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Abstract

Context: The history of the landscape directly affects biotic assemblages, resulting in time lags in species response to disturbances. In highly fragmented environments, this phenomenon often causes extinction debts. However, few studies have been carried out in urban settings.

Objectives: To determine if there are time lags in the response of temperate natural grasslands to urbanization. Does it differ for indigenous species and for species indicative of disturbance and between woody and open grasslands? Do these time lags change over time? What are the potential landscape factors driving these changes? What are the corresponding vegetation changes?

Methods: In 1995 and 2012 vegetation sampling was carried out in 43 urban grassland sites. We calculated six urbanization and landscape measures in a 500 m buffer area surrounding each site for 1938, 1961, 1970, 1994, 1999, 2006, and 2010. We used generalized linear models and model selection to determine which time period best predicted the contemporary species richness patterns.

Results: Woody grasslands showed time lags of 20 - 40 years. Contemporary open grassland communities were, generally, associated with more contemporary landscapes. Altitude and road network density of natural areas were the most frequent predictors of species richness. The importance of the predictors changed between the different models. Species richness, specifically, indigenous herbaceous species, declined from 1995 to 2012.

25   **Conclusions**: The history of urbanization affects contemporary urban vegetation assemblages. This indicates potential extinction debts, which have important consequences for biodiversity conservation planning and sustainable future scenarios.

Introduction

The study of patterns of biodiversity in the landscape is of considerable interest in ecology.

35   Theories have been proposed on the drivers of these patterns and numerous studies compare

current land-use effects with biotic assemblages (e.g. Godefroid and Koedam 2003; Hansen

and Clevenger 2005; Duguay et al. 2006; Vakhlamova et al. 2014). However, an often ignored

perspective is that of the impact of the history of the landscape. A study in France revealed

evidence of the irreversible impacts of ancient farming practices on soil nutrient availability

40   and plant diversity of contemporary forested landscapes (Dupouey et al. 2002). Other studies

also provided clear evidence, indicating that many current landscape patterns are directly

influenced by past anthropogenic activities (e.g. Foster 1992; Koerner et al. 1997; Gustavsson

et al. 2007; Rhemtulla et al. 2009). Such impacts are called legacy effects and are defined as

"*the impacts that previous conditions have on current processes or properties*" (Monger et al.

45   2015). Therefore, in order to understand current observed patterns and processes of ecological

systems it is critical to incorporate information on past human-mediated disturbances to

determine the influence of potential anthropogenic legacy effects (Hamburg and Sanford

1986).

Not only does history affect ecosystems, but communities are often slow in reacting to

50   disturbances, and time lags occur between causes and their effects (e.g. Magnuson 1990; Burel

1993; Tilman et al. 1994; Foster et al. 2003; Gustavsson et al. 2007; Koyanagi et al. 2012).

Time lags occur because processes operating in landscapes take time, relict species can remain

in altered landscapes, movements across the landscape may be slow, some biological events

require certain rare concurrent conditions to take place, and time lags can be accumulated by a

55   sequence of events (Magnuson 1990). Species respond in different ways to disturbances based

on their life history characteristics (Ewers and Didham 2006; Chiba et al. 2009; Kuussaari et al.

2009), therefore, observed time lags vary. In vegetation, longer living trees show longer time

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lags than grassland and herbaceous plants (Davis 1986). Time lags of 150 – 250 years were

estimated for Alaskan forests in response to climate change (Chapin and Starfield 1997; Lloyd

60   2005), while semi-natural grasslands in Sweden displayed a 50 -100 year time lag in species

diversity changes due to changes in habitat connectivity (Lindborg and Eriksson 2004).

Similarly, Helm et al. (2006) showed that in alvar grasslands of Estonia, current habitat

specialist species were best described by habitat configurations 70 years earlier. In Japanese

semi-natural grasslands, Koyanagi et al. (2012) found that time lags differed between 30 – 50

65   years depending on the specific plant species functional traits.

In studying time lags, it is important to distinguish between research on exotic and

indigenous species. Studies of time lags in exotic species usually pertain to the time lag

between introduction and eventual establishment and invasion; the focus is generally on the

increase of species richness with time (Sakai et al. 2001; Crooks 2005; Daehler 2009). Studies

70   focusing on indigenous species, however, invariably investigate time lags in the decrease of

species richness, i.e. declines in populations or even species extinctions (Brooks et al. 1999;

Hanski and Ovaskainen 2002; Kuussaari et al. 2009). Disturbances not only influence

vegetation composition but severe disturbances, such as habitat destruction or fragmentation,

can push species to extinction (Tilman et al. 2001). However, due to the existence of species

75   time lags in response to these disturbances, delayed extinctions can occur (i.e. extinction debts,

Tilman et al. 1994; Kuussaari et al. 2009). Therefore, a sobering picture is revealed of current

observed extant vegetation potentially already doomed by past disturbances; a situation calling

for critical reflection in fragmented contextual settings.

In urban ecological studies, there is a paucity of studies on anthropogenic legacy effects

80   and time lags. The limited number of studies documenting time lags in vegetation patterns in

urban areas almost exclusively pertains to the relationship between neighbourhood social

characteristics and woody vegetation cover (Pickett et al. 2008; Boone et al. 2009; Luck et al.

2009; Grove et al. 2014; Locke and Baine 2014). However, these do not document responses

of vegetation to a disturbance, but rather identify corresponding social contextual plant

85   establishment periods. Nonetheless, there are a few studies on extinction debts in urban areas.

Hahs et al. (2009) studied plant extinction rates in 22 cities worldwide and determined that

contemporary urban areas potentially have large extinction debts. A subsequent study of

European countries determined that "*irrespective of recent conservation actions, large scale

risks to biodiversity lag considerably behind contemporary levels of socioeconomic pressures.*

90   *The negative impact of human activities on current biodiversity will not become fully realized

until several decades into the future*" (Dullinger et al. 2013).

        This study aims to (i) enhance research on time lags in the response of urban remnant

natural vegetation to anthropogenic disturbances; (ii) address the paucity of urban re-visitation

studies (Williams et al. 2005), (iii) add to long-term vegetation change studies in new locations

95   in order to enhance global knowledge; and (iv) enhance urban research in temperate natural

grasslands. Moreover, no such study has been carried out in Africa. We answer the call in

urban ecological literature to include temporal dynamics (Ramalho and Hobbs 2012) and to

more fully understand mechanisms driving current vegetation patterns (McDonnell and Hahs

2013). The main objective is to determine if there are time lags in the response of temperate

100   natural grasslands to urbanization. More specifically, we asked (i) does it differ for indigenous

species and disturbance indicator species and between woody grassland communities and open

grasslands? (ii) Do these time lags change over time? (iii) What are the potential landscape

factors driving these changes? Additionally, (iv) what are the corresponding vegetation

changes over a 17-year time period?

105   We hypothesize that (a) indigenous species patterns will correspond to past landscape

patterns, (b) disturbance indicator species richness will correspond to periods of rapid urban

growth and will have longer time lags, (c) woody grassland communities will have longer time

lags than open grasslands, (d) intensification of disturbances (such as rapid urban growth) will

shorten observed time lags, and (e) indigenous species richness will decline while exotics and

110   species indicative of disturbances will increase with urbanization.

Methods

Study area and history

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The study was conducted in the city of Potchefstroom (26˚ 42' 53'' S; 27˚ 05' 49'' E) and its

immediate natural surroundings, situated in the North-West Province of South Africa (Fig. 1a).

The city covers a 55 km^2 area at an elevation of 1350 m, with a population of approximately

250 000 (Tlokwe City Council 2015). The city experiences average temperatures of 0˚C in

120   winter with frequent frost and 30˚C in summer months. The mean annual rainfall is about 550

mm received mainly in summer months (Supplementary Information Fig. S1). Potchefstroom

was established in its current location in 1841 (van den Bergh 1992). Simultaneous to town

settlement was the delineation of farms around the town boundary (van den Bergh 1990).

However, along the western boundary of the town, a town commonage area was demarcated

125   for use as grazing (Fig. 1b). The commonage reached a maximum area of 25 434 ha by 1889

due to the continuous demand for more grazing (van den Bergh 1992). The rapid advance of

the motorcar from 1929 to 1945 signalled the end of the large-scale use of the town

commonage for grazing purposes (Smit 1989). Therefore, the commonage area was continually

grazed for about 100 years. Thereafter, urbanization and its associated disturbances became the

130   major influence. In subsequent years, most of the urban development expanded into the town

commonage area, as the most readily available municipal land (Fig. 1c). A crucial factor in the

urban development of the town commonage area was the Group Areas Act of 1950, mandating

the compulsory zoning of separate racial residential areas. Development of these residential

areas of mostly poor residents started in 1956 in the town commonage area (Neser 1967). The

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135 democratic elections of 1994 and the lift of urban restriction laws resulted in an immense

growth of urban residential areas of the town commonage area (Fig. 1c).

#Figure 1 approximately here#

140 *Vegetation sampling*

Potchefstroom is situated in temperate natural grasslands at the confluence of three vegetation

types: the Rand Highveld Grassland, Carletonville Dolomite Grassland and the Andesite

Mountain Bushveld (Mucina and Rutherford 2006), the latter being Savanna elements found on

145 hills and ridges in the area (Supplementary Information Fig. S2), described in this study as

woody grassland communities. Vegetation sampling sites are all situated in the town

commonage area (Fig. 1b) with most on the urban-rural fringe and some existing as remnant

fragments within residential areas. Extensive vegetation sampling of the Potchefstroom area in

1995-6 (Cilliers et al. 1999) allowed us to compare vegetation composition before and after the

150 rapid urban expansion period (Fig. 1d and e). The original surveys were phytosociological

relevés sampled using Braun-Blanquet cover abundance values (Mueller-Dombois and

Ellenberg 1974). Seventy-eight sample plots were surveyed in 1995-6 of which 43 were re-

surveyed in 2012 comprising of 26 woody grassland sites and 17 open grassland sites. Eight of

the 78 sites were lost to urban development, the precise location of 15 sites are unknown and of

155 the remaining sites we only chose those that were historically untransformed, i.e. we excluded

old fields and any other direct anthropogenically-disturbed sites. Most of the sites are situated

in the western part of the study area in an unbroken extensive grassland area, some of which

later became fragmented. The rest of the sites are located on small remnant areas fragmented

due to urbanization (Supplementary Information Fig. S3). Resampled site locations were as

160 close as possible to the original sites, using datasheet site descriptions, aerial photographs on

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which some of the site locations were marked, and one of the author's (Cilliers) own

recollections. Woody grasslands were sampled in 10 x 10 m sample plots and open grasslands

in 4 x 4 m sample plots (Bredenkamp and Theron 1978), with one plot per site. Woody

communities are naturally occurring habitat 'islands' in the grassland matrix, mainly situated

165   on hills and ridges forming part of the Andesite Mountain Bushveld vegetation type (Mucina

and Rutherford 2006) with the dominant taxa represented by trees and large shrubs. However,

historically open grasslands can also be transformed by bush encroachment due to higher

rainfall frequencies (Ward 2005), which allows tree seedlings to survive in the grasslands or as

a result of over-grazing and unnatural fire regimes that stimulate tree growth when competition

170   with grassland species is lower (Kraaij and Ward 2006; Van Auken 2009).

        The percentage cover of all species within the sample plots was recorded. The 1995

Braun-Blanquet cover abundance data were converted to mean percentage values (Eckhardt et

al. 1993) to allow direct comparison between the resampled and original data. For this paper,

only the perennial species data were used as per Williams et al. (2005) to reduce the potential

175   for recording false absences of species. We calculated indigenous species richness (ISR),

exotic species richness (ESR) and species richness of plants that indicate disturbance (DSR)

per sample plot, as well as total species richness, percentage indigenous species and percentage

indigenous species cover. However, the last three measures were excluded from our analyses

because they all correlated with either ISR or ESR. For instance, ISR correlated highly and

180   significantly with total species richness in both years and for both woody and open grassland

communities (Person's $r \geq 0.98$). Furthermore, ESR correlated highly with percentage

indigenous species ($-0.86 < r < -0.97$) and percentage indigenous species cover ($-0.68 < r < -0.83$).

To calculate DSR, we identified 31 (indigenous and exotic) species from the recorded

species occurrences that indicate grassland vegetation in poor condition, specifically

185   overgrazing and trampling, pioneer species, weeds, invaders, and bush encroachment (e.g.

Louw 1951; Bredenkamp et al. 1989; Bezuidenhout et al. 1994a; Cilliers and Bredenkamp

1999; Cilliers et al. 1999). Because humans disturb natural areas in various ways, through trampling, plant removal, rubbish dumping etc., we wanted to determine whether these species that flourish in disturbed environments increase with increasing urbanization and if their

190   richness patterns correspond to urban landscape measures. These disturbance indicator species were identified from published studies of Potchefstroom and its surrounding regional grassland setting (Supplementary Information Table 1).

Urban landscape measures

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We digitized 500 m buffer areas around each site to quantify the landscape matrix. Optimal matrix scales have not been determined to study the effects of urbanization on vegetation (Dauber et al. 2003), therefore we decided on 500 m as some authors state this a suitable buffer area (e.g. Tscharntke et al. 2005; Duguay et al. 2006; Kleijn et al. 2009; Vakhlamova et al.

200   2014). Additionally, since we are interested in the anthropogenic effects on vegetation dynamics and the area of interest is mostly inhabited by poor residents, we analysed firewood collection distances. The field data sheets of Cilliers in 1995-6 revealed that sites where firewood was gathered were all situated within 200-500 m from residential areas. The limited literature on grassland species dispersal also indicate that most dispersal of grassland species,

205   excluding long-distance dispersal by animals, occur well within the 500 m limit of our buffer zone (O'Connor 1991; Morgan 1995).

        Measures were calculated for the time periods 1938, 1961, 1970, 1994, 1999, 2006, and 2010 as these were the dates for which we could readily obtain aerial or satellite imagery. For 1938-1994, we georeferenced digital aerial photographs, procured from government archives

210   (www.ngi.gov.za), in ArcMap 10 (ESRI 2010) using digital topographical maps of periods nearest to the imagery dates as reference material. For the periods 1999-2010 we obtained orthorectified satellite imagery. The chosen measures for this study included: age of

urbanization (Age), altitude, road network density of natural areas (RNDN), percentage natural area (PN), density of dwellings (CD) and landscape diversity (H'). These measures were

215   calculated in ArcMap 10, additionally using the Hawth's Analysis Tools version 3.27 (Beyer 2006) add-in to calculate RNDN, CD and H. To determine the age of urbanization we used the aerial and satellite images to determine when any form of urban buildings first occurred in the 500 m buffer, for example if urban infrastructure occurred in 1938, the age of urbanization in the 2012 models was 74 years. Because we could not accurately state in which year

220   urbanization occurred before 1938, all the urbanized sites in the 1938 GLM models were given the age of 1 year (in a sense presence/absence data). We included altitude (recorded with a GPS device: 1332 - 1432 m) since the sampling site locations varies from plains to foot slopes and small hills and ridges.

The effects of roads and trampling on vegetation are well documented (Cilliers and

225   Bredenkamp 2000; Gelbard and Belnap 2003; Hansen and Clevenger 2005; Kissling et al. 2009; Deng et al. 2011). We specifically wanted to determine the effect of roads (tar and dirt) and footpaths on the vegetation dynamics of natural areas as an index of fragmentation and disturbance, i.e. a proxy for habitat quality. Therefore, all roads and footpaths inside and traversing the natural areas were digitized. We modified the standard road network density

230   measure (e.g. Hahs and McDonnell 2006) by dividing only the digitized roads inside the natural area by the size of the natural area inside each 500 m buffer area. Thus, road network density of natural areas (RNDN) was measured as the length of roads per m^2 of natural areas. Percentage natural areas was simply the proportion of natural areas inside the 500 m buffer area. We used the measure density of dwellings as a surrogate for population density for two

235   reasons; first we could accurately digitize it for each time period as there are no reciprocal fine scale census data available for any of the time periods. Second, comparison in the literature showed that in PCA and FA analyses where both measures were used, it had similar loadings as the population density measure (Hahs and McDonnell 2006; Andersson et al. 2009; du Toit

and Cilliers 2011). Thus, the density of dwellings (CD) was calculated as the count of all

240 buildings per buffer area. Landscape diversity (H') was calculated using the proportion of

different habitats analysed with the Shannon Index (Shannon 1948) (after Romme and Knight

1982; Purschke et al. 2012; Janišová et al. 2014). The buffer areas were classified by manually

digitizing it from aerial and satellite images into the following classes: mine dumps and

excavations, natural, urban, cultivated land, plantations and water. The percentage area per

245 class was then used as input into Primer 6 (Clarke and Gorley 2006) to calculate the Shannon

index.

Data analysis

250 All analyses were performed with the statistical package R version 3.0.2 (R Core Team 2013).

Four sets of analyses were performed per vegetation type (woody and open grassland); two for

the 1995 vegetation data (ISR, DSR) and two for the 2012 vegetation data (ISR, DSR). We

were unable to analyse ESR due to very low numbers of exotic species in the dataset. For each

analysis, the following steps were followed: In the first step, spatial autocorrelation between

255 the sample plots were tested using Moran's I in the ape version 3.1-4 package in R. Site

longitude and latitude were used to perform this test. The presence of spatial structure was

further evaluated by comparing the AIC value of a null model with no covariance structure, to

AIC values of models including various covariate structures (including exponential, Gaussian,

spherical, linear and rational quadratics that are based on site longitude and latitude values)

260 (the procedure is explained in full here:

http://statistics.ats.ucla.edu/stat/r/faq/variogram_lme.htm). The lme command in the nlme

version 3.1-111 package in R was used to perform this analysis. No indication of spatial

structure was detected in any of the datasets.

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In the second step, generalized linear models were performed for each of the eight
vegetation parameters. The response variables were modelled following a Poisson error
distribution. Predictor variables for all models included altitude, age of urbanization (Age),
percentage natural area (PN), road network density of natural areas (RNDN), density of
dwellings (CD) and landscape diversity (H'). For the data collected in 1995, each response
variable (e.g., ISR of woody grasslands in 1995) was modelled against all predictor variables
for 1938, then for 1961, then 1970 and finally for 1994. Model selection was performed for
each year (e.g., ISR woody grasslands for 1995 against the 1938 landscape, ISR woody
grasslands for 1995 against the 1961 landscape, etc.) by removing less significant variables one
at a time until only variables of $p < 0.2$ were left in the models. AIC values of these final
models for, say ISR woody grasslands for 1995, were compared between the four years (1938,
1961, 1970, 1994) and the one with the lowest AIC was selected as the optimal model for this
particular vegetation parameter. For the data collected in 2012, the same procedure was
followed as described above, except that the response variables here were modelled against all
predictor variables for 1938, 1961, 1970, 1994, 1999, 2006, and 2010.

All variables were on a continuous scale, but a few had to be converted to categorical
variables due to highly irregular values in the variable. This was particularly true for variables
measured in 1938 and 1961, and a few variables in 1970.

Results

Landscape matrix change

The percentage natural area declined steadily with time; however woody grasslands situated,
on average, at higher altitudes, had consistently higher average percentage natural areas left
(Fig. 2a). The road network density of natural areas (RNDN) indicated that open grasslands

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290   had consistently higher densities of footpaths and roads, except in 2006. RNDN in both

habitats increased steadily with a noticeable increase in 1994 and then a drastic increase in

2010, consistent with rapid urban development in the area (Fig. 2b). The density of dwellings

measure showed a marked increase in population density since 1994 (Fig. 2c). Open grassland

landscape diversity was consistently more complex than woody grassland landscape diversity

295   and both increased from 1938 to 2010 (Fig. 2d).

#Figure 2 approximately here#

Vegetation community time lags

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Results of the GLM models indicate that in 1995 and 2012 the open grassland vegetation (ISR)

was best predicted by the 1994 and 2010 landscape variables as they returned the lowest AIC

value (Table 1). Since we did not have landscape data for 1995 and 2012 his can either be

interpreted as a 1 and 2 year time lag, respectively, or as no time lag as those are the most

305   current landscape variables available. The 1995 DSR, on the other hand, was best explained by

the 1970s landscape, indicating a 25 year lag. In 2012, this changed to a six year lag, best

predicted by the 2006 landscape. The woody grassland richness patterns (ISR and DSR),

however, showed longer time lags (Table 1). In 1995, ISR was best predicted by the 1970

landscape, indicating a 25 year time lag. In 2012, the best model was of the 1994 landscape,

310   indicating an 18 year time lag. The 1995 DSR was best predicted by the 1961 landscape, a 34

year lag. This changed to 42 years in 2012 as the 1970 landscape represented the best fit

model.

Altitude and road network density of natural areas (Table 1, Fig. 3) were the most

frequent predictors of species richness. Five of the eight vegetation models had a statistically

315   significant response to both altitude and RNDN. Open grassland species richness increased

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with altitude and RNDN, while woody grassland species richness decreased with altitude and

RNDN (Fig. 3). Percentage natural area was statistically significant in four models with open

grassland communities decreasing in species richness with increasing PN, while the woody

grassland DSR in 2012 increased with PN (Table 1, Fig. 4). The density of dwellings and

320 landscape diversity were each significant in three models. The age of urbanization was the least

important variable with only one statistically significant contribution in the 2012 open

grassland ISR model (Table 1).

#Table 1 approximately here#

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#Figure 3 approximately here#

#Figure 4 approximately here#

330 *Vegetation change between 1995 and 2012*

The open grassland sites gained 19 species between 1995 and 2012, but lost 58 species, with a

net loss of 39. The woody grasslands gained 26, but lost 51, with a net loss of 25. Collectively,

24 of the species (3 grasses, 10 herbs, 10 shrubs—1 exotic, 1 tree) lost in the open and woody

335 grasslands did not occur in any habitats surveyed in the recent literature (du Toit 2009; Jansen

van Rensburg 2010; van der Walt 2013), and have a potential local extinction risk

(Supplementary Information Table 2). These 24 species were all rare, occurring only in 3 or

fewer sites. None of the species gained are new additions to the area. Species were either

recorded in the alternate habitat in 1995 (e.g. if recorded in the 2012 woody grasslands it was

340 present in the 1995 open grasslands) or listed in older literature of the Potchefstroom area

(Bezuidenhout and Bredenkamp 1990, 1991; Bezuidenhout et al. 1994b; Bredenkamp et al.

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1994; Retief and Herman 1997; Cilliers et al. 1998; Cilliers and Bredenkamp 1998, 1999; Cilliers et al. 1999; Cilliers and Bredenkamp 2000). Both habitats in 1995 had 20% rare species (recorded in a single site and habitat only). This increased to 24 % for the open

345   grasslands and 22 % in the woody grasslands in 2012. Growth forms between years remained essentially the same, except that herbaceous species declined drastically (26 in open and 19 in woody grasslands, respectively) (Table 2). Exotic species declined in the open grasslands and increased in the woody grasslands, with very low percentage cover throughout the study periods. Sites that displayed high species richness in the open grasslands in 1995, also did so in

350   2012 (Supplementary Information Fig. S4a). Woody sites, however, had distinct variation with time (Supplementary Information Fig. S4b) For the disturbance indicator species (Table 2), the species richness declined in the open grasslands and stayed the same in the woody grasslands, with very low percentage covers throughout the study periods. All 14 DSR species recorded in the 2012 open grasslands were also present in 1995. The woody sites shared 22 DSR species

355   and the two newly recorded species in 2012 were both present in the 1995 and 2012 open grasslands.

       # Table 2 approximately here#

360   **Discussion**

       Time lags were observed for both the open and woody grassland vegetation. Time lags observed for the woody grasslands preceded major urban development in the study area. The township of Ikageng was established in 1957-1963 and in 1969 resettlement started in Promosa

365   (Neser 1967). In the period between 1961 and 1970 the township of Mohadin was established, and 1994 preceded the start of rapid urban growth (see Fig. 1). The woody grassland ISR lags remained constant at an average of 21 years, moving 'forward' with urban development. The

woody DSR averaged 38 years, corresponding to the first major urban development in the town commonage area.

370   The open grassland ISR patterns can either be interpreted as a 1 and 2 year lag, respectively, or as no time lag because of an absence of data for the specific years in which the sampling was done. A study by Adriaens et al. (2006) on semi-natural grasslands in Belgium found no time lags in connection with past habitat area and connectivity, however they also had a 19 year gap between their current landscape variables and the nearest historical one.

375   O'Connor (1991) researched local extinctions in perennial grasslands and reported that many palatable grass species are obligate seed producers that produce low numbers of seeds that are poorly dispersed. The seed bank of these 'extinction-prone' species need annual seed input as the seeds only survive for 2-3 years in the soil. If the extant plant is removed and the soil seed bank depleted or seedlings fail to establish due to disturbances, predation or low rainfall the

380   species can quickly become locally extinct (O'Connor 1991). Moreover, a soil seed bank experiment in temperate natural *Themeda triandra* grasslands in Australia found that perennial indigenous species (specifically herbs) were almost completely absent from the soil seed bank (Morgan 1998). This implies quick species turnover times in short-lived grassland species, which in combination with described hyperdynamism of highly fragmented areas (Laurance

385   2002) most probably accounts for the short or absent time lags observed in the open grassland ISR patterns.

        It is important to note that the accuracy of the time lag calculation is restricted by the time periods used. This is especially pertinent for the evaluation of the open grassland models. After the 1970 landscape there is a 24 year gap wherein we could not obtain accurate aerial

390   imagery before the 1994 dataset. All the models indicate comparative time lags between the two sampling periods, except the open grassland DSR models. The 1995 DSR corresponded to the 1970 landscape indicating a 25 year lag and the 2012 DSR corresponded to 2006 indicating a 6 year lag. However, close scrutiny of our results indicates that both of the time lags of the

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DSR models in the open grasslands are indicative of the last time period before the most

395 current landscape variables, i.e. in 1995 it was the 1970 landscape and in 2012 the 2006 landscape. Therefore, the 25 year gap displayed by the 1995 model could be inaccurate as it is the closest available historical landscape prior to the current landscape. Therefore, the 1995 open grassland DSR patterns could probably have better corresponded to the observed 6 year lag of the 2012 landscape if we had more landscape datasets in the 24 year interval.

400 Time lags observed for the open and woody grassland DSR patterns both exceeded that observed for the ISR patterns. Ecosystem response lags behind disturbances (Magnuson 1990; Hayashida 2005). For instance, the disturbance indicator species used in this study are pioneers or bush encroachers and their presence are the first indication that a site experienced disturbances. The resulting community changes and direct disturbance impacts in turn

405 influence the rest of the community. It is therefore expected that disturbance indicator species patterns will always lag behind extant indigenous species patterns. The presence of disturbance indicator species can subsequently potentially serve as an early warning sign that other species losses will occur. There are no equivalent time lag studies carried out in temperate natural grasslands with which to compare our findings. However, the observed time lags for the woody

410 community are relatively close to the 30-50 year time lags of Japanese semi-natural grasslands (Koyanagi et al. 2012). Other studies in semi-natural grasslands document 50-100 years (Lindborg and Eriksson 2004) and 70 years for Estonian semi-natural grasslands (Helm et al. 2006).

The 1995 open grassland indigenous species richness patterns were best predicted by

415 the 1994 landscape variables where higher altitudes, older urbanization influences with smaller percentage natural areas in the buffer, higher road network densities, and more heterogeneous landscapes had the highest ISR (Fig. 5a and b). The 2012 ISR patterns were best predicted by 2010 landscape variables; higher altitudes, older urbanization influences, higher road network densities, population densities and landscape diversity predicted higher ISR. The increase in

420 species richness with a decrease in percentage natural areas might be explained by the fact that species richness was positively related to urbanization age. Therefore, older sites closer to the urban area had higher quality habitats (as indicated by higher ISR) (Fig. 5b). The town commonage area in which the sites further from the urban area are situated was continuously grazed for approximately 100 years, thus the sites close to the urban area would have been

425 largely protected from grazers. This then could explain the counter-intuitive negative relationship with percentage natural areas in the buffer. Moreover, of the two variables only urbanization age remained significant in the 2012 ISR model. This relationship with urbanization age also explains the positive relationship with RNDN, as the vegetation fragments are smaller and many footpaths traverse them between the residential areas (Fig. 5b).

430 The same argument holds for the positive relationship of the 2012 ISR with the density of dwellings and landscape diversity. Further evidence is also provided when examining the ISR pattern changes per site from 1995 to 2012 (Supplementary Information Fig. S4a). In the open grassland DSR models, only a single variable best predicted the patterns in 1995 and 2012. The 1995 model indicated that lower percentage natural area sites of 1970 had higher DSR (Fig. 5c)

435 whereas sites with higher road network densities in 2006 predicted sites with higher DSR in 2012 (Fig. 5d).

For the indigenous species richness of woody grasslands, on the other hand, lower altitudes with smaller percentage natural areas in the buffer, but more homogenous and low dwelling densities in 1970 predicted sites with higher ISR in 1995 (Fig. 6a). In 2012, however,

440 lower altitudes, lower road network densities but higher dwelling densities in 1994 predicted sites with higher ISR (Fig 6b). The negative relationship with RNDN for both years can be explained by the fact that the footpaths in woody sites are indicative not only of thoroughfares but of direct disturbances i.e. firewood harvesting, whereas most of the footpaths in open grassland sites are only used as thoroughfares. The negative relationship with altitude might

445 also partly be explained by the ecotone concept (Risser 1995; Kark and van Rensburg 2006),

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where lower lying woody sites have more open grassland species as the community changes from woody to open grasslands enhancing species richness of these sites. Urban expansion mostly took place on lower lying areas, which in combination with higher species richness of ecotones might explain the negative relationship with PN in 1995 and the subsequent positive relationship with urbanization age and density of dwellings in 2012 (Fig. 6b). The percentage natural area in the buffer, as with the open grasslands, was again not important in the 2012 model.

#Figure 5 approximately here#

The woody grassland DSR in 1995 was best predicted by the 1961 landscape, indicating that lower altitude, lower road network density, and more homogenous sites had higher species richness (Fig. 6c). In 2012, lower altitudes with less natural area in the buffer had higher DSR values (Fig. 6d). The sites nearest to urban areas are on average situated at lower altitudes, and the contradictory lower road network densities can be ascribed to the fact that RNDN values for 1961 was highest in sites situated in small grassland fragments on the opposite side of the densely populated informal residential areas (Fig. 6c and Supplementary Information Fig. S3). Many footpaths traversed this area, due to the vicinity of military grounds and a water purification plant. In contrast, sites in the non-fragmented homogenous western part of the study area—despite the nearness of many to urban areas— still had fewer roads and footpaths in relation to the size of natural areas.

#Figure 6 approximately here#

The loss of indigenous species in both the woody and open grassland vegetation is in line with documented loss of species in urban areas with time (Chocholoušková and Pyšek 2003; Tait et

al. 2005; Williams et al. 2006; Stehlik et al. 2007). Long time-lags in the response of woody grassland communities might be the reason why these communities lost fewer species and shared more species between the time periods than the open grasslands. The decline in exotic

475   species and disturbance species richness of the open grasslands seem to indicate that these sites do not receive as much direct disturbances as that of woody sites, which are particularly targeted for firewood collection (Madubansi and Shackleton 2007). Of specific concern is the major loss of herbaceous species in both habitat types. Moreover, despite the presence of time lags to indicate possible extinction debts, the high proportion of rare species and its slight

480   increase from 1995 to 2012 for both the open and woody grasslands might also be an extinction debt signature (Hanski and Ovaskainen 2002).

Natural stressors in these grasslands are grazing, climate and fire. In our study area, fire is largely suppressed at sites in the city (however mowing can simulate the effects of fire due to biomass removal (Williams et al. 2006; Cilliers et al. 2008)) and those on the fringe experience

485   irregular burning. Anthropogenically-caused and suppressed fires together with natural fires cause changed disturbance regimes, which impact indigenous species richness (Williams et al. 2006) and bush encroachment (Friedel 1987). In their study, Williams et al. (2006) linked changed fire regimes (as a proxy of habitat quality) to declines in indigenous species and indicated that habitat quality rather than patch size or isolation determined local extinction

490   risks of grassland species. Similarly, in explaining the distribution of herbaceous species in woodlands, Dupré and Ehrlén (2002) found that habitat quality (measured by soil properties) was more important than spatial configuration. However, fragmentation effects can be masked by confounding factors (Ewers and Didham 2006). In the current study, some small fragmented areas harboured higher diversity than sites situated in the extensive grassland area in the

495   western part of the study area, emphasizing the conservation value of smaller natural remnants (Lawson et al. 2008). However, the overall loss of species from 1995 to 2012 in almost every site indicates the negative effects of urban anthropogenic disturbances and subsequent

21

fragmentation on vegetation communities, as also indicated by Krauss et al. (2010). Other important factors influencing vegetation patterns are precipitation and climate, not explicitly

500 incorporated in this study. However, in their study on semi-arid sagebrush steppe Anderson and Inouye (2001) found that vegetation cover and density lagged 2-4 years in response to precipitation. The rainfall patterns prior to the sampling periods in this study indicate that both periods received rainfall close to the overall mean of the study area (Supplementary Information Fig. S1). Therefore, despite above average rainfall during the 1995-6 sampling

505 period this would probably not have profoundly influenced cover abundance at the time of sampling (Supplementary Information Fig. S1). Results indicate that urban areas are complex and that different components of plant communities react differently to urbanization-related disturbances. This study is unique in the sense that we had two sampling periods with which to test time lags and as a direct result thereof we highlighted the importance of the selection of

510 landscape measures. The relevance of the measures changed in explaining the observed vegetation patterns for different sampling periods. Moreover, between the different years, some of the relationships between species richness and the variables changed (e.g. from negative to positive). The urban landscape measures were determined for a 500 m radius buffer and we acknowledge that the scale we used to determine the landscape measures can have an impact

515 on the reliability of our results. The nature of the sites that were chosen, i.e. relevés (representative sample plots) instead of entire fragmented areas and the specific landscape measures used can also influence our results; the possibility arises that grasslands might respond better to other variables not measured or at different scales.

520 **Conclusions**

Our first hypothesis that indigenous species richness patterns correspond to past landscape patterns was partly confirmed, as indigenous woody grassland species richness showed long

22

time lags, while open grassland had very short or even no time lags. The second hypothesis

525   that disturbance indicator species correspond to periods of rapid growth and exhibit longer time

lags was partly supported, as woody DSR was linked to initial urban expansion periods (the

establishment of Ikageng and Promosa) but not to rapid urbanization after 1994. However,

DSR time lags were consistently longer that ISR time lags for all habitats. We believe that

DSR time lags can act as an early warning system and proxy for changes to local vegetation

530   communities. The third hypothesis that woody grassland will have longer time lags was

confirmed. The fourth hypothesis the time lags will shorten as urbanization intensifies was not

confirmed, except in the case of grassland DSR, however this could be as a result of the

available data. Of specific significance is that despite rapid urbanization in the area, all other

models showed relatively constant time lags. The last hypothesis was partly supported as

535   indigenous species richness declined, however exotic species richness declined in open

grassland sites but increased in woody grasslands, whereas disturbance species richness also

declined in open grasslands but remained the same in woody grasslands.

Our study is the first to specifically test for time lags in the response of remnant natural

vegetation to urbanization. Additionally, we tested two different vegetation sampling periods

540   indicating potentially constant time lag periods in the response of remnant natural vegetation to

urbanization influences, despite rapid urban expansion in the intervening years. The modified

measure of road network density of natural areas shows potential as it was one of the most

frequent predictors in the models. However, it will have more ecological utility if equally sized

sites are compared with one another. The results of this study highlight the importance of

545   legacy effects on patterns observed in contemporary communities (Burel 1993; Ewers and

Didham 2006). Indigenous species losses over the 17-year period and the presence of clear

time lags in the woody grasslands indicate that these communities at least have a probable

extinction debt (Kuussaari et al. 2009; Krauss et al. 2010) to pay in the future.

550 **Acknowledgements**

555 **Tables**

Table 1 GLM results. Model coefficients (± SE) are presented, as well as p-values. Int = model intercept, Alt = altitude, Age = age of

urbanisation, PN = percentage natural area, RNDN = road network density of natural areas, CD = density (the number) of dwellings, H' =

Shannon's diversity index of landscape diversity. AIC = Akaike's Information Criterion. AIC values represent the model with the highest AIC

value (and year), and the model with the lowest AIC (and year, in bold). GLM model coefficients and SE and p values presented here are from

560 models with the lowest AIC values. L2 and L3 represent the second and third levels of a variable classified as a factor. See Data analysis.

	Int	Alt	Age	PN	RNDN	CD	H'	AIC (model year)
Open grassland								
1995								
ISR	-19.992	0.017	0.006	-0.007	39.058			153.40 (1938) ->
	(5.030)	(0.004)	(0.004)	(0.004)	(14.328)			135.38 (**1994**)
	<0.001	<0.001	0.133	0.045	0.006			
DSR	3.388			-0.026				70.91 (1994) ->
	(0.387)			(0.005)				67.51 (**1970**)
	<0.001			<0.001				

2012								
ISR	-20.550	0.016	0.011		18.750	0.001	0.752	130.06 (1938) ->
	(5.139)	(0.004)	(0.003)		(8.713)	(0.0003)	(0.376)	116.21 (**2010**)
	<0.001	<0.001	0.002		0.031	0.003	0.046	
DSR	-0.935				107.187			69.58 (1938) ->
	(0.507)				(25.946)			59.40 (**2006**)
	0.065				<0.001			

Woody grassland

1995

ISR	20.647	-0.012		-0.285	-43.493	-0.460	-1.429	211.05 (1938) ->
	(3.585)	(0.003)		(0.211)	(24.447)	(0.144)	(0.355)	178.76 (**1970**)
	<0.001	<0.001		0.175 (L2)	0.075	0.001 (L2)	<0.001	
				-0.553		-0.126		
				(0.228)		(0.239)		
				0.015 (L3)		0.600 (L3)		
DSR	53.572	-0.037			-68.388		-0.731	157.33 (1970) ->

(9.026)	(0.006)			(34.550)	(0.255)	125.66 (**1961**)
<0.001	<0.001			0.048	0.004 (L2)	

2012

ISR	8.980	-0.004	0.005		-39.360	0.001	197.46 (2006) ->
	(3.196)	(0.002)	(0.003)		(15.070)	(0.0003)	187.98 (**1994**)
	0.005	0.080	0.116		0.009	<0.001	
DSR	21.426	-0.015		-0.036			113.04 (2010) ->
	(7.815)	(0.006)		(0.271)			109.21 (**1970**)
	0.006	0.010		0.894 (L2)			
				0.612			
				(0.294)			
				0.037 (L3)			

Table 2 Species composition of each habitat type for all species and the disturbance indicator species specifically in 1995-6 and 2012. Percentage values are given in brackets.

All species	SR	Indigenous	Exotic	Grass	Herb	Shrub	Tree
Grasslands 1995	153	142 (92.8%)	11 (7.2%)	38 (24.8%)	95 (62.1%)	19 (12.4%)	1 (0.7%)
Grasslands 2012	114	107 (93.9%)	7 (6.1%)	31 (27.2%)	69 (60.5%)	13 (11.4%)	1 (0.9%)
Woody 1995	164	150 (91.5%)	14 (8.5%)	29 (17.7%)	80 (48.8%)	38 (23.2%)	17 (10.4%)
Woody 2012	139	120 (86.3%)	19 (13.7%)	29 (20.9%)	61 (43.9%)	32 (23%)	17 (12.2%)
Disturbance species							
Grasslands 1995	26	21 (81%)	5 (19%)	8 (31%)	12 (46%)	6 (23%)	0
Grasslands 2012	14	11 (79%)	3 (21%)	4 (29%)	8 (57%)	2 (14%)	0
Woody 1995	24	17 (71%)	7 (29%)	7 (29%)	13 (54%)	4 (17%)	0
Woody 2012	24	17 (71%)	7 (29%)	7 (29%)	13 (54%)	4 (17%)	0

565

Figure Captions

Fig. 1 The location of Potchefstroom in South Africa (a), the town commonage area (black outline) and the location of the sites (see legend of map c) (b), urban development from 1863 to 570 2010 (1863 obtained from an early hand drawn map, 1944-2006 were digitized from government topographical maps and 2010 from a satellite image) (c), sites and urban area in 1995 (d), sites and urban area in 2010, indicating the 1995 urban area (hatched) (e).
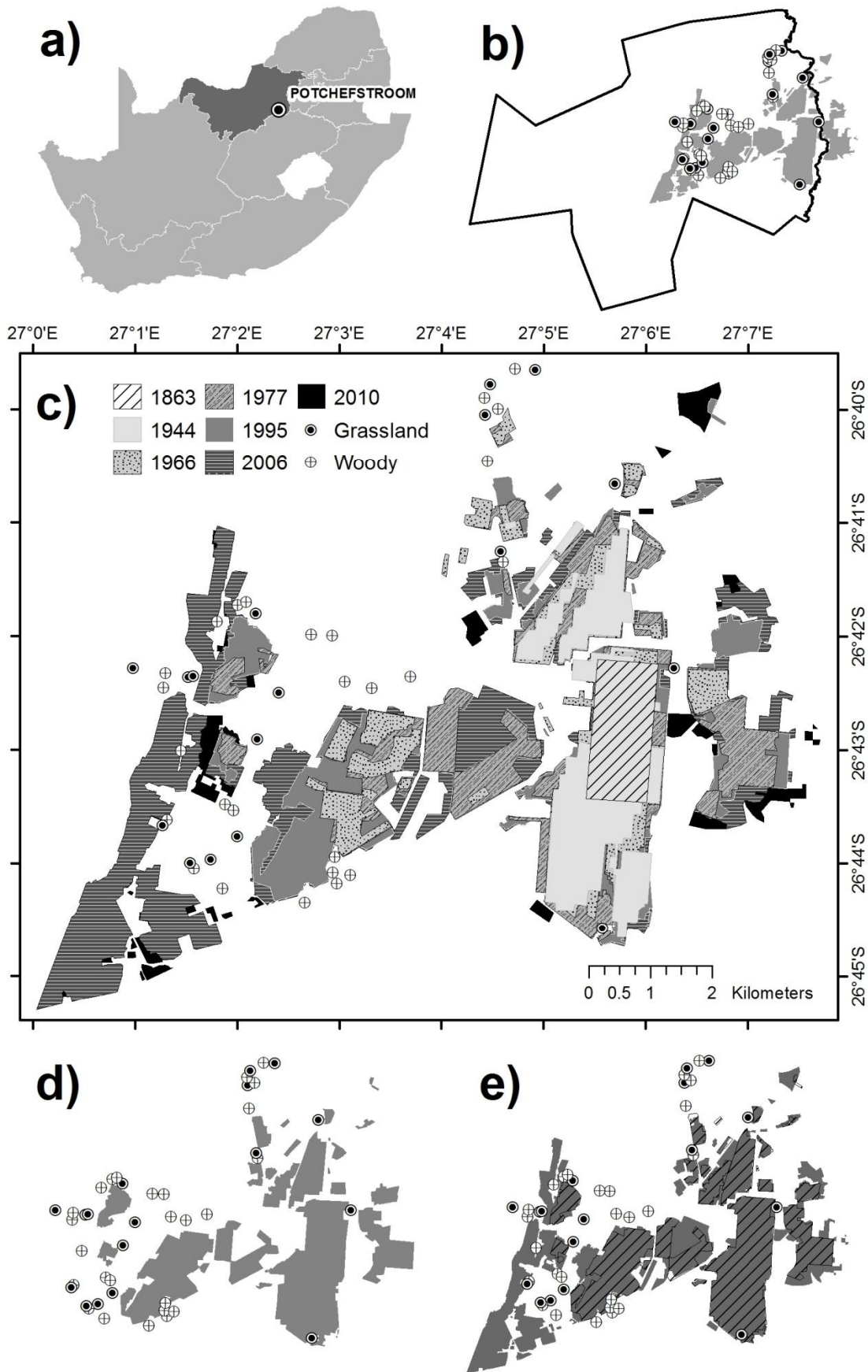
Fig. 2 Plots indicating change in a) the percentage natural (PN) area, b) the road network 575 density of the natural areas (RNDN), c) the density of dwellings (CD), and d) landscape diversity (H') for the open grassland (G) (open boxes) and woody (W) (black boxes) communities spanning the period 1938-2010. Means ± SE's are shown.

Fig. 3 The relationships between species richness and altitude (top plot) and the road network 580 density of natural areas (bottom plot) as indicated in Table 1. Codes indicate open grassland (G) or woody community (W) patterns in 1995 (95) or 2012 (12) for indigenous (ISR) and disturbance (DSR) species richness.
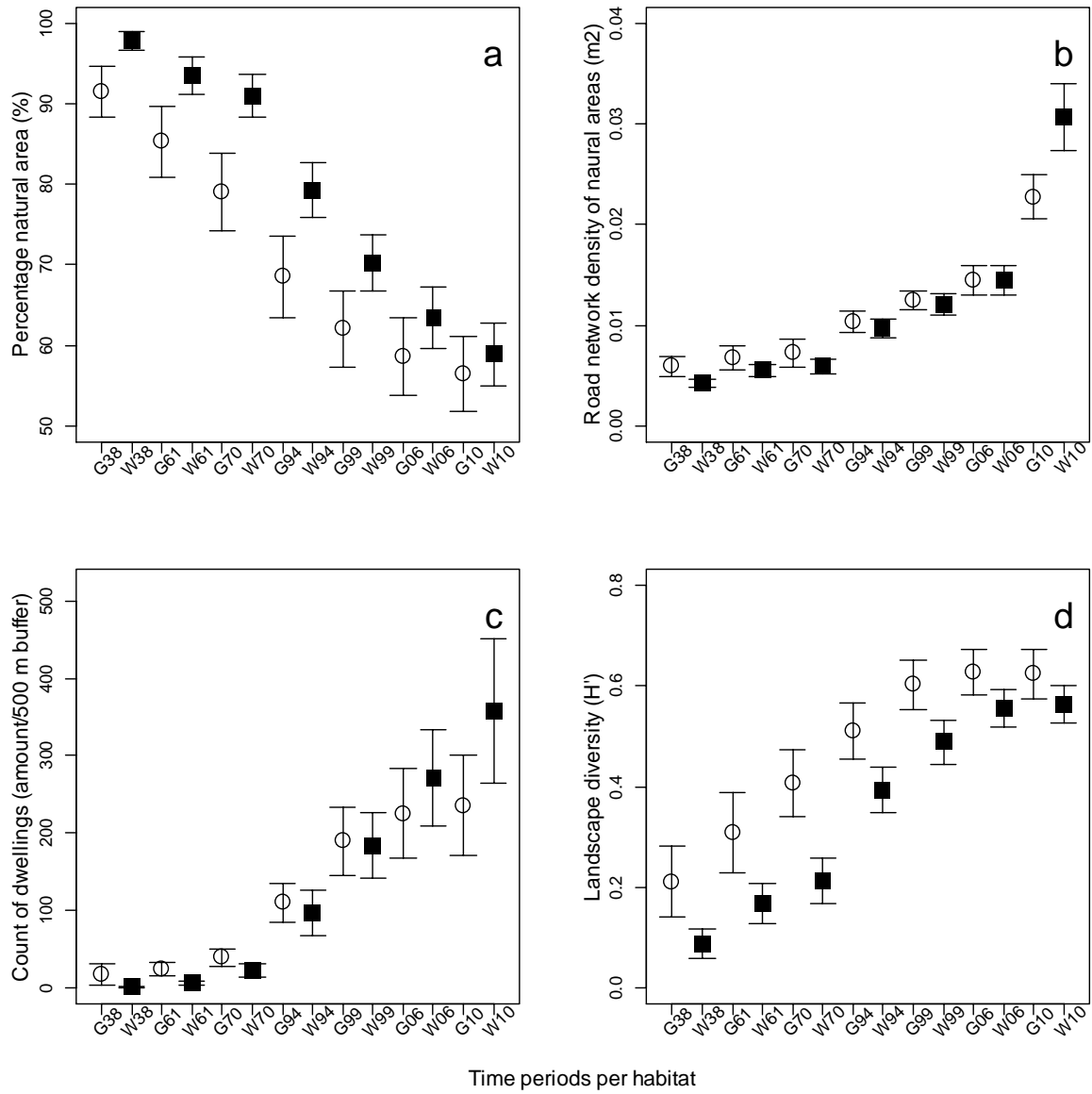
Fig. 4 The relationships between species richness and the percentage natural area as indicated 585 in Table 1. Codes indicate open grassland (G) or woody community (W) patterns in 1995 (95) or 2012 (12) for indigenous (ISR) and disturbance (DSR) species richness.

Fig. 5 Open grassland indigenous (a, b) and disturbance (c, d) species richness per site for 1995 and 2012. Indicated in each map are the extent of the urban area and the roads and footpaths in 590 the natural areas (RN Natural) corresponding to the best predicted model.
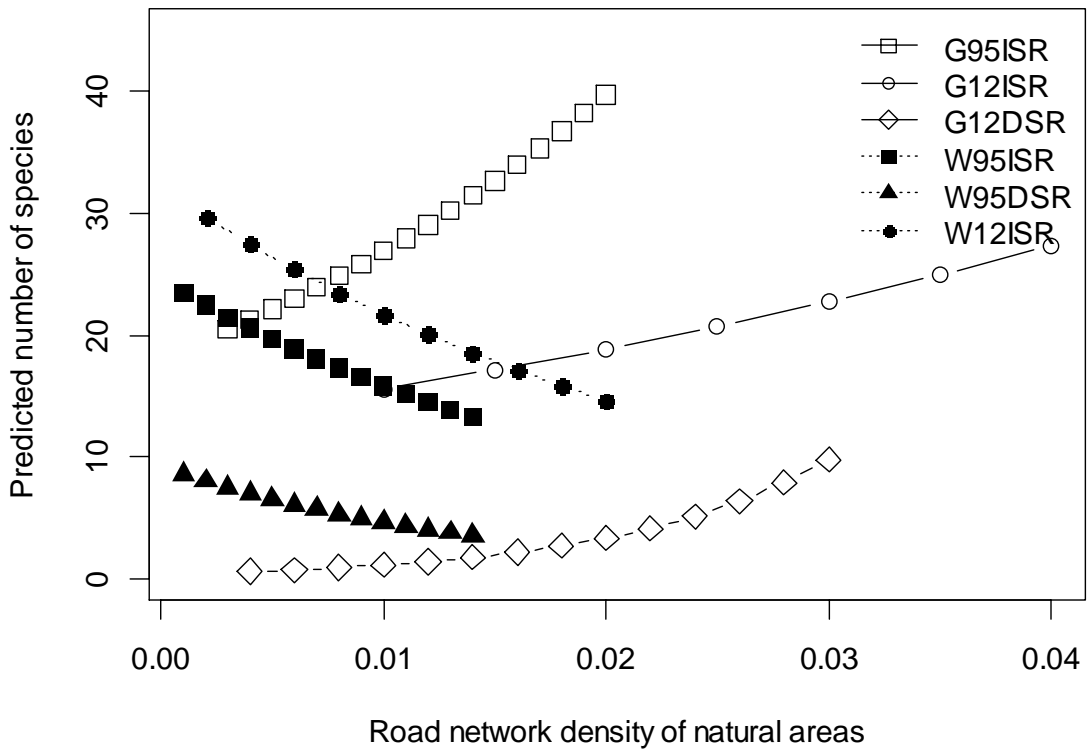
29

Fig. 6 Woody grassland indigenous (a, b) and disturbance (c, d) species richness per site for 1995 and 2012. Indicated in each map are the extent of the urban area and the roads and footpaths in the natural areas (RN Natural) corresponding to the best predicted model.
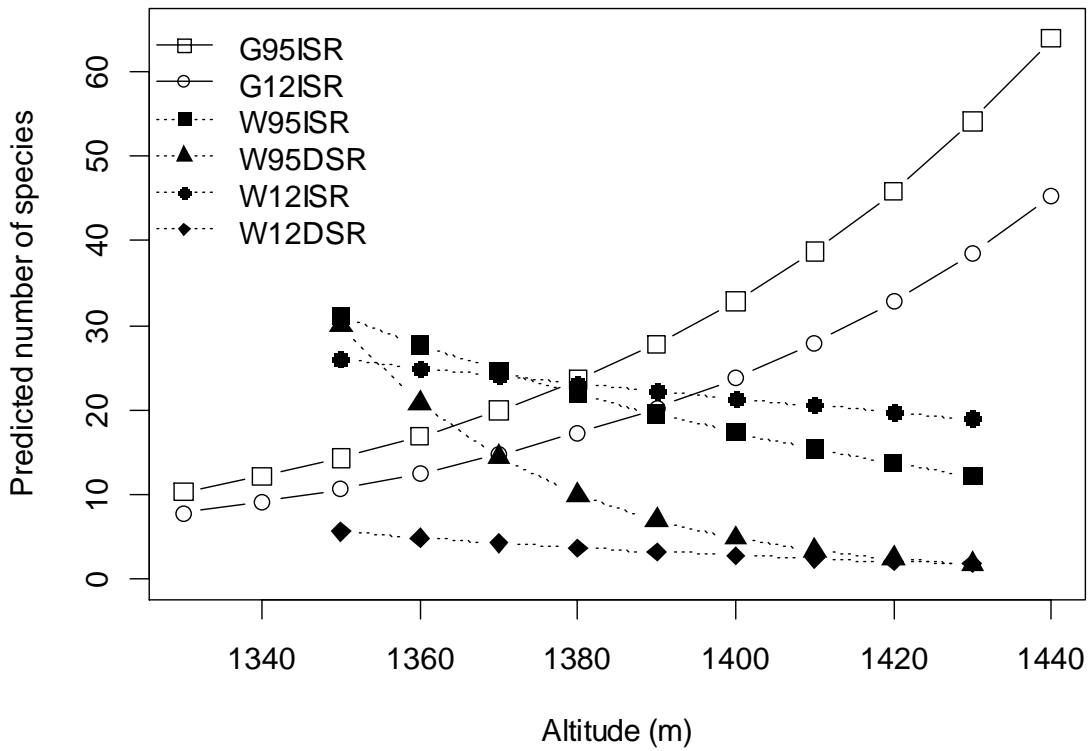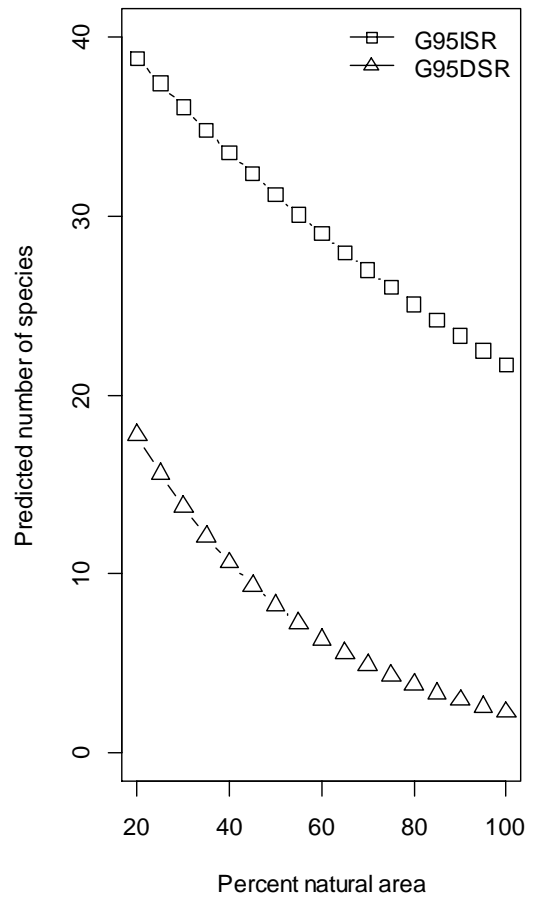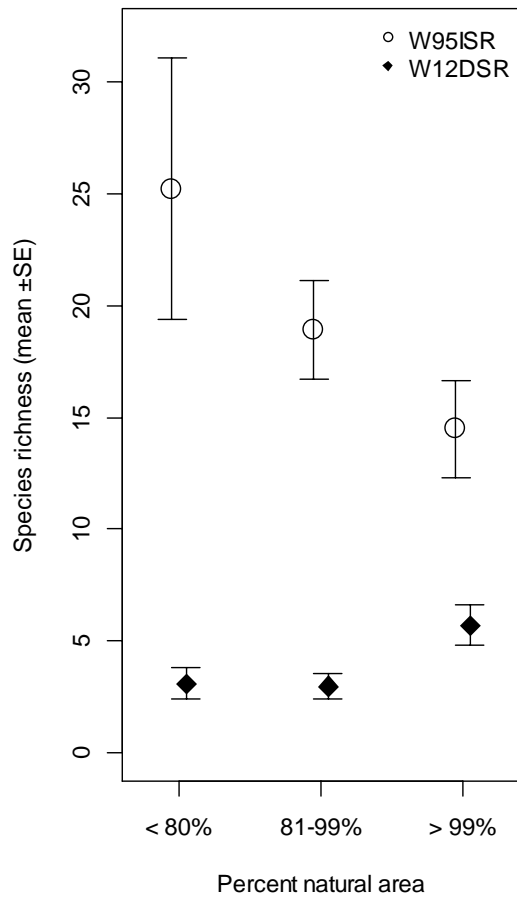
595

Fig. 1

Fig. 2

600

Fig. 3

Fig. 4

605

Fig. 5

a) 1995 ISR
1970 RN Natural
1970 Urban Area

b) 2012 ISR
1994 RN Natural
1994 Urban Area

ISR
7 - 15
16 - 25
26 - 35
36 - 42

c) 1995 DSR
1961 RN Natural
1961 Urban Area

d) 2012 DSR
1970 RN Natural
1970 Urban Area
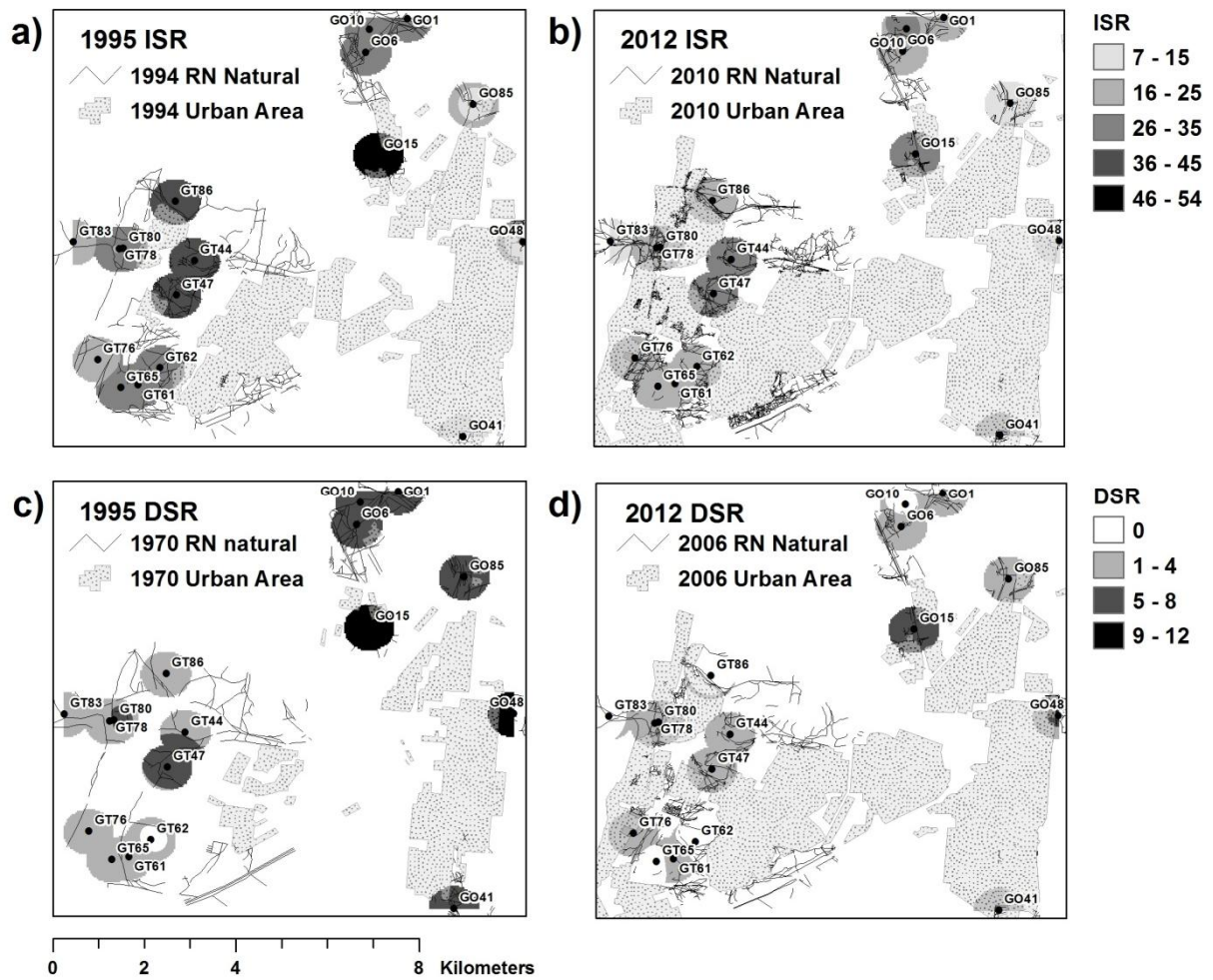
DSR
0
1 - 4
5 - 8
9 - 12

0 1 2 4 Kilometers
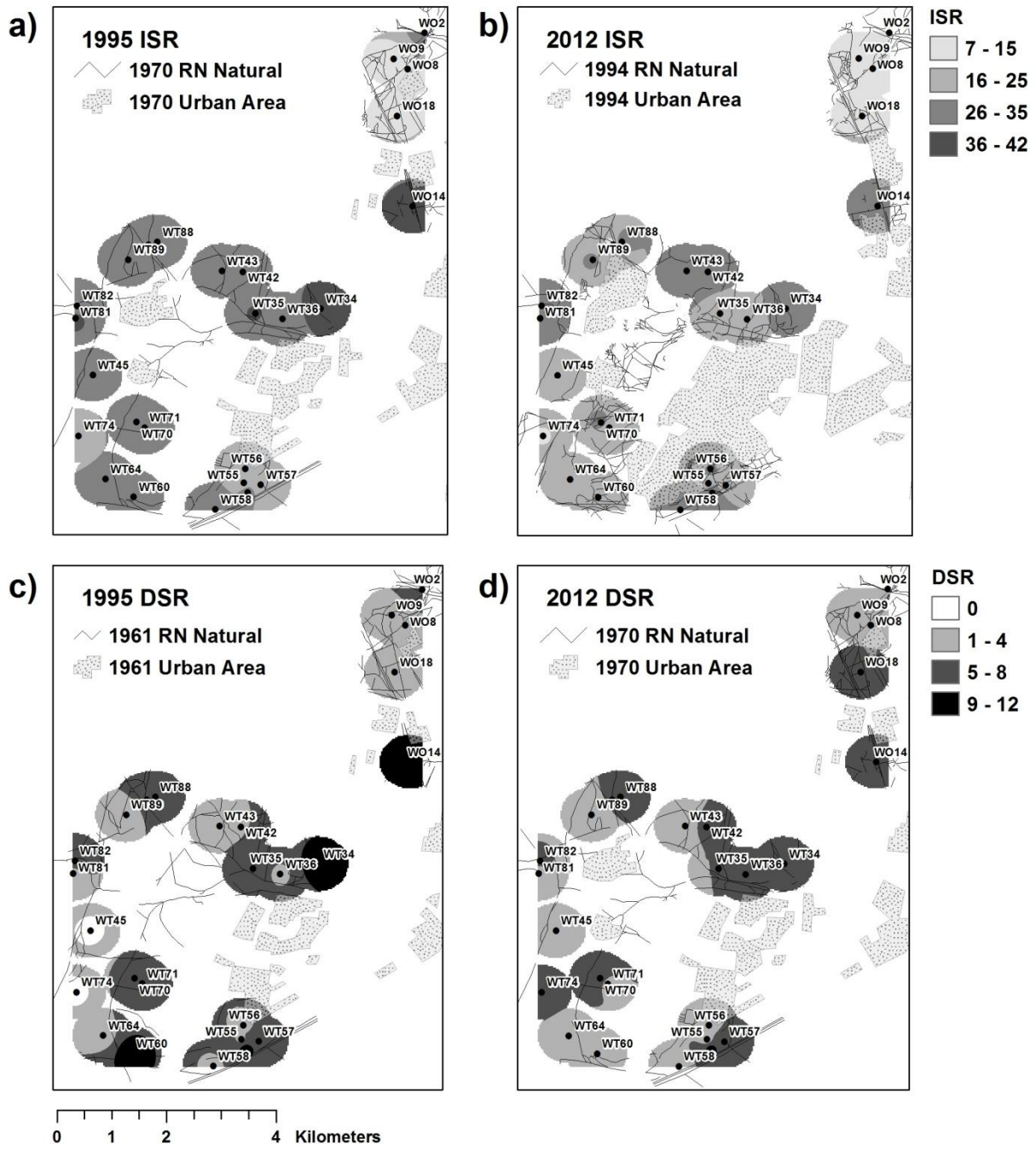
610 **Fig. 6**

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