 sites for vegetation surveys along the Shingwedzi (n = 69), Phugwane (n = 68) and Mphongolo (n = 6) rivers (Figure 4.19). Selection of sites was based primarily on incorporating patchiness across a range of surface water proximities, spatial configurations and persistences through the dry season, while remaining sufficiently accessible from the Shingwedzi base camp. Vegetation surveys were carried out annually at the end of each of three dry seasons (1997 – 1999), in order to capture the entire dry season's impacts. During the first season, all trees encountered within each of five 30 x 30-m quadrats were surveyed at each site. Asymptotes of species-area (Rosenzweig, 1995) and similarly plotted "impact-area" curves (signifying when the cumulative proportion of trees with impacts reached an asymptote) indicated that this method was oversampling trees at each site. Consequently, in subsequent years the same survey method was employed, but along variable-length transects, rather than in quadrats. The length of each transect was determined by surveying trees until species-area and impact-area curves reached an asymptote. This ensured that (i) sufficient and representative samples of the species present and trees impacted had been surveyed at each site, (ii) that it was possible to increase the number of survey sites, and hence incorporate more variability in water distribution, in the available time. Transect width was also variable so as not to underestimate large trees (Mueller-Dombois, 1972) – each tree whose stem fell within 2 m of the transect line, as well as each tree >5 m in height whose canopy fell within 2 m of the transect line, was surveyed.

For each tree encountered either in the quadrats or along the transects, an expert field ranger confirmed whether the impact had been caused by elephants or other agents such as fire, wind or other browsers. Each tree was then assigned an impact severity class based on the percentage of the tree impacted by elephants (none = 0%, light = <25%, moderate = 25 – 50%, severe = 50 – 75% and very severe = >75%; sensu (Anderson and Walker, 1974, Smallie and O'Connor, 2000, MacGregor and O'Connor, 2004). Impacts that had accumulated over previous years were distinguished from fresh impacts by means of the colour of the exposed wood in the affected area, since previous seasons' impacts turn grey after being exposed to rainfall (Anderson and Walker 1974, Ben-Shahar 1993). I was interested only in

old impacts for this component of the study, since this represented several years' accumulation of elephant impacts, and hence the outcome of variable disturbance regimes over time. As such, impacts accumulated over several seasons were expected to signify the outcome of varying spatial and temporal determinants of elephant feeding over several years, and with varying rainfall conditions. It was not possible to determine exactly how many previous years' impact could be discerned. Therefore, henceforth I simply refer to this impact as impact accumulated over the longer term (as opposed to the fresh impacts accumulated over the course of a single dry season).

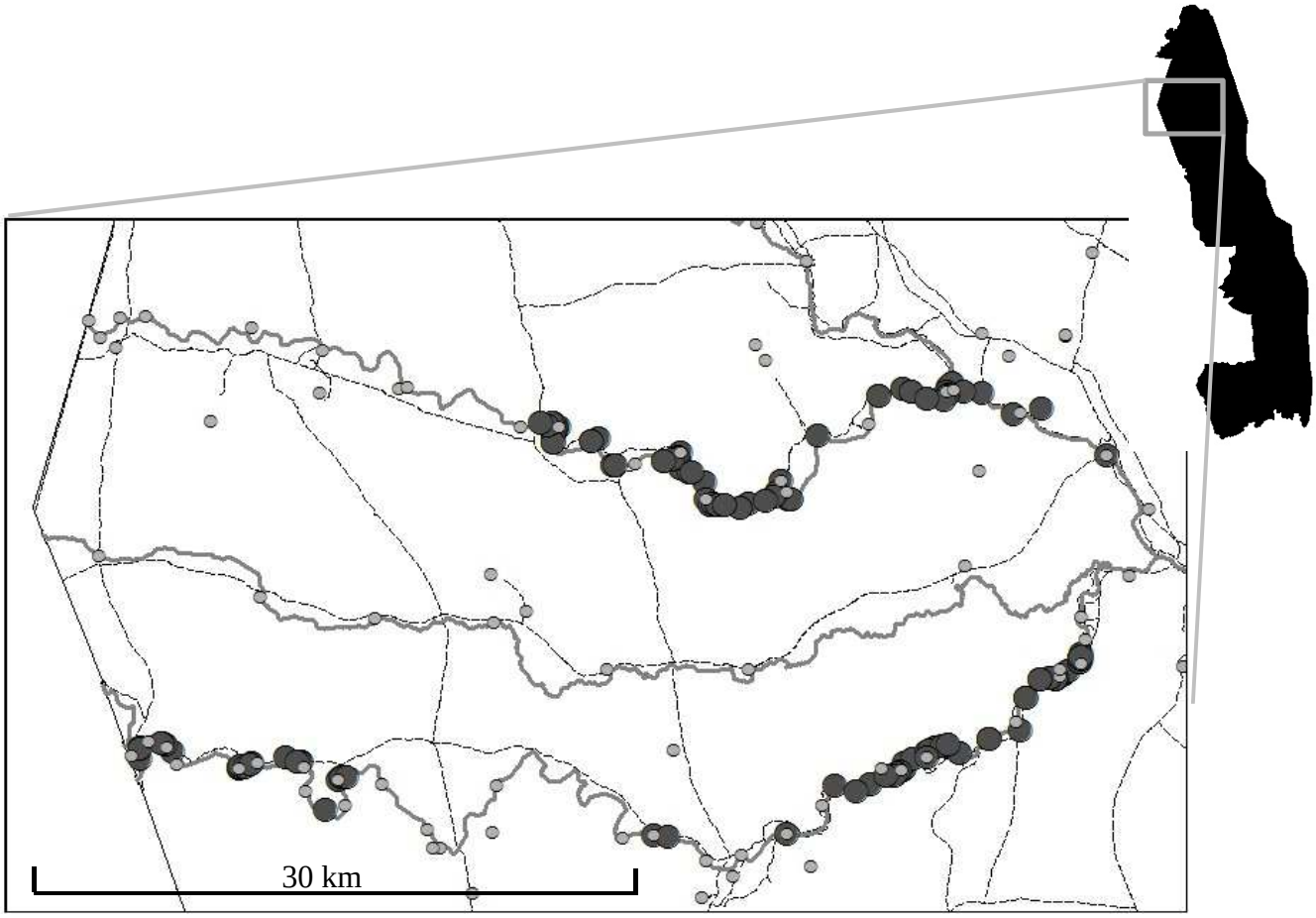

Figure 4.19 Location of vegetation survey sites along three ephemeral rivers in northern KNP (dark grey dots are survey sites, light grey dots are waterpoints, stipled lines are roads)

4.2.2. Quantifying patchiness in the levels of elephant impact

Analysis of the frequency distribution of accumulated impacts revealed that impacts were relatively low (Figure 4.20), given that elephants were at their highest densities in the park's

history at the time of the study (Whyte et al., 1998). An average of nearly 40% of trees had no accumulated impacts at all, and a further 38% had only light levels of accumulated impact (Figure 4.20). Therefore I pooled the proportion of trees with moderate, severe and very severe impacts at each site to obtain a single value for the higher levels of accumulated impact there over the longer term (henceforth referred to as severe accumulated impacts).

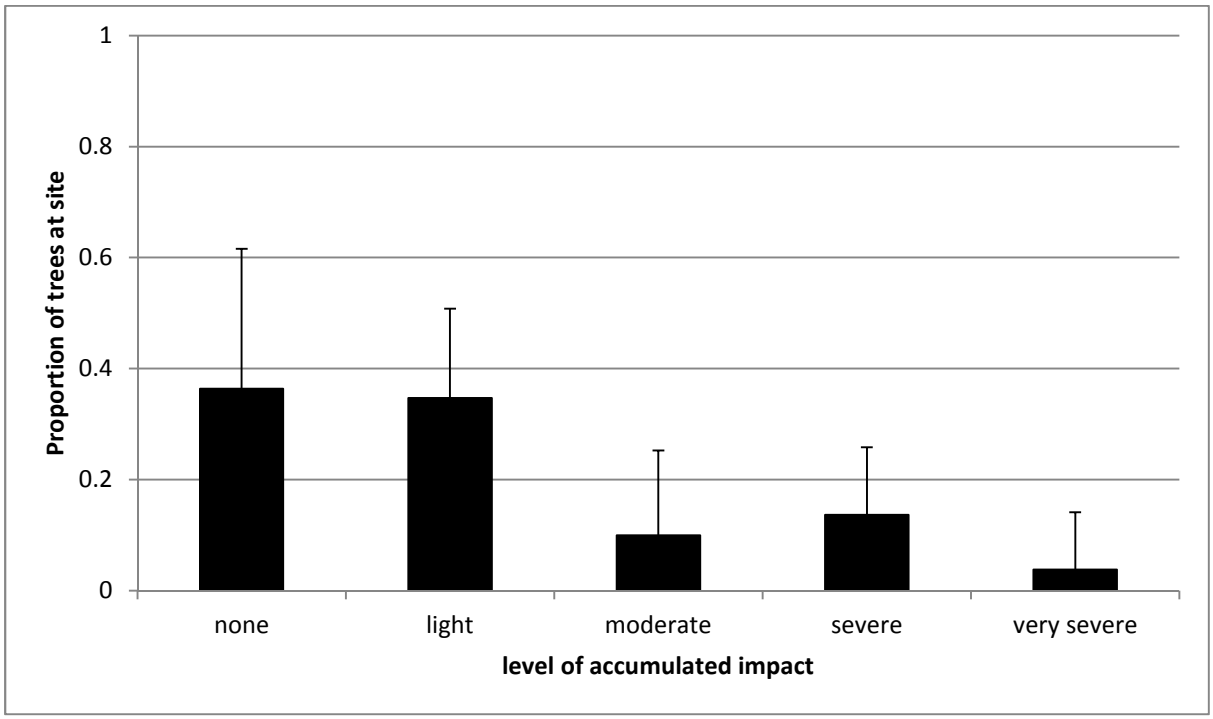

Figure 4.20 Frequency distributions of the levels of accumulated elephant impact along three ephemeral rivers in northern KNP. Values are mean proportions of trees with severe accumulated impact over n = 146 sites; error bars are standard deviations

In keeping with the proposed heterogeneity approach outlined above, and that taken in the previous chapters, I quantified the patchiness of accumulated impacts over the study area by beginning with the test for Incremental Spatial Autocorrelation (ArcMap 10.1; (ESRI, 2001)). This tool measured the intensity of spatial clustering of impacts (Scott and Janikas, 2010), enabling me to identify the peak scale in the levels of impact patchiness to use in the ensuing regression analysis (section 4.2.3).

4.2.3. Investigating the role of surface water heterogeneity in determining patchiness in the levels of elephant impact

Having demonstrated that elephants preferred patches that were in the vicinity of clustered waterpoints in the previous chapter (Chapter 3, section 3.3.2), I used the same linear (though spatial) regression technique to test the role of surface water heterogeneity in generating patterns of accumulated elephant impacts.

I therefore hypothesized that the predictions depicted in Figure 4.17 would be approximated as:

$$y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \beta_4 year1 + \beta_5 year2 + \beta_6 year3$$

Where β is the constant term associated with each explanatory variable in a linear regression, x_1 is the distance to the nearest waterpoint, x_2 is the site's patch context (provided by neighbouring waterpoints), and x_3 is the persistence of the nearest waterpoint through dry periods. Waterpoint persistence was categorised by a dummy variable signifying whether the waterpoint was perennial (persisted through the dry seasons of all years during the study period) or ephemeral (persisted through only the wet year of the study period), using the water database compiled for Chapter 2. The years of the study were included to account for the fact that consecutive sampling years would inherently accumulate additional impacts to those observed in previous years. As in the previous chapter, I tested the possible modulating effects of differences in elephant gender, varying rainfall conditions and natural versus artificial water, by including these as interactions terms with the surface water variables described above.

I determined water proximity from each survey site to its nearest waterpoint using the water database compiled in Chapter 2 (section 2.2) and the Near tool in ArcMap 10.1 (ESRI, 2001). Since the previous chapter's results indicated that elephants focused patch choice around natural water, at least over the short term, I also included proximity to the nearest natural source of water as a possible explanatory variable. The patch context for each site was determined by creating a neighbourhood around each site using ArcMap 10.1's Buffer tool. The neighbourhood size was determined using the peak scale of impact patchiness found by the Incremental Spatial Autocorrelation described above (this chapter, section 4.2.2), since this peak signifies the scale(s) at which there are underlying spatial processes at work (Scott and Janikas, 2010). I then used the Spatial Join tool (ESRI, 2001) to count the number of

waterpoints falling within each site's neighbourhood. This value represented the site's patch context, or spatial configuration of waterpoints neighbouring the survey sites (including those in the adjacent interfluves).

In keeping with the heterogeneity approach developed thus far in the thesis, I made use of the local form of linear regression (Geographically Weighted Regression (GWR); (Fotheringham et al., 2003)) to account for possible nonstationarity in the relationship between surface water heterogeneity and severe levels of accumulated elephant impact. As explained in detail in Chapter 3 (section 3.2.2), this involves first finding a properly specified global Ordinary Least Squares (OLS) regression model (Scott and Janikas, 2010), using ArcMap 10.1's (ESRI, 2001) Exploratory Regression tool. This tool identifies the full set of explanatory variables that effectively capture the inherent spatial structure in the dependent variable, trying all possible combinations of explanatory variables to see which models pass all of the necessary OLS requirements. I made use of an Inverse Distance weighting method to create the required spatial weights matrix (Fortin et al., 2012), based on the assumption that vegetation survey sites further away were less likely to contribute to a focal site's neighbourhood than sites closer by.

Before finding a properly specified OLS model, I used the resultant Summary of Variable Significance output to test the prediction that more severe impacts would accumulate in patches with more persistent patterns of preferred surface water heterogeneity, as identified in the previous chapter (Chapter 3, section 3.3.3). I inferred persistent patterns of surface water heterogeneity from the patterns I had observed during the driest year of the study period (1998; see Study Area in section 1.7, Chapter 1), when the study area experienced less than half (255 mm) of the long term mean annual rainfall (450 mm; Gertenbach (1980)), assuming that water that persisted through this driest year was likely to persist through other dry years over the longer term. I included patterns of surface water heterogeneity in the average (1997) and wet (1999) years to represent comparative patterns of surface water heterogeneity in wetter conditions. The Summary of Significance tables were then used to test whether the dry year's surface water heterogeneity patterns were most strongly associated with levels of accumulated impact, as predicted.

4.2.4. Predicting the effect of complete closure of artificial water sources on patterns of elephant impact

Having obtained the GWR model as described above, I assessed the effect of complete closure of artificial water sources in the study area on patterns of accumulated elephant impact using the predictive component of the GWR tool in ArcMap 10.1 (ESRI, 2001). This involved re-running the GWR model with the addition of the DtW and patch context variables without any artificial water sources in the tool's predictive input (Scott and Janikas, 2010). The GWR output then provides a new variable representing the predicted response. In this way I could compare the observed patterns of elephant impact in the presence of artificial water sources with the expected patterns after complete closure of all artificial water sources. I also used the Incremental Spatial Autocorrelation tool to test how the scale(s) of elephant impacts might change after complete borehole closure.

4.3. Results

4.3.1. Patchiness in the levels of elephant impacts across the riparian landscape

Despite the fact that sources of surface water in the study area were seldom >5 km apart, levels of elephant impact were patchily distributed rather than homogenous across the riparian landscape (Figure 4.21). This patchy accumulation of impacts was to be expected, given the patchy patterns of movement and feeding uncovered in the previous chapter (Chapter 3, section 3.3.1). Furthermore, patchiness of elephant impacts peaked at 1500 m (Figure 4.21), matching the scales of elephant patch choice and feeding during visits to these riparian zones (Chapter 3, section 3.3.1).

A second peak in the patchiness of accumulated impacts was observed at 7500 m (Figure 4.21). In cases where more than one peak in patchiness is identified, further analyses are usually undertaken using the scale that most closely fits the process being examined, often the first peak (Scott and Janikas, 2010). Since elephant patch choice and feeding most closely matched the first peak in impact patchiness (1500 m), I focused the ensuing analyses at this scale and did not explore the drivers of accumulated impacts at any other scales.

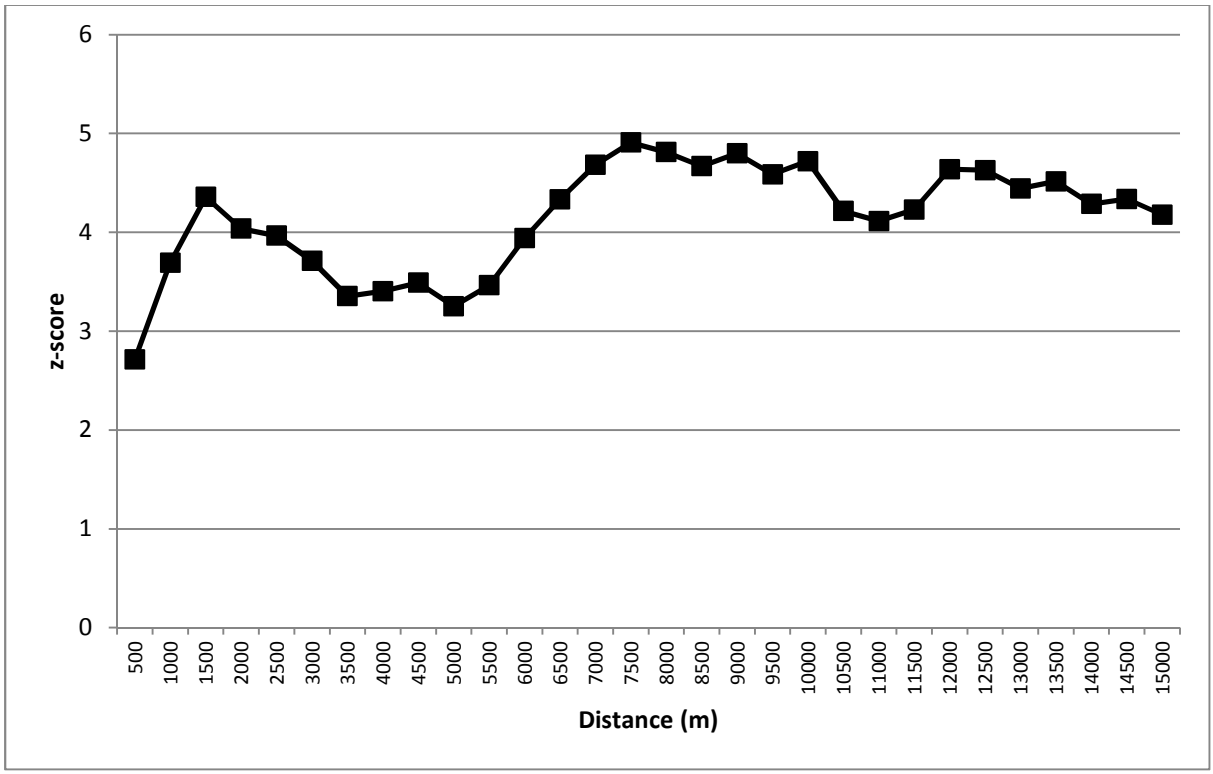

Figure 4.21 Incremental spatial autocorrelation of patches of severe accumulated elephant impacts on riparian woody trees along three ephemeral rivers in northern KNP, indicating peaks in impact clustering at 1500 m and 7500 m

4.3.2 Role of surface water heterogeneity in generating patchiness in the levels of elephant impact

Overall, the variables describing impact accumulation closely resembled those describing elephant patch choice and feeding. For example, the distance to natural water sources was a stronger determinant of impacts than when all sources of water were considered together (Table 4.4), reflecting elephant preferences for moving through the riparian zone in the vicinity of natural surface water (Chapter 3, section 3.3.3). Similarly, the consistently good explanatory power of patch context (84% of models) reflected elephant preferences for clustered waterpoints when crossing the riparian-upland boundary (chapter 3, section 3.3.1). Interestingly, even though elephant impacts accumulated in the vicinity of natural waterpoints, both natural and artificial water sources contributed to the patch context of these waterpoints as perceived by elephants.

Variables representing the most consistent patterns of surface water heterogeneity, lasting even through the driest year of the study period, provided the best explanatory power for levels of impact accumulation in the riparian zone (Table 4.4). This supported the prediction that impacts were likely to accumulate where intervals between bouts of elephant disturbance were smaller, in patches with consistently preferred patterns of surface water heterogeneity. The lower levels of impact accumulated in the vicinity of ephemeral waterpoints further substantiated this argument (Table 4.4).

Accordingly, the best fit global OLS model describing levels of accumulated impact in this landscape included distance to water, patch context and waterpoint persistence (Table 4.5), as predicted by the linear equation proposed in section 4.2.3. However, although the OLS model supported all of my predictions, and was statistically significant ($p < 0.00005$, d.f. = 6, 136), it only explained 44% of the variability in levels of accumulated impact (Table 4.5).

Table 4.4 Consistency of significant variables explaining levels of elephant impact, determined by exploratory regression. "Average", "dry" and "wet" refer to years during the study period with annual rainfall at, below and above the long-term annual mean rainfall for the study area, respectively

Variable	%significant	%negative	%positive
distance to natural water (dry)	96.96	100	0
year 1 (average)	96.56	100	0
distance to natural water (average)	95.13	99.96	0.04
year 3 (wet)	86.64	0	100
nearest waterpoint ephemeral	84.9	100	0
waterpoint configuration (dry)	83.82	0	100
nearest waterpoint perennial	56.53	10.67	89.33
landscape water context (average)	49.62	1.68	98.32
waterpoint configuration (average)	45.55	0.04	99.96
year 2 (dry)	40.85	75.94	24.06
distance to any source of water (dry)	33.8	57.05	42.95
natural surface water context (dry)	31.6	23.25	76.75
waterpoint configuration (wet)	25.61	8.19	91.81
distance to any source of water (wet)	23.25	77.07	22.93
distance to natural water (wet)	23.05	49.42	50.58
distance to any source of water (average)	11.39	84.86	15.14
natural waterpoint configuration (wet)	1.4	41.75	58.25

Table 4.5 Comparison of global (OLS) and local (GWR) models of factors associated with the accumulation of elephant impacts. "Average", "dry" and "wet" refer to years during the study period with annual rainfall at, below and above the long-term annual mean rainfall for the study area, respectively

Response variable	**OLS adjusted r^2**	**OLS AICc**	**Jarque-Bera p-value (df)**	**Koenker (BP) p-value (df)**	**Joint F-statistic p-value$_{df}$**	**factors included**	**t-statistic**	**(robust) p-value**	**GWR adjusted r^2**	**GWR AICc**
Proportion of trees at each site with moderate, severe or very severe levels of accumulated impact	**0.441**	**-103.16**	0.367	0.266_6	<0.00005 $df_{6,136}$	year 1 (average) year 2 (dry) nearest waterpoint ephemeral distance to nearest natural waterpoint (dry) distance to any waterpoint (dry) waterpoint configuration (dry)	-0.254 -0.165 -0.193 -0.00002 0.00003 0.049	0.000001 0.000891 0.000027 0.000209 0.0051 0.0005	**0.528**	**-116.31**

A thematic map of the levels of accumulated impact at each of the vegetation survey sites provided clues as to this relatively poor explanatory power. Only 15 of the 143 sites had high levels of accumulated impact (>50% of the trees with moderate, severe or very severe accumulated impacts), while the remainder of the sites had few or no trees (<40%) with high levels of accumulated impact (Figure 4.22). Moreover, the heavier impacts occurred in hotspots around waterpoints, rather than attenuating with distance from water (Figure 4.22). However, patches of low impact between these hotspots could not be differentiated among patches between clustered versus dispersed or randomly configured waterpoints as predicted.

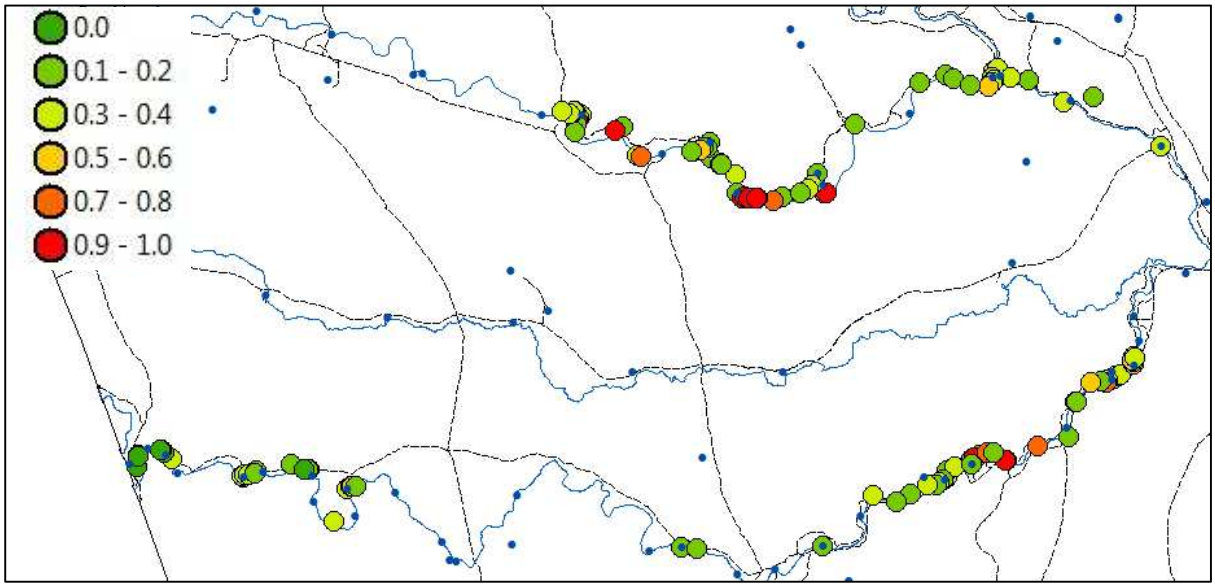

Figure 4.22 Levels of accumulated elephant impact along three ephemeral rivers in northern KNP (displayed as the proportion of trees at each site with moderate, severe, or very severe levels of impact)

Accordingly, patterns of accumulated impact coincided well with patches of preferred movement and feeding in the riparian zone that had been identified in Chapter 3 (section 3.3.1). For example, all of the patches with higher levels of accumulated elephant impact (specifically, Zari, Boomplaas and Sandpiper windmills along the Phugwane River, and the Redrocks and Joao-Spirowiri waterpoint complexes along the Shingwedzi River), were also patches preferred for movement through the riparian zones of these rivers (Chapter 3, section 3.3.2). In contrast, only two preferred patches were not patches of greater impact. The local GWR model only increased explanatory power to 53% after accounting for regional variation (Table 4.5). However, it revealed significant regional variation in the relationship between surface water heterogeneity variables and the accumulation of elephant impacts across the

riparian landscape (Table 4.5). Specifically, the model explained impact accumulation much better (up to 61%) along the western reaches of the Shingwedzi River, and a lot poorer (as little as 36%) in the eastern portions of the study area (Figure 4.23).

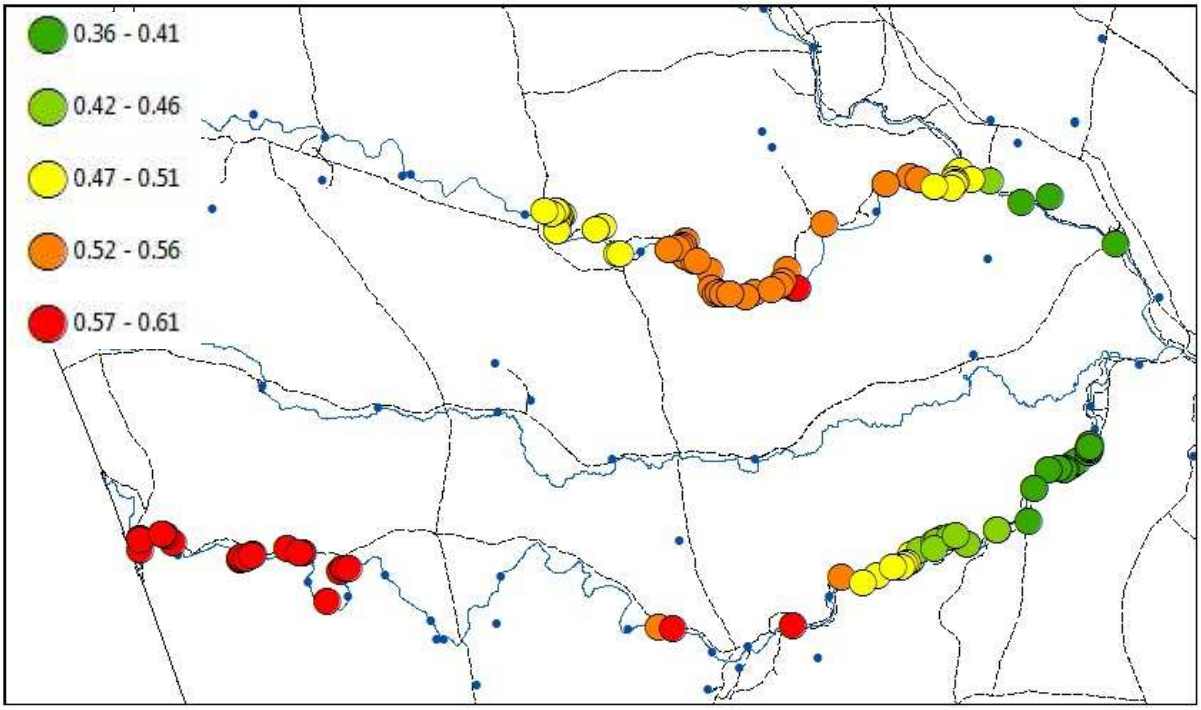

Figure 4.23 Local r^2 values describing the strength of the relationship between levels of elephant impact and surface water heterogeneity along three rivers in northern KNP

Mapping the GWR co-efficients of the surface water variables in the best-fit model provided insights into possible sources of this nonstationarity. For example, along the western reaches of the Shingwedzi River, where ephemeral waterpoints were more abundant, having an ephemeral waterpoint nearby meant lower levels of accumulated impact. However, this relationship did not hold very strongly elswhere in the study area (Figure 4.24). Similarly, although proximity to natural waterpoints emerged as an important explanatory variable, it was strongest along the eastern reaches of the Shingwedzi River (Figure 4.24). In contrast, along the Phugwane River, which had few ephemeral or natural water sources, impacts accumulated close to any source of surface water (Figure 4.24). Patches with larger numbers of neighbouring waterpoints consistently generated higher levels of accumulated impact, although the strength of this relationship was modulated by which other surface water variables were important for that patch (Figure 4.24).

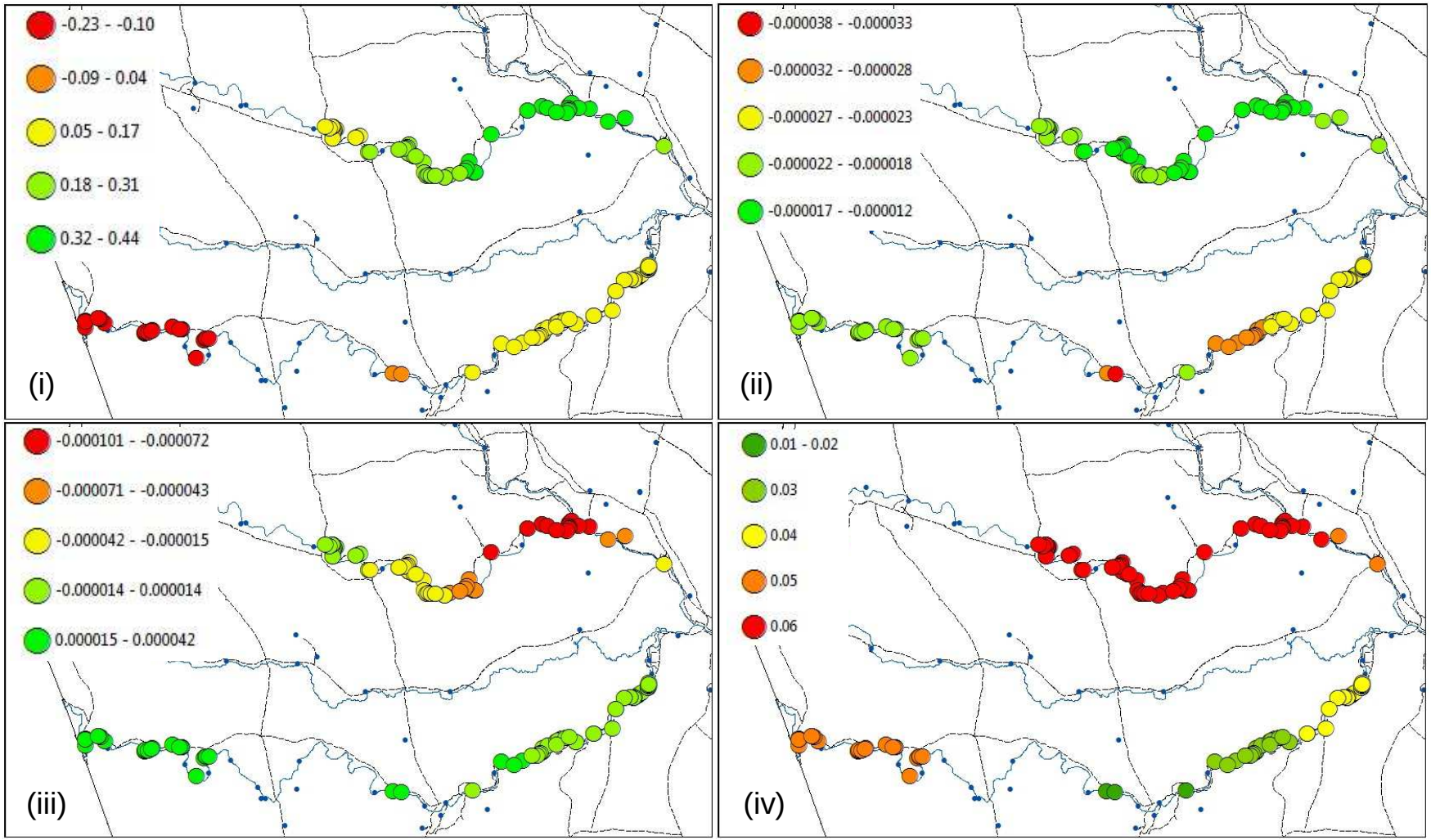

Figure 4.24 Local co-efficient values for (i) the nearest waterpoint being ephemeral, (ii) distance to the nearest natural waterpoint, (iii) distance to any waterpoint, and (iv) patch context provided by neighbouring waterpoints, as determinants of the accumulation of elephant impacts in different parts of the riparian landscape in northern Kruger National Park

4.3.3 Predicted patterns of elephant impact under a natural surface water scenario

Removal of artificial water sources was predicted to alter both the location and levels of accumulated elephant impacts dramatically. Although the proportion of patches with severe levels of accumulated impact would experience negligible change, fewer patches were predicted to have no accumulated impacts at all, indicating an overall increase in moderate levels of impact (Figure 4.25). Contrary to my expectations, this suggests an homogenisation of impacts upon reverting to natural patterns of surface water heterogeneity, rather than increasing heterogeneity as suggested by Owen-Smith et al. (2006).

Patches of high impact were predicted to shift away from the Redrocks-Spirowiri and Zari waterpoints under a natural surface water scenario, and instead became focused primarily along the western reaches of the Shingwedzi River where most of the ephemeral waterpoints occurred (Figure 4.25). Again this result was contrary to my prediction that impacts would accumulate around the more persistent natural waterpoints. Instead, removal of artificial water sources would leave this area with the highest number of neighbouring waterpoints, emphasizing the importance of patch context.

Using the impact levels predicted under a natural water scenario by the GWR, Incremental Spatial Autocorrelation revealed that these dramatic changes to the locations and levels of elephant impact were accompanied by equally dramatic shifts in the scales of impact patchiness (Figure 4.26). Reflecting the apparent homogenisation of elephant impacts reported above, the scales of patchiness were predicted to increase three- to six-fold. Furthermore, the first peak in patchiness would increase from 1500 m to 9000 m (Figure 4.26).

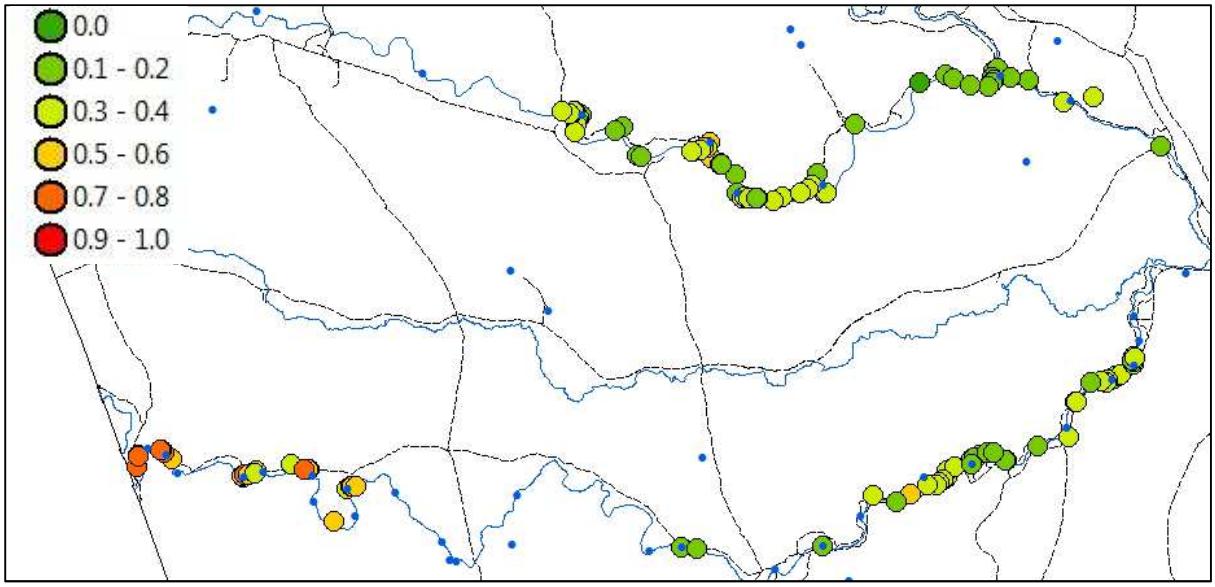

Figure 4.25 Predicted elephant disturbance regimes across the riparian zones in the study area after the removal of all artificial sources of surface water. Levels of impact indicate the proportion of trees at a site with moderate, severe or very severe impact

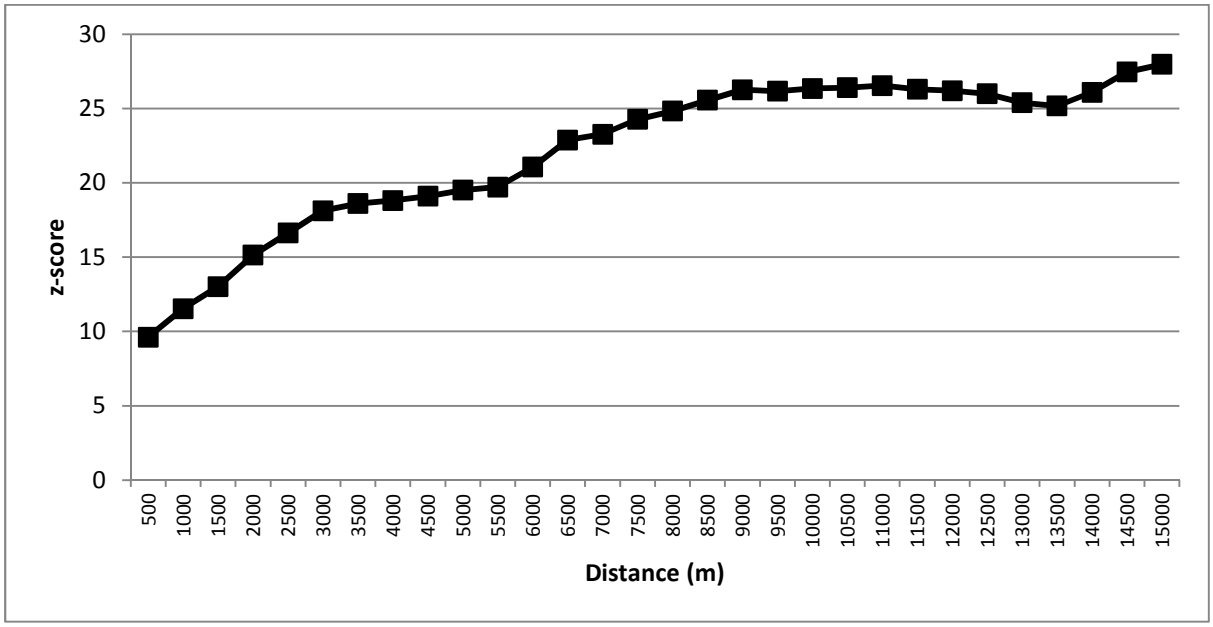

Figure 4.26 Predicted scales of patchiness in the levels of elephant impacts in the study area following the closure of all artificial sources of water, as calculated by Incremental Spatial Autocorrelation (ArcMap 10.1). The first peak in patchiness was predicted to increase from 1500 m to 9000 m

4.4. Discussion

In this chapter, I explored the role of surface water heterogeneity in generating patchy levels of elephant impact across a savanna landscape with abundant water supplies. The work differed from previous studies (Pellew, 1983, Wackernagel, 1993, Kerley and Landman, 2006, Holdo, 2007, Stokke et al., 2014{Parker, 1999 #3713, Asner et al., 2009, Landman et al., 2012, Cumming, 1982, Cumming et al., 1997, Buechner and Dawkins, 1961, Van Wyk and Fairall, 1969, Laws, 1970, Anderson and Walker, 1974, Rutina et al., 2005, Hofmeyr and Eckardt, 2006, Guldemond and Van Aarde, 2008, Kerley et al., 2008, Landman et al., 2008, Barnes et al., 2008, Moe et al., 2009, Teren and Owen-Smith, 2010, Lagendijk et al., 2011, Fullman and Child, 2012, Rutina and Moe, 2014, Skarpe et al., 2014a)}by quantifying the actual levels of elephant impact to infer underlying spatial processes, rather than relying on purported elephant effects on woody composition and structure that are difficult to tease apart from other drivers of vegetation dynamics. Using the scaled, contextual approach developed in earlier chapters, the role of surface water heterogeneity in generating these impact patterns could be explored beyond previous distance to water measures, using a local regression technique that could account for the spatial autocorrelation and nonstationarity common in complex, heterogeneous systems. This heterogeneity approach exposed the peak scale of elephant impact (1500 m) in this landscape for the first time, revealing a match with the scale of the underlying disturbance regime created by elephant preferences to feed in patches with clustered and/or natural waterpoints (Chapter 3). Incorporating the predictive component of the local regression technique demonstrated that removal of all artificial water sources would not necessarily increase the patchiness of elephant impacts unless these closures were associated with an increase in the remaining clustered natural waterpoints. However, by removing perennially open artificial water sources, the intervals between return visits to these patches would become greater, resulting in reduced levels of elephant impact. In contrast to the contentions of earlier studies, the understanding developed in this chapter indicates that patchy elephant impacts are indeed possible across landscapes with abundant surface water, as long as these water sources have variable spatial configurations and persistence.

4.4.1 Understanding how elephants generate patchy patterns of impact across a heterogeneous landscape

Despite the constraints on measuring amounts of elephant feeding, rather than biomass, in the preceding chapter, the scales of impact patchiness uncovered here (1500 m) matched those of elephant patch choice and feeding demonstrated in Chapter 3 (section 3.3.1). This finding supports the identification of these spatial responses by elephants to the presence and spatial configuration of natural water sources, as the underlying mechanism of patchy impact generation in this landscape.

As with elephant spatial responses to surface water heterogeneity, the accumulation of impacts across the landscape over the longer term more closely approximated "hotspots" of elephant disturbance patterns than a gradual attenuation away from water. This result supports the contention made in the preceding chapter, that linear models based on the piosphere concept of zones of impact nearer to water (Thrash and Derry, 1999, Derry, 2004, Landman et al., 2012) are inappropriate for describing elephant disturbance regimes in this landscape.

This study was restricted to riparian zones, since elephants focus their dry season activities in this part of the landscape. It therefore remains important to determine how the insights gained here apply to the adjacent upland areas where other ecosystem drivers such as fire also play a role in generating vegetation patterns (Levick, 2008). Floods are another type of disturbance that can substantially alter vegetation patterns in riparian zones (Jacobs et al., 2007). Extreme flooding events are predicted to be increase under the influence of global climate change (Jacobson, 1997). Hence it will be important for future studies to consider the interacting effects of elephants and hydrological drivers on riparian vegetation change, particularly given the important contribution that the riparian zone makes to biodiversity (Naiman et al., 1993).

Disturbances typically create spatial heterogeneity in ecological systems (Connell, 1979, Pickett, 1985, Pickett et al., 1989). Even very severe natural disturbances usually do not homogenize the landscape (Turner, 2010). Accordingly, disturbance theory (Pickett and White, 1985, Caswell and Cohem, 1991) provided a useful conceptual framework for understanding how the spatial and temporal heterogeneity of surface water in this landscape resulted in the accumulation of varying levels of elephant impact across the riparian zone. As predicted, the severity of elephant disturbances was highest in patches with preferred

(clustered) waterpoint spatial configurations and/or natural waterpoints, presumably because more elephants visited these patches, and they did so more frequently. As a result, the smaller disturbance return intervals in these patches left these patches with less time to recover before elephants returned to disturb them again. As expected, disturbance intervals were also influenced by waterpoint persistence, with lower impacts at the less predictable, ephemeral water sources, as well as at waterpoints that were less consistently clustered over time. These smaller disturbance return intervals were reflected by lower levels of elephant impact severity.

4.4.2. Implications for the use of water provision to generate variable elephant disturbances

The current understanding generated from DtW studies predicts that complete closure of artificial water sources will increase levels of impact patchiness through greater proportions of the landscape remote from water (Owen-Smith, 1996). In contrast, the scaled, contextual perspective of surface water heterogeneity employed in this thesis predicts that complete closure would cause an overall elevation of impacts, spread more evenly across the landscape. Rather, the key to generating hotspots of elephant impact would be strategic closures or placements of boreholes to create clustered waterpoint configurations, leaving the remaining areas with significantly lower impacts. This underscores the importance of incorporating the spatial configuration of waterpoints into future considerations of water provisioning policies.

Even though elephants preferred natural water, the distribution of artificial waterpoints contributed to the clustering patterns of these natural waterpoints, and hence strategic placement of artificial water sources to generate such clustering is expected to enhance impact patchiness in this landscape. Accordingly, this new contextual understanding suggests that water provisioning as a tool to maintain, restore or even enhance impact patchiness has been underestimated, and therefore prematurely dismissed, in protected areas with abundant water supplies. However, the preference by elephants for clustered waterpoints may differ in landscapes where the distribution and relative abundance of various critical resources differs, because of the particular trade-offs that elephants must make to achieve metabolic balance. Therefore, it is important to gain an understanding of the particular scales and patterns of elephant response to surface water heterogeneity in a landscape before

developing a water provisioning strategy aimed at generating patchy elephant impacts. Spatial tools now exist to optimize such water provisioning strategies.

4.4.3 Avenues for future research

A potentially important omission from this work is that it did not address how the distribution of preferred woody species may potentially modulate the generation of patchy elephant impacts across the landscape. Although elephants are able to tolerate a low quality diet (Stokke and Toit, 2000), and therefore don't need to be selective, it is well known that they do cherry-pick certain plant species (see Chapter 1, section 1.4). Hence, it is possible that the presence or relative abundance of preferred species may play a role in modulating the patterns of accumulated impact in this landscape (Shrader et al., 2012). Finally, the extent to which patches with low levels of impact act as true refuges from elephant disturbance will depend on the susceptibility of the woody species to elephant impacts (O'Connor et al., 2007) in these patches. It is therefore important to include considerations of susceptibility to elephant impact into understanding of the generation of true refuges. Having exposed the underlying mechanism of elephant space use resulting in patchy elephant impacts in this landscape, patterns of woody plant diversity can now contextualised. I will examine this in the next chapter (Chapter 5).

Chapter 5 - Elephant-mediated modifications to biodiversity along a trajectory of change in a heterogeneous landscape

5.1. Introduction

Although elephant populations have declined dramatically over most of Africa (Gillson and Lindsay, 2003), they are still steadily increasing in the southern portion of the continent (Scholes and Mennell, 2008). Consequently, there is widespread concern for loss of susceptible plant species and tall trees through increasing elephant impacts (Pienaar, 1969, Van Wyk and Fairall, 1969, Anderson and Walker, 1974, Coetzee et al., 1979, Sise, 1986, Swanepoel and Swanepoel, 1986, Guy, 1989, Spinage, 1990, Midgley and Joubert, 1991, Addy, 1993, Ben-Shahar, 1993, Cowling, 1994, Cumming et al., 1997, Trollope et al., 1998, Johnson et al., 1999, Kelly, 2001, Cowling and Kerley, 2002, MacGregor and O'Connor, 2004, Skarpe et al., 2004, Hofmeyr and Eckardt, 2006, Holdo, 2007, Kerley et al., 2008, Shannon et al., 2008, Lagendijk et al., 2011, du Toit et al., 2014b, Skarpe et al., 2014a, Skarpe et al., 2014b). Past approaches to this “elephant problem” (Caughley, 1976) were centered around keeping elephant population sizes below a particular ceiling or carrying capacity (Van Wyk and Fairall, 1969). At this level, it was believed that elephant impacts would be in equilibrium with vegetation regeneration. However, over the past two decades, the failure of carrying capacity approaches to protect susceptible species and tall trees (Eckhardt et al., 2001), along with societal pressure about elephant culling, have compelled scientists and managers to search for a new approach to solving the “elephant problem” (Owen-Smith et al., 2006, O’Connor et al., 2007, Scholes and Mennell, 2008).

In the Introductory Chapter, I outlined how the Intermediate Disturbance Hypothesis (IDH; Connell (1979)) has provided a framework for predicting how biodiversity may be reduced under increasing elephant densities (Chapter 1, section 1.5). Under the past Balance of Nature paradigm (Wu and Loucks, 1995), the IDH predicted that maximum diversity

would be found in landscapes where intermediate levels of elephant disturbance were high enough to reduce competitively dominant plant (and associated) species, but not so high as to eradicate impact intolerant species (Figure 5.27).

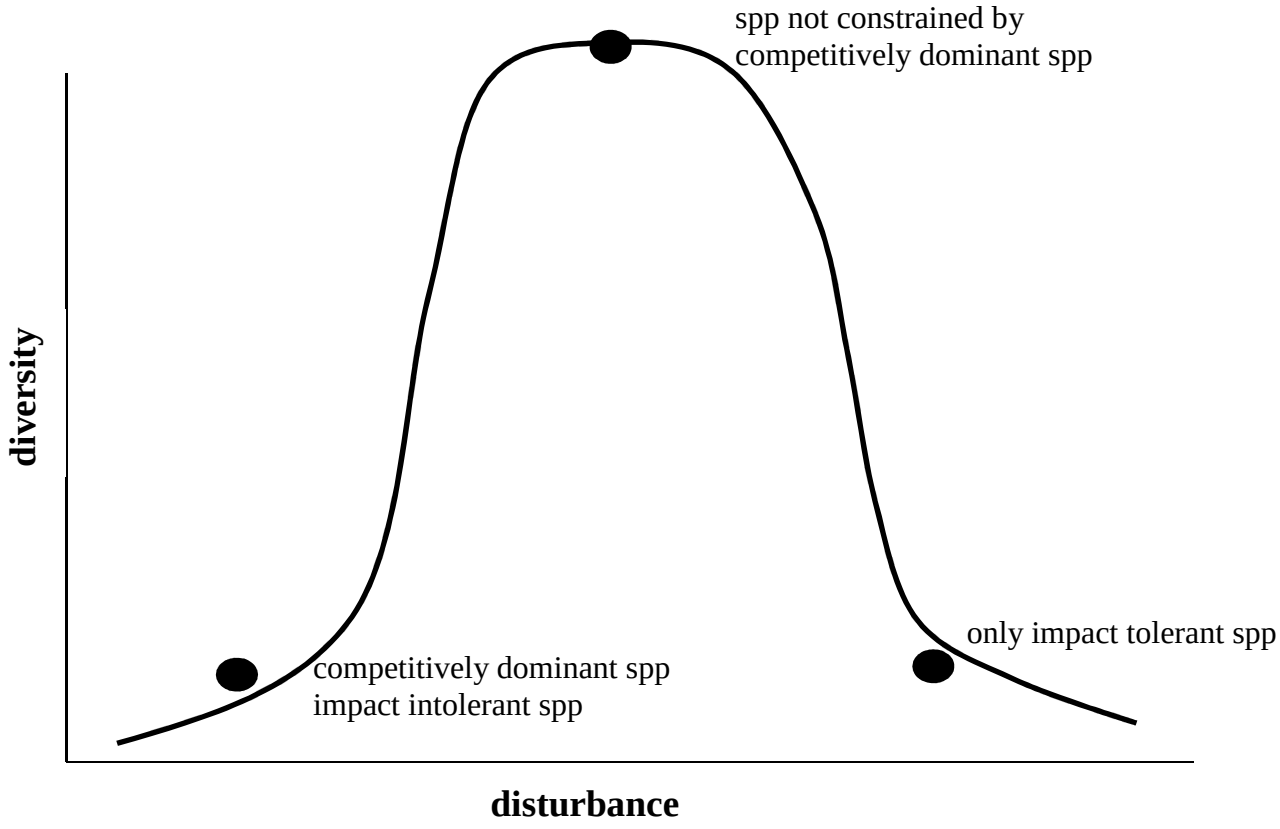

Figure 5.27 Diversity predictions of the Intermediate Disturbance Hypothesis

With the paradigm shift to heterogeneity in the mid-1990's (Wu and Loucks, 1995) came a heterogeneity interpretation of the IDH. Consideration of space and scale (Reynolds et al., 1993, Roberts and Gilliam, 1995) led to the recognition that local elephant-mediated biodiversity losses did not necessarily extrapolate up to broad-scale, regional losses of biodiversity (Chamaillé-Jammes et al., 2007, Kerley et al., 2008). Instead, patches of varying elephant impact could potentially generate metastability (Wu and Loucks, 1995), compensating for local losses at the landscape level (Owen-Smith et al., 2006). Consequently, rather than aiming for a single optimal level of intermediate disturbance across the entire landscape, a heterogeneity interpretation of the IDH promotes the generation of a patch mosaic (Bormann and Likens, 1979, Wiens, 1996, Pickett and Rogers, 1997) of varying disturbance in different parts of the landscape (Hobbs and Huenneke, 1992, Roberts and

Gilliam, 1995, Whyte et al., 1999, Whyte, 2004). The spatially explicit interpretation of the IDH predicts that, as long as these patches of disturbance remain distinct, reduced local biodiversity in patches of high impact will be compensated for at broader levels (Roberts and Gilliam, 1995). In fact, locally severe impacts may even promote local diversity by providing conditions preferred by disturbance tolerant species that would otherwise not colonise a patch (Connell, 1979, Roberts and Gilliam, 1995).

These principles underpin KNP's current elephant management policy, which aims to ensure patchy elephant impacts, rather than to regulate elephant population size or carrying capacity (Whyte et al., 1999, Whyte, 2004). Surface water heterogeneity has been proposed as a means of maintaining such discrete patches of elephant impact (Owen-Smith, 1996, Gaylard et al., 2003, Chamaillé-Jammes et al., 2007, O'Connor et al., 2007, Landman et al., 2012). However, until now understanding the conditions that would generate sufficiently heterogeneous surface water patterns to constrain elephant impacts in this way, as well as the role of water provisioning in reducing or enhancing this heterogeneity, have been restricted to measures of distance to water (DtW; (Redfern, 2002), Redfern et al. (2005), Chamaillé-Jammes et al. (2007), Chamaillé-Jammes et al. (2007), Smit et al. (2007a), Smit et al. (2007c), Grant et al. (2008), Smit and Grant (2009)).

Over the course of the preceding chapters, I have developed a heterogeneity approach that has enabled me to advance this understanding beyond simple DtW, by quantifying the scale(s) and patterns of surface water heterogeneity in a spatially explicit manner that describes waterpoint spatial configurations (Chapter 2). Hence, incorporating the patch context of waterpoints in this way not only provided new insights into the surface water template available to elephants in this landscape, but also as to how elephants responded to this template by selecting patches with clustered spatial configurations (Chapter 3). Understanding these spatial responses to surface water heterogeneity contextualised how these elephant disturbance regimes resulted in a range of impact levels across the landscape, with higher levels of impact in patches with clustered waterpoints, and lower levels where disturbance return intervals were longer due to the lack of preferred surface water traits (Chapter 4). However, whether this patchiness results in true refuges from elephant impact depends on how susceptible the species in these patches are, given their regeneration capacity relative to elephant disturbance return intervals (O'Connor et al., 2007).

The concept of biodiversity itself has shifted from a past focus on species richness to a more comprehensive definition that incorporates hierarchically nested components of compositional, structural and functional diversity (Aubert et al., 2003, Rogers, 2003). This broader perspective of biodiversity across a range of scales and levels of organisation has important implications for understanding elephants as agents of change. For example, losses of a particular component of biodiversity don't necessarily translate into losses of the other components (Roberts and Gilliam, 1995, Aubert et al., 2003, Zebisch et al., 2004). Moreover, changes in one component of biodiversity may be a precursor to changes of the other components of biodiversity, thereby providing an early warning signal of impending change (Roberts and Gilliam, 1995, Aubert et al., 2003). There is still a lack of understanding about which of these components are most susceptible to elephant impacts.

In this chapter I investigate patterns of riparian woody diversity along the ephemeral rivers in northern KNP, incorporating Noss's (1990) more comprehensive perspective of biodiversity by examining several different measures of riparian woody diversity, and inferring the role of elephants by using the heterogeneity interpretation of the IDH. Rather than testing narrowly-focused hypotheses of elephant-induced biodiversity change, which would require controlling or accounting for all other factors potentially driving riparian woody diversity, I make use of multiple lines of evidence gathered in the preceding chapters, with which to interpret the observed patterns of riparian woody diversity. In so doing, I make use of such an adaptive inference method of scientific enquiry (Holling and Allen, 2002) as the final component of the heterogeneity approach developed thus far in the thesis, to pinpoint where the study area lies along a predicted trajectory of change mediated by elephants. Specifically, I made use of the findings about elephant patch choice and feeding from Chapter 3, along with the patterns of elephant impact demonstrated in Chapter 4, to make the following predictions about elephant-mediated patterns of riparian woody diversity along such a trajectory of change in the study area, according to a heterogeneity interpretation of the IDH (Figure 5.28):

i) given the patchy, but relatively low, levels of elephant impact demonstrated in Chapter 4 (nearly 40% of trees measured had no signs of accumulated elephant impact at all), riparian woody diversity would be patchy at scales matching the spatial patterns of elephant patch choice and feeding, and hence at the scales of impact patchiness across the landscape; and therefore

ii) patches of higher biodiversity would coincide with the patches representing less preferred (randomly configured or dispersed) waterpoints or longer elephant disturbance return intervals (ephemeral or less consistently clustered waterpoints; Chapter 4); consequently

iii) even though this landscape has some patches of severe elephant impact, regional diversity would be higher than local diversity, since the refuge patches away from severe elephant impacts compensate for local biodiversity losses; however

iv) levels of elephant impact may not be severe enough, even in the most heavily impacted patches, to eliminate susceptible species or to induce the growth of impact tolerant species. If this is the case, I expect diversity patterns either to be (a) homogenous (because elephant impacts are not severe or frequent enough relative to the vegetation's capacity for regrowth), or (b) patchy, with an inverse relationship to impact levels, but restricted to changes in riparian woody structural diversity; accordingly, I expect that

v) patterns of riparian woody diversity will be only weakly associated with levels of accumulated elephant impact across the landscape

By providing the first empirical test of a heterogeneity interpretation of the IDH, this study aims to contribute towards evaluating the basis of current elephant management philosophies in African savannas. In addition, illuminating the extent of elephant-induced biodiversity changes in this landscape will place KNP along a trajectory of biodiversity change, facilitating the prediction of how biodiversity is expected to change in the face of a growing elephant population there. Finally, by inferring elephant-induced changes to the patterns of three different components of riparian woody diversity, the results will have implications for which indicators would be best for monitoring the early warning signals of elephant-induced biodiversity loss in this landscape.

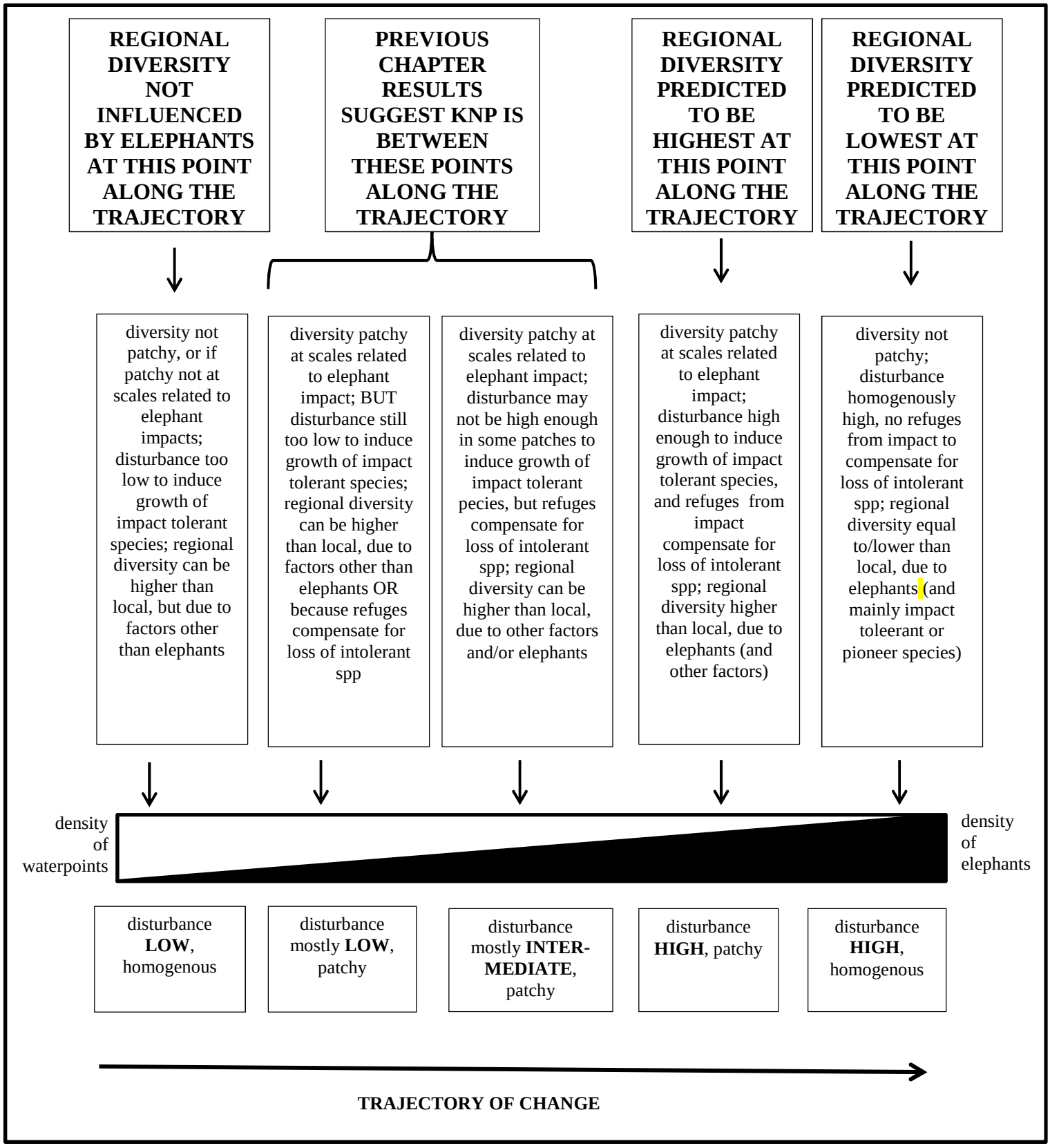

Figure 5.28 Diagrammatic representation of the hypothesized trajectory of change following increasing elephant densities and varying patterns of surface water heterogeneity in riparian zones in northern KNP. The hypothesized trajectory of change stems from a heterogeneity interpretation of the Intermediate Disturbance Hypothesis (Connell, 1979), using the patterns of elephant patch choice, feeding and impact distribution uncovered in Chapters 3 and 4

5.2. Methods

Having used the understanding developed in previous chapters in the context of a heterogeneity interpretation of the IDH, and using this framework to predict a trajectory of elephant-mediated change in this riparian landscape (Figure 5.28), the methodology for this chapter comprised three key steps. The first step involved quantifying multiple measures of riparian woody diversity, and assessing the scale(s) and patchiness of these diversity patterns across the riparian landscape, to evaluate whether the contention that elephants have homogenised woody diversity is supported. Secondly, I assessed how closely patterns of patchiness in riparian woody diversity matched patterns of elephant impact, in terms of both the scale and the location of impact hotspots and altered woody diversity, to look for evidence that elephants were the cause of these patterns. The final step involved searching for evidence of regional compensation for local diversity losses, through comparisons of regional and local levels of diversity, as well as by investigating whether any local losses of diversity may have been replaced by commensurate gains in other forms of riparian woody diversity. In this way I could infer whether patchy impacts were severe enough to induce the generation of impact tolerant versus impact intolerant species in different parts of the landscape. Making use of the same survey sites and study area as the previous chapters enabled me to integrate all the evidence from my findings about the patterns of surface water heterogeneity, elephant space use and associated patterns of impact accumulation, into the heterogeneity interpretation of the IDH. In this manner, I adaptively inferred the contribution of elephants to the observed patterns of riparian woody diversity in this landscape.

5.2.1. Quantifying patchiness in patterns of riparian woody diversity

During the field surveys undertaken to measure elephant impacts for the previous chapter (Chapter 4, section 4.2.1), I identified each tree encountered to species level, wherever possible. In addition, I incorporated tree height as an index of woody structure by estimating trees relative to a 2-m reference board, and placing them into one of six height classes: <50cm, 50 – 100 cm, 100 – 200 cm, 200 – 400 cm, 400 – 800 cm or >800 cm. I then calculated the structural diversity, species diversity and species richness at each site. In this way, I incorporated a measure of evenness for both height class distribution and riparian woody species (diversity), as well as the traditionally evaluated number of species (richness).

Structural and species diversity were calculated using the Shannon index of evenness (Shannon, 1948):

$$H' = -\sum_{i=1}^{R} p_i \ln p_i$$

Where p_i is the proportion of individuals belonging to the *i*th type of height class or species. Species richness was simply quantified as the total number of woody species encountered at each survey site (Spellerberg and Fedor, 2003).

In keeping with the heterogeneity approach developed in the preceding chapters, I made use of Incremental Spatial Autocorrelation in ArcView 10.1 (ESRI, 2001) to test the prediction that patterns of riparian woody diversity would be patchy in the study area. By investigating the spatial autocorrelation of the three local diversity measures over a series of distances, this approach provided an objective means of identifying the scale(s) at which these patterns were patchy (Scott and Janikas, 2010). Accordingly, the three measures of riparian woody diversity served as the response variables for each of the three independent tests of Incremental Spatial Autocorrelation (for details of the method, refer to previous chapters).

5.2.2. Testing for regional compensation for locally reduced riparian woody diversity

Testing the next prediction involved assessing whether patches of high elephant disturbance that had lower local diversity were compensated for in patches that had escaped severe elephant impacts. To do this, I tested whether the levels of any of the three measures of riparian woody diversity that may have been reduced in patches of high impact were retained elsewhere in the riparian landscape. I did this by plotting local elephant disturbance (measured as the proportion of trees at each site with moderate, severe or very severe accumulated impacts) against each measure of riparian woody diversity for each of the survey sites. I then pooled the data from all the study sites to calculate regional values for structural and species diversity, as well as for species richness, and plotted these as separate series along with the plots of local diversity values. I inferred the possibility of local

compensation for biodiversity losses in other patches if regional diversity values were higher than local diversity values.

However, since increased diversity at regional scales could simply be an artefact of species-area relationships (Rosenzweig, 1995) or other drivers of woody diversity (van Wilgen et al., 2003, Holdo, 2007, Holdo et al., 2009, Levick and Rogers, 2011, Colgan et al., 2012, Levick et al., 2012, Baldeck et al., 2014), it was necessary for me to test how well any observed differences in diversity patterns coincided with patches of varying impacts, and could therefore be attributed to elephants. I did this by comparing thematic maps of each of the diversity measures to levels of elephant impact, using ArcMap 10.1 (ESRI, 2001).

5.2.3. Assessing the contribution of elephant impacts to patterns of riparian woody species composition

Since the thematic map of impact accumulation across the landscape more closely approximated hotspots of damage than attenuation of damage with distance away from a patch and linear regressions explained this attenuation poorly (Chapter 4, Figure 4.22), I performed a multivariate Canonical Correspondence Analysis (CCA; Ter Braak (1986), Ter Braak (1987)) to test the prediction that riparian woody species composition would be only weakly associated with varying levels of elephant impact in this landscape. CCA is a constrained multivariate statistical technique traditionally used to explore the relationship between biological assemblages and their environment (Ter Braak, 1987, Borcard et al., 1992, Levick, 2008). Accordingly, I inferred that the severity of elephant impacts was indeed great enough to induce changes to local riparian woody species composition if the CCA demonstrated strong, statistically significant associations between levels of elephant impact and particular suites of riparian woody species.

5.3 Results

A total of 49 species was identified from the 6569 trees encountered in the study area. However, only 10 species made up 88% of the trees found, with *C. megalobotrys* (18%), *G. heterophylla* (15%), *C. mopane* (10%), *P. violaceae* (10%) and *D. mespiliformis* (10%) being the most numerous (Figure 5.29), while 27 of the species were represented by less than 10

individuals each in the survey sites. Hence the survey results indicated a plant community dominated by a few riparian woody species, with several uncommon species making up the balance in only a few sites. Furthermore, very few trees in the seedling or sapling size classes were encountered at the survey sites, with nearly 60% of the trees measured being between 1 – 4 m (Figure 5.30).

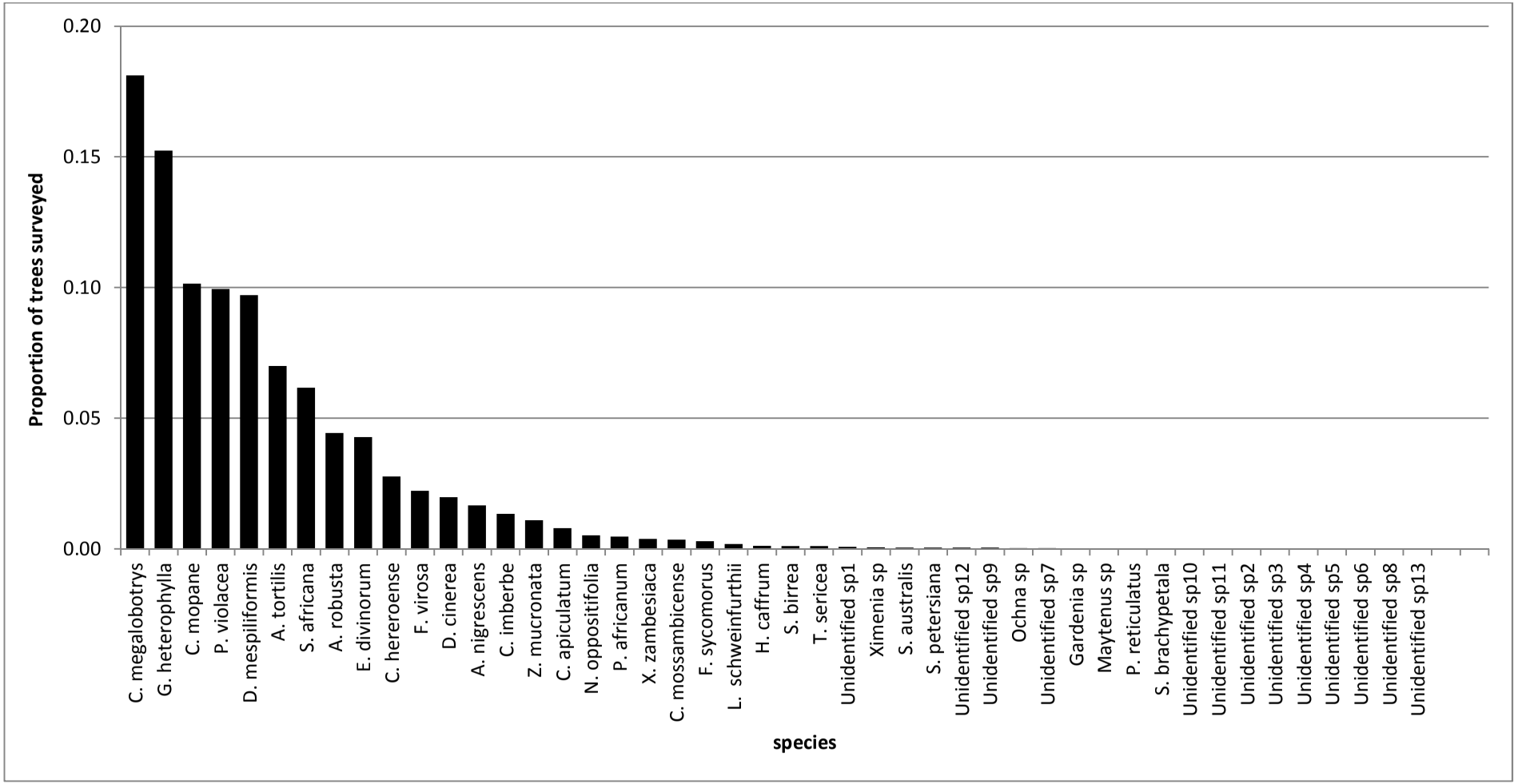

Figure 5.29 Proportional representation of riparian woody species surveyed along three ephemeral rivers in northern KNP (n = 6569 trees)

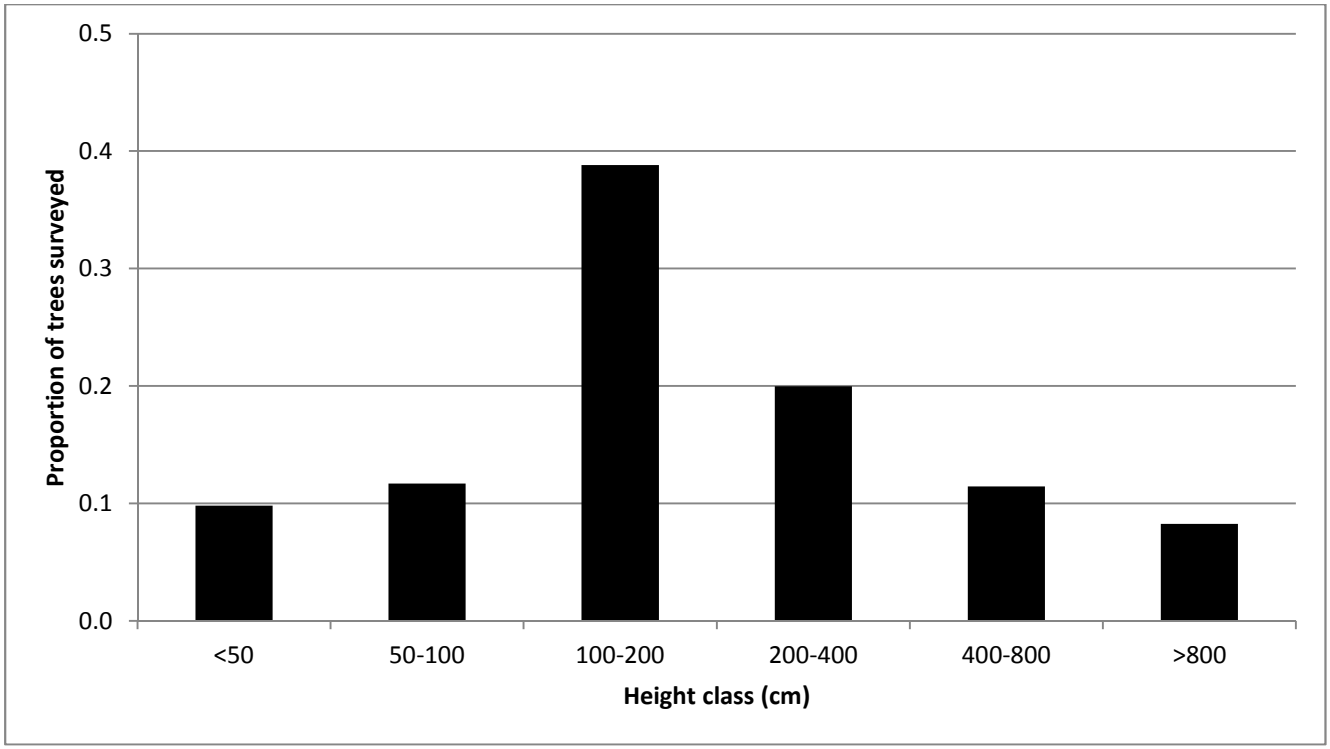

Figure 5.30 Frequency distribution of woody height classes (n = 6569 trees)

5.3.1 Patchiness in the patterns of riparian woody diversity

Contrary to my predictions, there were no significant peaks in structural diversity across the survey sites at any scale (Figure 5.31). Instead, only riparian woody species diversity and species richness were significantly patchy across the study area (Figure 5.31). Species diversity reached a first peak in patchiness at 1000 m ($z = 2.95$; $p = 0.003$), closely matching the scale of patchiness of elephant patch choice and patches of severe accumulated impact (1500 m) identified in previous chapters (Chapter 3, section 3.3.1 and Chapter 4, section 4.3.1). A second significant peak in the patchiness of species diversity occurred at 9500 m ($z = 6.22$; $p < 0.00005$; Figure 5.31). In contrast, patchiness in riparian woody species richness peaked at 3000 m ($z = 7.739$; $p < 0.00005$) and 5500 m ($z = 8.45$; $p < 0.00005$; Figure 5.31), respectively. These scales were unrelated to the previously identified scales of elephant patch choice or patches of elephant impacts, suggesting that patchiness in the patterns of riparian woody species richness were unrelated to the elephant disturbance regime.

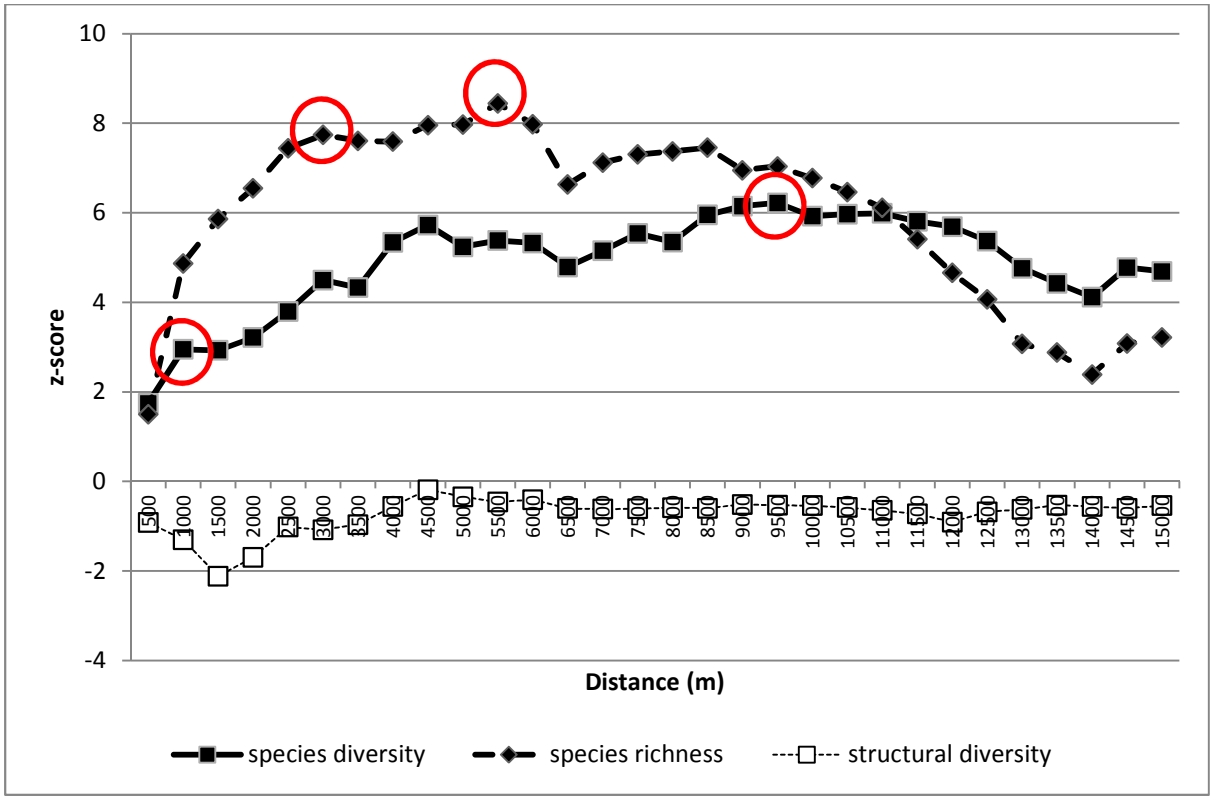

Figure 5.31 Incremental spatial autocorrelation of the patterns of woody species diversity and richness, as well as structural diversity (measured as tree heights) along three ephemeral rivers in northern KNP. Red circles signify statistically significant peaks in patchiness, indicating the presence of underlying spatial processes at these scales

5.3.2 Evidence for regional compensation for locally reduced riparian woody diversity

As predicted by the heterogeneity interpretation of the IDH, regional levels of structural diversity, species diversity and species richness were higher than their local counterparts (Figure 5.32), suggesting that any local losses of riparian woody diversity (even though none were statistically significant) were compensated for by patches elsewhere that had maintained their diversity. In the case of species richness, the occurrence of uncommon species in some patches resulted in a higher overall count of species at the regional level (Figure 5.32). However, this regional compensation for local reductions in riparian woody diversity cannot be ascribed to the patchy accumulation of elephant impacts alone, and could indeed simply reflect the known relationship of a species-area curve (Rosenzweig, 1995) or other drivers, as

pointed out above (section 5.2.2). Nevertheless, this result does confirm the prediction that that riparian woody diversity in the study area had not yet been homogenised by elephants.

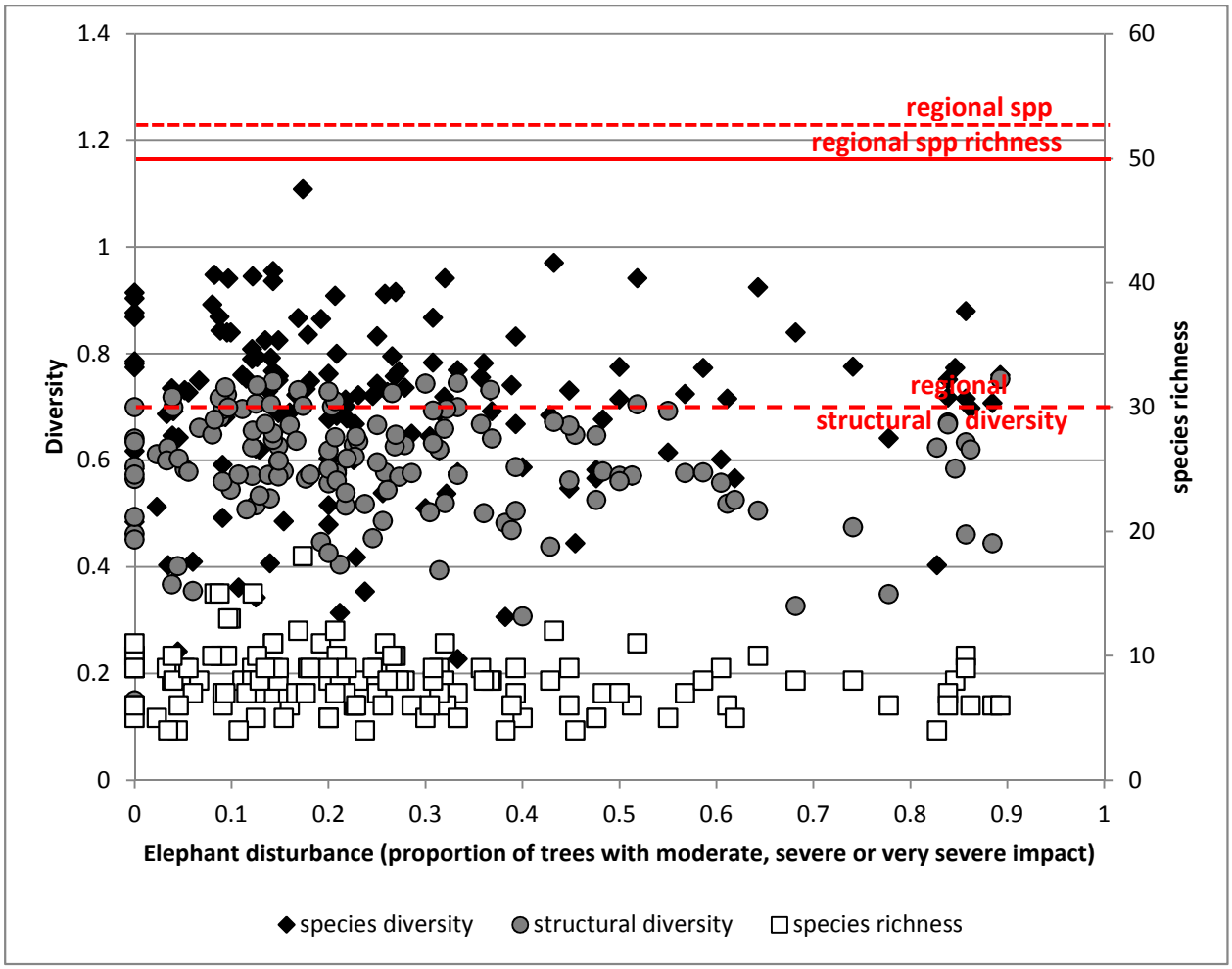

Figure 5.32 Three measures of riparian woody diversity along ephemeral rivers in northern KNP, comparing local and regional values as a function of varying levels of elephant disturbance

Thematic maps of riparian woody structural diversity, species diversity and species richness across the study area exhibited patches with varying riparian woody diversity (Figure 5.33). Although structural diversity was found to be homogenous across the study area (section 5.3.1), it was in fact homogeneously high relative to the three patches of lower (H' = 0.31 – 0.45) structural diversity. A patch of higher structural diversity (at Sandpiper windmill near the confluence of the Mphongolo and Phugwane rivers; (Figure 5.33), as well

as two localised patches of lower structural diversity (along the western and central reaches of the Shingwedzi and Phugwane rivers, respectively; Figure 5.33). However, the patches of high elephant impact did not coincide with the patches of low structural diversity (Figure 5.33). Similarly, patches of low elephant impact did not coincide with the patch of significantly higher structural diversity (Figure 5.33). These results therefore suggest that factors other than elephant impacts were responsible for generating these patterns of riparian woody structural diversity.

In contrast, two of the four patches of severe accumulated impacts coincided with patches of low species diversity (Figure 5.33). These patches of severe impact were associated with the two clustered waterpoint complexes along the Shingwedzi River (the Redrocks and Joao-Spirowiri waterpoint complexes). In addition, one of the six patches of low impact, along the western reaches of the Shingwedzi River, coincided with a high species diversity patch (Figure 5.33). These results suggest that elephant impacts were responsible for generating these patterns of species diversity. However, it should be noted that other patches of high/low diversity in the study area did not coincide with elephant impacts (Figure 5.33), indicating the presence of other drivers of riparian woody species diversity.

As predicted, patches of high/low riparian woody species richness coincided least well with patches of varying elephant impact, with only one patch of low elephant impact associated with higher species richness (Figure 5.33). This result supports the prediction that elephant impacts in the study area had not yet begun to alter this component of woody diversity.

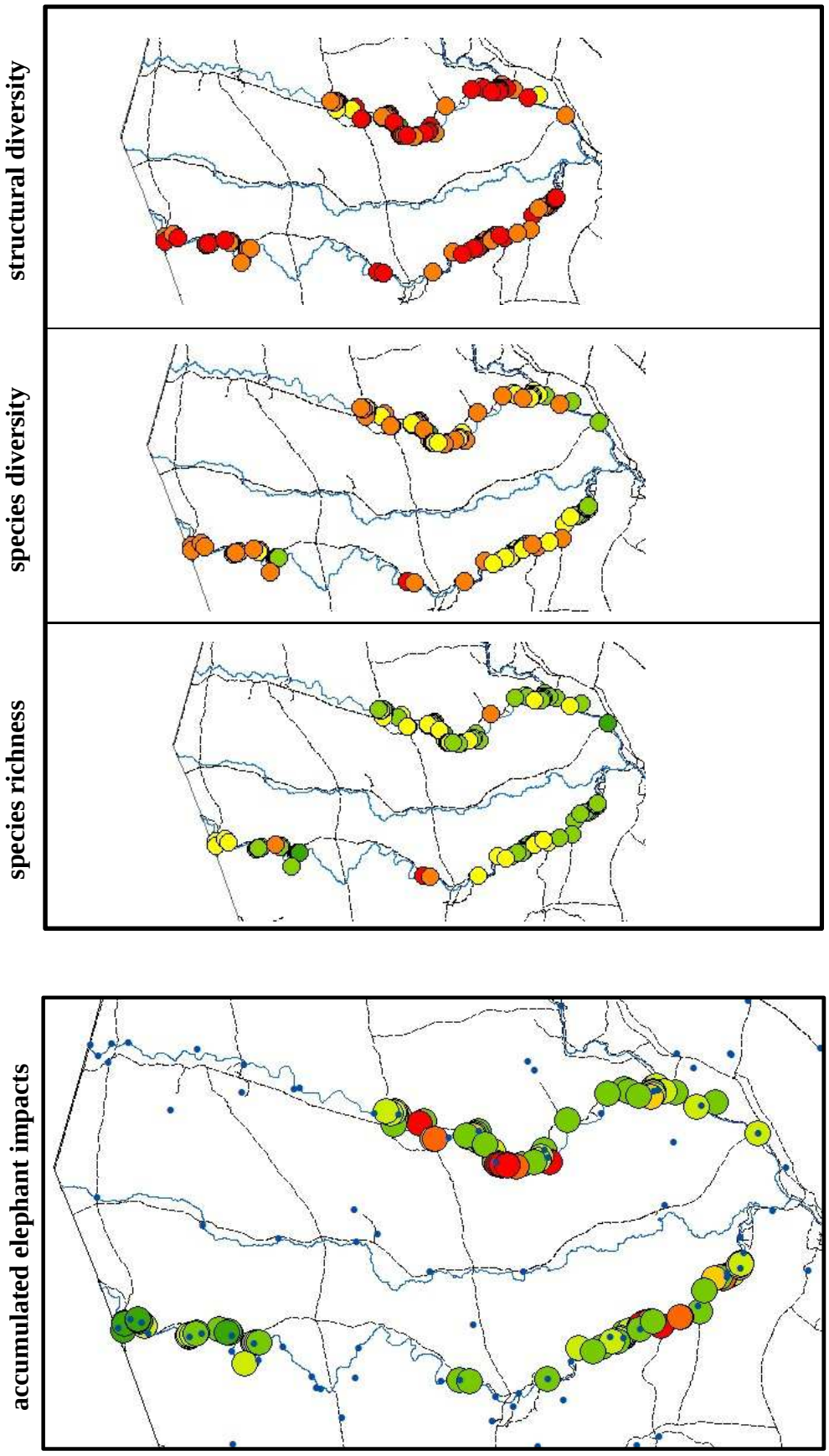

Figure 5.33 Spatial patterns of riparian woody diversity (top) compared with accumulated elephant impacts (bottom) along three ephemeral rivers in northern KNP. Green patches represent lower diversity values, whereas redder patches represent higher diversity values, for each measure

5.3.3 Contribution of elephant impacts to patterns of riparian woody species composition

The CCA ordination diagram revealed that 10 of the woody species encountered were associated with particular levels of accumulated elephant impact (Figure 5.34). For example, the *Gardenia* sp. was associated with sites with very low levels of elephant impact (<10% of trees with moderate, severe or very severe impacts), while *Z. mucronata*, *F. virosa*, *C. mossambicense*, *G. heterophylla*, *Phyllanthus reticulatus* and *Ximenia* sp. were associated with higher levels of elephant impact (>40% of trees with moderate, severe or very severe impacts; Figure 5.34). However, the particular suites of species revealed by the ordination diagram did not coincide with known groups of impact tolerant or intolerant species. Furthermore, the poor explanatory power of levels of elephant impact reported by the CCA (<10% of total variation explained) provided support for the prediction that elephant disturbances were not yet severe enough in this landscape to induce changes to riparian woody species composition.

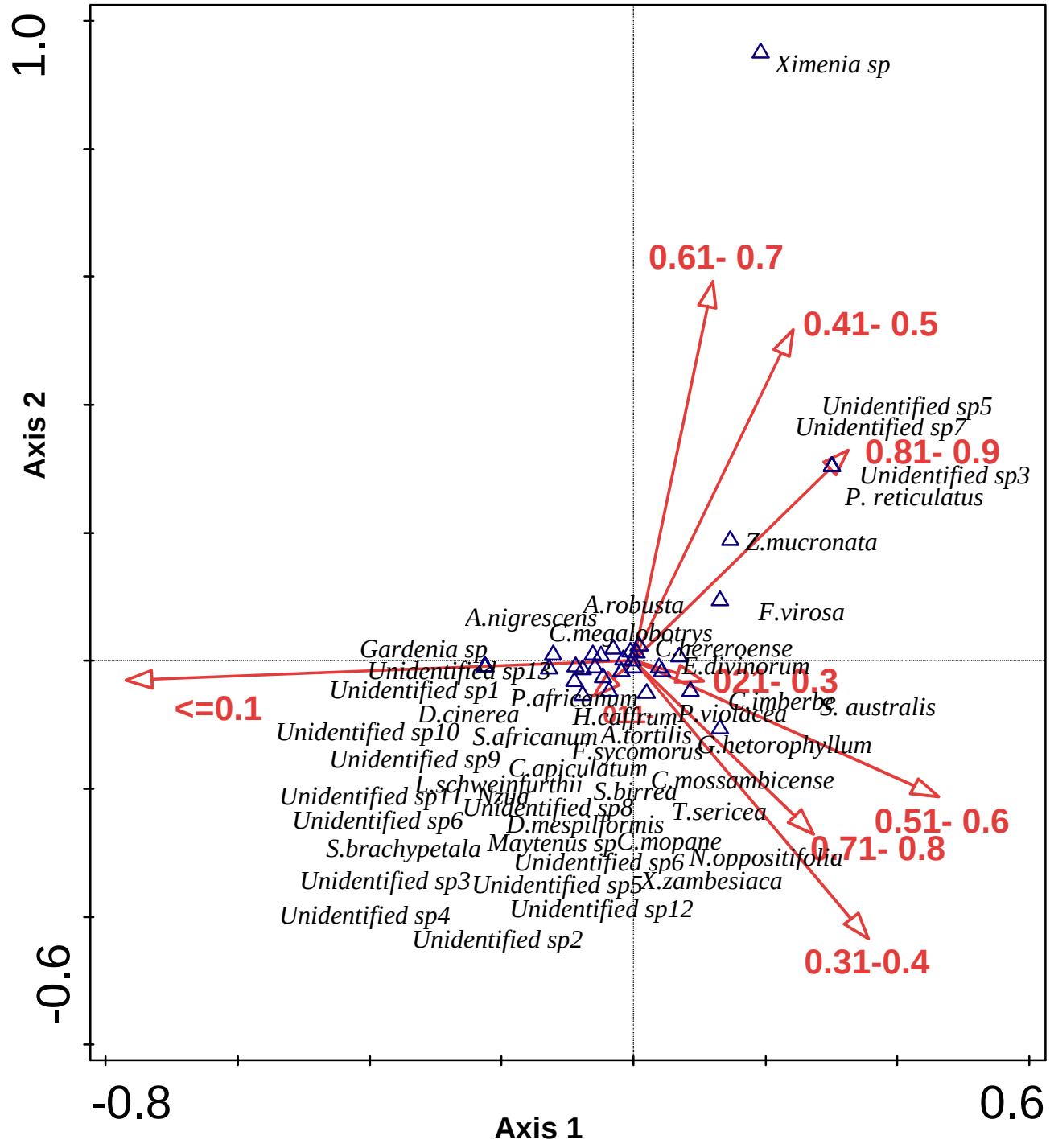

Figure 5.34 CCA of riparian woody species in patches with varying levels of elephant impact (indicated in red as proportions of trees with moderate, severe or very severe elephant impacts). Axis 1 represents distance to water, axis 2 represents waterpoint spatial context or configuration (number of waterpoints within 1500 m)

5.4 Discussion

In this chapter, I assessed to what extent the patchy elephant disturbances generated by their responses to surface water heterogeneity had altered riparian woody diversity in the drier northern region of KNP. I did so by testing a series of predictions emanating from a heterogeneity interpretation of the IDH, to locate the study area along an hypothesized trajectory of elephant-mediated change. The chapter therefore represents the final component of the heterogeneity approach that I have proposed for understanding and managing elephants, and developed through the course of this thesis. The framework for this approach has, as its basis, spatially explicit analyses to determine the nature and scales of resource heterogeneity, as well as elephant responses to this resource heterogeneity, and the resultant patterns of impact accumulation across the landscape. The work in this chapter advanced the heterogeneity approach further, by introducing adaptive inference as an alternative scientific method of enquiry to the narrowly-focused hypothesis testing associated with typical reductionist approaches (Holling and Allen, 2002). Together the findings indicated that the study area in northern KNP was at the low end of an elephant-mediated trajectory of biodiversity change, with elephant spatial and temporal responses to surface water heterogeneity sufficiently patchy to generate a range of impact levels even though the elephant population size was at its highest in recorded history at the time of the study. Accordingly, there was little evidence to suggest that the patterns and scales of riparian woody species richness and structural diversity had been shaped by elephant disturbance. In contrast, riparian woody species diversity exhibited early signs of elephant-mediated losses, although these were confined to patches of high impact.

5.4.1 Diversity changes brought about by elephant disturbances

Although woody structural diversity was homogenous across the riparian landscape, which was contrary to my predictions, species diversity and species richness exhibited a patchy distribution. In the absence of a reference point, structural diversity, though homogenous across the landscape, appeared relatively high. However, high structural diversity is not necessarily indicative of a healthily regenerating plant population, which typically exhibits a negative-J growth curve (Midgley et al., 2010). This was not the case for the riparian plant community in this landscape, which exhibited a shortage of the younger age classes. However, given the scales of patchiness in elephant impacts and hotspots demonstrated in the

preceding chapter, it is unlikely that elephants created this widespread absence of woody vegetation recruitment. Instead, the study period may simply not have coincided with an episodic recruitment event (Pettit and Froend, 2001).

In contrast, the scales of patchiness in species diversity closely matched the scale of elephant patch choice, feeding and impacts. Moreover, the few patches of particularly low species diversity coincided with hotspots of accumulated impact, suggesting that elephants were responsible for reducing woody species diversity in these patches. Nevertheless, this lower species diversity was compensated for in the patches between the impact hotspots. Finally, woody species richness was patchy at larger scales than elephant disturbances in this landscape, and woody species composition was only weakly associated with levels of elephant impact. According to the heterogeneity interpretation of the IDH, this signifies that elephant impacts were not yet high enough to reduce species richness or induce the generation of new, impact tolerant species, even in disturbance hotspots (Figure 5.28). Together these findings indicate a non-linear relationship between elephant density and diversity, created by the spatial patchiness and temporal respite from elephant disturbances. Accordingly, this illustrates that the previous carrying capacity model used to manage elephants (Pienaar, 1969, Van Wyk and Fairall, 1969) is inappropriate for predicting biodiversity changes with changing elephant population size.

These results have implications for understanding the underlying mechanism of elephant-mediated biodiversity change. Specifically, and in contrast to my predictions, the evidence presented here suggests that species diversity, rather than structural diversity, is the first component of riparian woody diversity to be affected by elephant impacts. This suggests that the mechanism of riparian woody species loss mediated by elephants is through changes to the relative abundance of woody species, rather than through loss of woody biomass affecting the regeneration of riparian plant communities. Although, this hypothesis requires further testing, this work suggests that monitoring woody species diversity may provide an earlier warning signal of elephant-mediated biodiversity loss than either structural diversity or species richness and composition. Finally, these results emphasize how restricting diversity asssessments to a single scale or component of diversity is likely to provide a skewed understanding of changes to patterns of biodiversity (Magurran, 2004). In particular, without quantifying the scales of elephant impacts and diversity patterns, along with the patterns of other measures of woody diversity, the patterns of homogenous structural diversity demonstrated here may have been erroneously attributed to elephants.

5.4.2 Placing KNP along a trajectory of elephant-mediated biodiversity change

The high proportion of patches with low levels of accumulated elephant impact, together with the patchy patterns of riparian woody diversity and the lack of evidence for widespread elephant involvement in generating patterns of structural diversity or species richness, places this driest region of KNP at the low end of the trajectory of change predicted by a heterogeneity IDH (Figure 5.28). This result is in contrast to the prediction that elephant densities beyond 1/km^2 would inevitably lead to biodiversity losses (Van Wyk and Fairall, 1969, Cumming et al., 1997). However, since this study was restricted to the riparian zone, an important avenue for future research would be to test whether the mechanisms of change identified here operate similarly in the adjacent upland areas where fire is a significant driver of vegetation patterns (van Wilgen et al., 2003).

Since the elephant population in KNP has increased to over 15000 individuals since the time of this study (South African National Parks, unpublished census results 2014), examining how far riparian woody diversity in this area has shifted along the hypothesized trajectory of change since then will provide valuable insights into the rates of woody diversity change brought about by elephants at rising densities. In addition, it would be enlightening to test whether structural diversity and species richness have since been altered at the two patches of persistently clustered waterpoints. Such a follow-up study would provide an opportunity to test the trajectory of change predicted by the heterogeneity interpretation of the IDH under increased elephant densities, specifically, whether hotspots of accumulated impact have begun to coalesce, and whether the scales of patchiness in diversity patterns have changed since the time of this study.

5.4.3. Implications for biodiversity management and decision-making

Having identified where KNP is along the predicted trajectory of change provided an important insight for managing biodiversity in the presence of growing elephant populations. As elephant populations increase, their impacts on biodiversity are expected to coalesce (Figure 5.28). It is therefore important to stratify monitoring of these effects in such a way that the detection of such coalescing is possible. These results also demonstrate the importance of monitoring multiple measures of diversity change simultaneously (Roberts and Gilliam, 1995, Aubert et al., 2003) in order to be able to interpret the emergent patterns of

biodiversity generated by elephant disturbances. Monitoring spatial trends in the elephant impacts relative to surface water heterogeneity will provide an earlier warning signal of impending widespread biodiversity loss as the elephant population increases. Loss of refuges from impact is therefore recommended as a Threshold of Potential Concern (Biggs et al., 2003) for elephant herbivory in this landscape.

5.4.4 Implications of using the heterogeneity approach for understanding elephant-mediated changes to biodiversity

This work represents the first attempt to quantify the scales of diversity patterns related to elephant disturbance regimes in this savanna, and elsewhere, and provides supporting evidence for the prediction that elephants had not yet homogenised this riparian landscape despite the fact that the population size was the highest in recorded history at the time of the study. However, these patterns and underlying mechanisms need to be tested in the adjacent interfluves, as well as in other systems, where the drivers of vegetation dynamics (and the interactions and feedbacks between them) may differ (Levick and Rogers, 2011).

The differences in diversity patterns exhibited by the three riparian woody diversity measures examined in this study emphasized how restricting investigations of biodiversity patterns to single measures can skew the interpretation of elephant-mediated changes (Reynolds et al., 1993, Pollock, 1998, Aubert et al., 2003). Interpreted on their own, the differences in the scales of riparian woody species richness and structural diversity with that of elephant impacts suggested that no elephant effects had yet occurred in this landscape. In addition, elephants effects on species diversity patterns would have been exaggerated without the context of lack of changes to species richess and structural diversity. Furthermore, the fact that structural diversity was not the first component of diversity to be affected by elephants indicates that the hypothesized relationship between diversity components is not supported and requires further investigation.

Since patterns of elephant disturbance and the resultant diversity were not simply linearly related to DtW, quantifying the scale and patchiness of riparian woody diversity was central to illuminating how surface water heterogeneity modulated the role of elephants as agents of change. This quantification of scale and patchiness enabled comparisons of the scales of the elephant disturbance regimes associated with surface water heterogeneity, and of

the scales of patchiness in the patterns of riparian woody diversity. The fact that (i) impact patchiness resembled hotspots rather than a gradual attenuation of impacts, (ii) spatial autocorrelation was present because of significant patchiness, and (iii) nonstationarity in disturbance regimes produced emergent patterns of diversity with different drivers in different parts of the landscape, makes it likely that elephant effects would not have been identified (Type II error) or may have exhibited spurious trends (Type I error; (Mills et al., 2006)) using traditional statistical approaches and reductionist methods of scientific enquiry. For example, interpreted on its own, and without the lines of reasoning obtained from patterns of elephant patch choice and feeding, or the severity and patchines of impacts, the lack of patchiness in the patterns of structural diversity would have provided support for the hypothesis that elephants had homogenised structural diversity across this riparian landscape.

Contextualising differential elephant effects in different patches of the riparian landscape using an hypothesized trajectory of change under increasing elephant populations provided a framework for integrating all the lines of evidence obtained from the preceding chapter. In this manner, the trajectory represents a conceptual model of how diversity would be expected to change under an increasing elephant population, rather than to simply quantify elephant effects at one point in time. Furthermore, conceptualising elephant-mediated biodiversity effects as trajectories of change are in keeping with managing for heterogeneity and flux of ecosystems (Wu and Loucks, 1995), shifting management focus from a single desired state to a dynamic range of conditions.

Chapter 6 - How has the heterogeneity approach advanced our understanding of elephants as agents of change in complex systems?

6.1 Introduction

In this thesis, I have argued that a new approach, which explicitly accounts for the heterogeneity that is characteristic of complex systems (Kay and Schneider, 1995, Kolasa, 2005, Cadenasso et al., 2006), is required to advance our understanding and management of elephants as agents of change in savannas. Specifically, the study set out to illuminate the conditions under which a spatially and temporally variable surface water resource might provide a sufficiently patchy template for elephant disturbances, to allow refuge for susceptible plant species. The study therefore addressed a central question in ecology - how organisms respond to, and thereby generate, patterns of heterogeneity (Pickett et al., 2000, Pickett et al., 2003). By exposing the complex patterns and underlying processes of vegetation change associated with elephant disturbances in this landscape, I sought not only to improve our predictive understanding of elephant-vegetation interactions, but also to assess more broadly the value of taking such a heterogeneity approach for understanding and managing the interactions and feedbacks between organisms and their environments in complex systems.

6.2 What is the heterogeneity approach?

Since the departure from Balance of Nature paradigm (Wu and Loucks, 1995), most scientists implicitly recognise the importance of scale and heterogeneity in understanding ecological patterns and processes (Rogers et al., 2013). However, this link tends to be an intellectual

link, while there is still a lack of recognition of the implications of complexity for the mode of science or analytical approach required (Rogers et al., 2013).

In this thesis I have developed such an approach specifically for understanding elephants as agents of biodiversity change in savanna ecosystems. The approach has, as its basis, the quantification of scale of the particular patterns of heterogeneity under investigation, using spatial autocorrelation to expose underlying spatial processes. In this manner, the method allows peak scales of heterogeneity to emerge (Figure 2.2), providing an objective means of selecting the scale of analysis of the heterogeneity patterns themselves (Legendre and Fortin, 1989, Fortin et al., 2006, Fortin et al., 2012). This is a key component of the approach, since patterns of heterogeneitiy are scale-dependent (Turner et al., 1989, Kotliar and Wiens, 1990, Milne, 1991, Levin, 1992). Moreover, the analysis of heterogeneity patterns is spatially explicit to incorporate patch context, a key contributor to heterogeneity (Thies et al., 2003, Levick and Rogers, 2011).

In order to explore the drivers of these heterogeneity patterns, I made use of statistical tests that used the presence of spatial autocorrelation to help to identify important spatial explanatory variables (Legendre, 1993), rather than to have to eliminate it to satisfy the requirements of traditional parametric statistics such as OLS regression (Scott and Janikas, 2010). This is a key component of the heterogeneity approach (Figure 3.9), since spatial autocorrelation is a common feature of heterogeneous systems (Legendre, 1993). In addition, because of the non-linearities, feedbacks, contingencies, site-specific contexts and multiple causal factors in complex systems (Kolasa, 2005, Cadenasso et al., 2006, Zellmer et al., 2006, Mazzocchi, 2008), there is often regional variation (or nonstationarity) in the relationships between response and predictor variables, which cannot be accounted for using traditional linear OLS regression techniques (Samuels, 1993, Levick, 2008). Local regression techniques such as Geographicallly Weighted Regression can accomplish this (Brunsdon et al., 1998, Fotheringham et al., 2003, Wheeler, 2014).

Finally, Holling and Allen (2002) suggest that the emergent patterns resulting from the above-mentioned features of complex systems are unlikely to be uncovered by narrowly focused hypotheses, and therefore require an adaptive inference approach that draws on multiple lines of evidence. This method of enquiry made up the final component of my heterogeneity approach.

6.3 How did the heterogeneity approach provide new insights and understanding about elephant responses to, and generation of, heterogeneity?

By identifying scale(s) of surface water patchiness and using a spatially explicit technique to incorporate the spatial configurations of waterpoints, the heterogeneity approach developed here made it possible to illuminate the template of surface water available to elephants beyond simple DtW. Comparing these spatially implicit and explicit approaches revealed how DtW measures that do not incorporate patch context underestimate the spatial heterogeneity of surface water by (i) failing to account for multiple neighbouring waterpoints that occur within the same distance band, (ii) underestimating temporal fluctuations in surface water distribution by failing to detect the drying up of key waterpoints that fall within a distance band already occupied by at least one other waterpoint, and hence (iii) underestimating the dampening effect that water provision has had on the scales and patterns of natural surface water heterogeneity.

Using an identical scaled and spatially explicit approach made it possible to demonstrate that not only were elephant patch choices and feeding associated with the presence of natural sources of surface water in the riparian zone, but also that elephants preferred patches with clustered waterpoints. By demonstrating these elephant responses to surface water heterogeneity even where DtW were small relative to their maximum daily foraging ranges, the heterogeneity approach refuted the long held notion that the scales of surface water heterogeneity in KNP are too fine to shape elephant space use (Smit et al., 2007a, Grant et al., 2008, Smit and Grant, 2009).

Incorporating GWR into the approach as a local regression technique (Brunsdon et al., 1998, Fotheringham et al., 2003, Levick, 2008, Scott and Janikas, 2010, Wheeler, 2014) revealed the presence of spatial autocorrelation in patterns of elephant patch choice and feeding, as well as nonstationarity in the relationship between surface water heterogeneity and elephant space use responses. As a result, by virtue of its ability to account for spatial autocorrelation and nonstationariy (Scott and Janikas, 2010), the local GWR significantly improved the explanatory power of the best-fit model over the global OLS regression. In addition, plotting the local r^2 values revealed the presence of Simpson' Paradox (Simpson, 1951, Samuels, 1993), indicating that the traditional global OLS regression produced

spurious relationships due to the presence of nonstationarity. The heterogeneity approach therefore improved understanding of how elephants respond to heterogeneity by revealing that preferences for clustered waterpoints became greater with reduced resource availability during dry periods, and that even though elephants preferred natural waterpoints, the distribution of artificial waterpoints contributed towards the spatial configuration of these natural waterpoints. This raised the possibility of strategic placement or closure of artificial water sources to generate variable elephant disturbance regimes, which had been dismissed as unfeasible using the previous DtW approach (Grant et al., 2008).

The scales of elephant impact distribution matched the underlying disturbance regime generated by elephant patch choice and feeding, confirming this space use as the mechanism generating patchy elephant impacts over space and time. Mapping this patchiness revealed that impacts occurred as hotpots in the riparian landscape, rather than attenuating linearly away from water (Figure 4.18). The use of traditional, non-spatial linear regressions would dilute these patterns (Scott and Janikas, 2010), making it difficult to uncover the causal relationships between elephant impact distribution and heterogeneity of surface water.

By virtue of the multiple, often overlapping causes in complex systems, the traditional scientific method of testing competing hypotheses by means of a single unambiguous test may increase the risk of Type II errors (the erroneous conclusion that results are non-significant; Holling and Allen (2002), Mills et al. (2006)). Hence the final component of my heterogeneity approach involved an adaptive inference (Holling and Allen, 2002) method of enquiry that assessed multiple lines of converging evidence (including patterns and processes uncovered throughout the thesis) to draw conclusions about the contribution of elephant disturbances to prevailing patterns of riparian woody diversity. By making use of these multiple lines of evidence obtained from all of the preceding chapters in the thesis, the adaptive inference method of scientific enquiry winnowed out unsupported hypotheses (Holling and Allen, 2002). This made it possible to integrate the understanding of patterns of surface water heterogeneity, elephant space use responses to this heterogeneity and the resultant patterns of impact, and hence to infer that only patterns of riparian woody species diversity were associated with elephant effects in this landscape, confined to patches of severe impact.

6.4 Water provisioning strategies for maximizing savanna heterogeneity under growing elephant populations

Given the important contribution of artificial water sources towards the spatial configuration of natural waterpoints, the predictive component of the GWR (Figure 4.18) enabled me to assess how water provision might be used to manipulate the template for elephant disturbances provided by surface water heterogeneity. The most surprising insight derived from this component of the study was that returning to an entirely natural surface water scenario resulted in a degree of spatial homogenization of elephant impacts, rather than enhancing impact patchiness. This was a direct result of the particular changes to waterpoint spatial configuration that occurred by removal of artificial waterpoints. This finding has important implications for elephant management philosophies based on manipulating impacts rather than setting an elephant population ceiling (Whyte et al., 1999, Whyte, 2004). Firstly, there is still scope for water provisioning to manipulate the patchiness of elephant effects on biodiversity. However, rather than complete closure of all artificial water sources, water provisioning policies should be based on strategic closures, or even new placements, of key waterpoints to generate clusters of waterpoints that shift impacts away from sensitive areas, or provide areas with temporal respite from impacts.

6.5 How do the insights gained by using a heterogeneity approach influence decision-making for protected areas with growing elephant populations?

Although there were signs that woody species diversity had been reduced in hotspots of accumulated impact, surface water heterogeneity proved adequate to allow for refuges that could compensate for these losses, at least at the prevailing elephant densities. Decision-making to prevent widespread losses of biodiversity through elephant impacts should therefore involve monitoring outcomes at two different time frames (Gaylard and Ferreira, 2011) - Thresholds of Potential Concern involving the loss of refuges from elephant disturbances to act as early warning signals, as well as (multiple) components of riparian woody diversity signifying the eventual outcome of elephant impacts.

The findings of this study suggest that quantifying the spatial extent of impact hotspots relative to patches with lower levels of elephant disturbance would provide an early warning signal of impending biodiversity loss through homogenously high elephant impacts. Consequently, a follow-up study to investigate whether refuge areas have remained intact in the study area since the elephant population has increased, or whether zones of high impact have begun to coalesce instead, would provide valuable insights into the functional heterogeneity (Owen-Smith, 2004, Fahrig et al., 2011) provided by the prevailing patterns of surface water in this landscape. Running various water provision scenarios to optimize the patchiness of elephant impacts using the variety of predictive spatial analysis tools now available (Turner and Gardner, 1991, Haase, 1995, Scott and Janikas, 2010) will help to pinpoint the placement or closure of key artificial water sources. Accordingly, I propose that Thresholds of Potential Concern (Biggs et al., 2011) around elephant-mediated biodiversity loss should be based on the severity and spatial extent of hotspots of impact. This approach is aligned with a management focus on maintaining a dynamic patch mosaic (Wiens, 1996, Pickett and Rogers, 1997), that provides metastability against catastrophic regime shifts (Scheffer et al., 2001, Folke et al., 2004), rather than focusing on the loss of species (Wu and Loucks, 1995).

6.6 How applicable are these insights to other agents of change, or other systems?

Understanding how organisms generate heterogeneity requires an understanding of how these organisms respond to resource heterogeneity (Pickett et al., 2000, Pickett et al., 2003, Jones et al., 2010). The scales of their resource utilisation depend on their movement decisions, patch choice and perceptual scales (Milne, 1989, Johnson et al., 1992, Pearson et al., 1996). Resource availability differs among landscapes and over time, and therefore the particular scales and patterns of resource heterogeneity, and hence elephant responses to this heterogeneity, are likely to be site and context specific (Levick and Rogers, 2011).

As such, the empirical findings from this study area do not necessarily apply to elephants in other savannas, or even in other parts of KNP. Instead, this work has demonstrated that elephant effects on ecological patterns are expected to emerge as a result of the context-specific trade-offs that elephants must make between resources with different

availabilities, subject to ecological contingencies such as previous years' rainfall or disturbance regimes, and hence generating different feedbacks (O'Neill et al., 1988, Carson and Pickett, 1990, Illius and O'Connor, 2000, Owen-Smith, 2002, Owen-Smith, 2004). Consequently, even the scales of elephant response to, and generation of, heterogeneity are likely to differ in other systems. However, the study has demonstrated a heterogeneity approach that was successful in uncovering the patterns and processes generating elephant-mediated patterns of heterogeneity that can be used for other organisms and in other complex systems. Specifically, this thesis has contributed to the broader discipline of ecology by developing a heterogeneity approach that (i) exposed the importance of spatially explicit analyses for understanding patterns of spatial and temporal heterogeneity; (ii) demonstrated how spatial autocorrelation can be used to infer important underlying spatial processes, rather than being eliminated to satisfy the requirements of traditional parametric statistics; (iii) revealed how local spatial regression models account for the non-stationarity that is common in pattern-process relationships in complex systems, thereby avoiding the spurious relationships produced by non-spatial, global regression models in the presence of such regional variation; (iv) illuminated how spatially explicit modelling using the predictive capabilities of local regression techniques can expose nonlinearities in the dynamics of heterogeneous systems; and (v) demonstrated how adaptive inference can provide an alternative, pluralistic scientific method to overcome the pitfalls of more narrowly-focused, reductionsist methods for understanding causation in complex systems.

Together these findings emphasize the need for a new mode of scientific enquiry moving beyond the tacit acceptance of scale and heterogeneity, towards a "lived complexity" (Rogers et al., 2013) that permeates study approaches, analysis techniques and interpretations of complex systems.

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