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Cover photograph: Giraffes on the game farm Omatako Ranch (Observatory S04 Toggekry) in the Namibian Thornbush Savanna.
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Patterns and dynamics of vascular plant diversity along the BIOTA transects in southern Africa

Ute Schmiedel*, Jürgen Dengler, Jona Luther-Mosebach, Alexander Gröngröft, Gerhard Muche, Andreas Petersen, Ben J. Strohbach & Norbert Jürgens

Summary: Patterns of vascular plant diversity were studied at different spatial scales (100 m², 1000 m², 1 ha and 1 km²) along the BIOTA Southern Africa transects from the Kavango in northern Namibia to the Cape of Good Hope in South Africa, covering six biomes in the western part of southern Africa and a steep rainfall gradient. We analysed family richness, species richness, as well as z-values (i.e. the slopes of power-law species-area relationships as measures of β-diversity) on all these spatial scales in order to provide baseline data for biodiversity assessment in the region and an understanding of the influence of potential drivers on various dimensions of biodiversity. For the last purpose, we related our biodiversity parameters via correlations, linear and polynomial regressions as well as analyses of variance (ANOVAs) to potential drivers such as geography, landuse, climate, and soil. Finally, we used the time-series data of the BIOTA Observatories to analyse whether a change in species richness occurred during the project period.

The mean species density along the transects was 23.9 species for 100 m², with an absolute minimum of 0 (Desert Biome) and an absolute maximum of 128 (Fynbos Biome). The mean value for 1000-m² plots was 40 species (maximum: 169; Fynbos Biome), and 159 species (maximum: 385; Elandsberg Observatory, S32, Fynbos Biome) at the 1-km² scale. Elandsberg Observatory in the Fynbos Biome showed exceptionally high species richness at all spatial scales.

The following environmental factors showed the strongest relationship with species richness at the 1000-m² scale: mean annual precipitation (positive), precipitation seasonality (winter rainfall >> summer rainfall), mean annual temperature, length of dry season, and median pH values (all negative). The complex-factor soil ecotype richness, as an expression of the variability of plant-relevant soil features per 1 km², was only related to species richness at the 1-km² scale. Spatial species turnover (expressed as z-values), was highest in the arid parts of the transect (Desert and Succulent Karoo) and lowest in the Fynbos Biome.

The time series of annual monitoring data of up to nine years revealed a slight but significant mean annual increase in woody plant species richness at the 1000-m² plot level for most of the Observatories along the transect. The maximum mean annual increase recorded was +2.2 woody plant species in the Koeroegap Vlakte Observatory (S18, Succulent Karoo). The positive increase corresponds well with the findings of our individual-based plant population monitoring in the Succulent Karoo, which also indicated a stable to increasing development of the plant populations, irrespective of inter-annual variability. The only Observatory with a significant decrease was Wlotzkasbaken (S16) with on average –1.0 woody plant species per year. We discuss the role of the various drivers of plant diversity at different spatial scales along the transect and relate them to previous studies on regional and global plant diversity patterns. Finally, we highlight that the vascular plant data of BIOTA Southern Africa are a highly valuable, globally unique macroecological dataset in as far as they (i) combine large spatial extent with fine to medium grain, (ii) use a highly standardised sampling approach, including (iii) various spatial scales, (iv) time series, and (v) direct measures of many potential drivers of biodiversity.

Introduction

Southern Africa is renowned for its rich biodiversity (Barnard et al. 1998, Simmons et al. 1998, Goldblatt & Manning 2002, Burke 2003, Linder et al. 2010). The region accommodates two of the global biodiversity hotspots (i.e. Cape Floristic Region and Succulent Karoo, Jürgens 1986, Myers et al. 2000, Kier et al. 2005) and numerous local centres of plant-diversity and endemism (Nordenstam 1969, Davis et al. 1994), several of which are covered by the BIOTA Southern Africa transects: e.g. Cape Peninsula (Goldblatt & Manning 2002), Nieuwoudtville (Snijman & Perry 1987), Knersvlakte, Kamiesberg, Richtersveld (Nordenstam 1969, Hilton-Taylor 1994), and the Okavango Region (Maggs et al. 1998). Despite this species richness and numerous studies on local or regional plant diversity patterns and their drivers (e.g. Cowling 1990, Cowling et al. 1989,

Photo 1: Small-scale richness of succulent plants in the Succulent Karoo. Photo: U. Schmiedel.

Photo 2: Mosaic of different habitats at the Observatory Gellap Ost (S10) in the Nama Karoo. Photo: N. Dreber.

1992, 1994, 1996, 1997, 1998, Goldblatt 1997, Goldblatt & Manning 2002, Linder et al. 2010), studies that provide measures of species richness at different spatial scales in a standardised manner and which relate them to site-specific environmental drivers are scarce. A first comprehensive approach towards a regional comparison has been provided by Cowling et al. (1989).

The landscapes in the study region are prone to transformation and subsequent species loss due to unsustainable landuse (Hoffman & Todd 2000, Hoffman & Ashwell 2001) and projected climate change (Midgley et al. 2003, Thomas et al. 2004, Thuiller et al. 2006, Midgley & Thuiller 2007, Biggs et al. 2008). Vascular plants, the main primary producers, are likely the first to be affected by transformation, which has strong knock-on effects on other groups of organisms (e.g. Blaum et al. 2007, 2009, Siramin et al. 2009, see also Articles III.4.4, III.4.6, III.5.7, III.5.8) and the abiotic environment, such as the soil (Article III.5.4) and microclimate. The consequences might be irreversible losses of biodiversity, with negative effects on the resilience and productivity of the systems.

The extent of changes is hard to quantify, because benchmark data on current and historical states of the environment, which are required to reconstruct the changes over time at a given site, are scarce. Where such data have been available, it has provided valuable insight into environmental changes (Kraaij & Milton 2006, Rahlao et al. 2008). Historical

landscape photographs are valuable substitutes for quantitative site-specific data on historical vegetation cover and species composition (Articles III.1.2, III.1.3). Several case studies have used space as a substitute for time by analysing landuse impacts along fence-line contrasts or gradients of landuse intensity around stock posts and water points. These studies, which have been conducted in different biomes of southern Africa, have shown that unsustainable land management may result in changes to the species- and life form composition of vascular plants (Todd & Hoffman 1999, 2009, Riginos & Hoffman 2003, Anderson & Hoffman 2007, Haarmeyer et al. 2010, Wesuls & Lang 2010, and Article III.5.5).

The analysis of fence-line contrasts or resampling of historical permanent plots enables quantification of changes over a given time period, but it does not provide information on the responsible processes and their drivers. Only continuous long-term monitoring of biodiversity and their potential drivers (i.e. climatic factors, landuse management) can provide process-oriented information. The objective of the BIOTA Observatories in southern Africa is to provide baseline data for analysis of biodiversity patterns in southern Africa and, based on annual monitoring, to provide the required evidence for changes in species composition, and the processes and drivers of such change.

In this article, we analyse current patterns of vascular plant species richness at different spatial scales (i.e. 100 m², 1000 m², 1 km²) along the BIOTA South-

ern Africa transect and relate them to major environmental drivers (i.e. mean annual precipitation, rainfall season, soil heterogeneity). Based on nine years of monitoring data, we further provide a quantitative analysis of the changes in species richness of perennial plant species at the BIOTA Observatories.

Methods

Sampling was carried out on 36 of the 37 BIOTA Observatories (see Subchapter II.1.2; insufficient data for Nieuwoudtville, Observatory S45, for our analysis) along the BIOTA transects in southern Africa (see Subchapter II.1.1). From these Observatories, we used 29 environmental variables as predictors, and 12 parameters describing various "dimensions" of vascular plant diversity at different spatial scales as dependent variables. The data availability ranged from 22 to 36 Observatories, depending on the type of variable. The Electronic Appendix 1 gives an overview of the data used, while precise information on their measurement and calculation can be found in Subchapter II.1.3.

Two variables with strongly skewed distributions (electrical conductivity and organic carbon) were log-transformed for the analyses, while all other variables showed distributions sufficiently close to normal to allow the application of parametric statistical tests (see Quinn & Keough 2002). Box-whisker plots were used to display the biodiversity

Table 1: Variables used in the statistical analyses
The majority are metric variables, while ordinal or categorical variables are indicated in square brackets. Similarly, transformations applied to achieve approximate normality of the data are given in square brackets. Detailed information on each of the variables is available in Sub-chapter II.1.3

Type	Variable group	Variable(s)
Predictor	General data	Latitude; Longitude; Altitude; Rainfall season [2 categories]; Biome [6 categories]; Intensity of landuse [4-point ordinal, in correlations treated as quasi-metric]
	Climate (modelled data from Worldclim, Hijmans et al. 2005)	Mean annual temperature; Minimum annual temperature; Maximum annual temperature; Annual temperature range; Diurnal temperature range; Annual precipitation; Percentage winter precipitation; Length of dry season; Aridity index (De Martonne)
	Climate (data from BIOTA weather stations)	Inter-annual precipitation variability; Relative humidity; Wind speed; Solar radiation; Potential evapotranspiration; Aridity index (UNEP)
	Soil (chemistry)	pH; Electrical conductivity [log-transformed]; Organic carbon [log-transformed]
	Soil (pedodiversity, after Petersen 2008, see also Petersen et al. 2010)	Reference group richness; Soil unit richness; Soil unit evenness; Soil ecotype richness; Parametric space
Biodiversity (dependent variable)	α-diversity	Cumulative family richness (1 km^2); Cumulative species richness (1 km^2); Species richness (1 km^2, selected year); Mean species richness (1 ha); Mean species richness (1000 m^2); Maximum species richness (1000 m^2); Mean species richness (100 m^2); Maximum species richness (100 m^2)
	β-diversity	z-value (1000 m^2 to 1 km^2); z-value (1000 m^2 to 1 ha); z-value (100–1000 m^2, calculated for individual pairs of nested plots); z-value (100–1000 m^2; "mean-to-mean", i.e. calculated between the mean richness values per Observatory at that scales)

values of the individual hectare plots on the Observatories along the transects, arranged according to decreasing summer and increasing winter rainfall. Although analysis of variance (ANOVA) with post hoc tests had revealed that Observatories could be arranged in many distinct groups according to their diversity values, we did not include them as we do not consider them as particularly meaningful here.

For the inferential statistical tests, we used only one value for each Observatory, i.e. mean, median, minimum, or maximum, depending on the specific variable. The analyses were carried out in a two-step approach. First, we established Pearson correlation matrices among the predictors (Electronic Appendix 2), among the dependent variables (Electronic Appendix 3), and between predictors and dependent variables (Electronic Appendix 4). Then we applied linear regression analyses for combinations of predictors and dependent variables with significant and strong correlations and for which a causal relationship was plausible. We used both simple linear and second-order polynomial regressions when the data

distribution suggested the latter as the more appropriate model. In this case, we used the Akaike information criterion (AIC), calculated in PAST (Hammer et al. 2001) as an additional measure of goodness-of-fit in comparison of models with different complexity (see Quinn & Keough 2002). In one case, we applied the regression analyses separately for the Observatories of the two rainfall regions (i.e. winter vs. summer rainfall), as the correlations had indicated a strong additional effect of rainfall season. In order to analyse the effects of categorical or ordinal variables on biodiversity measures, we applied ANOVAs.

Finally, we calculated the mean annual change (between consecutive years) in species richness of perennial woody plants (i.e. phanerophytes and chamaephytes) for the 1000-m^2 plots. We did this calculation for each of the 1000 m^2-plots sampled within an Observatory. This resulted in typically 20 values per Observatory (depending on the number of 1000 m^2-plots sampled; see Part II) of a linear increase/decrease rate per Observatory. These change rates per plot were

then graphically displayed and subjected to a t-test in order to see whether the observed mean change was significantly different from zero.

Results

Relationships among the biodiversity parameters

The majority of the biodiversity parameters were strongly positively correlated to each other (see Electronic Appendix 1). The only exceptions were the z-values, which showed—apart from one case—negative and only partly significant correlations to the various richness parameters. Since z-values are a measure of β-diversity, this finding means that the relative increase in species richness with spatial scale was generally lower when the small-scale richness was already high. The richness values for the four different spatial scales (100 m^2, 1000 m^2, 1 ha, 1 km^2) within individual years showed the highest Pearson correlation coefficients among all parameter pairs ($r = 0.783$–0.985), with the values

increasing with decreasing plot size differences. The correlation of species richness for 1 km² cumulated over all years with the single-year richness values was clearly lower ($r = 0.535–0.887$), indicating biases caused by the different numbers of years sampled as well as varying "identification rates". The latter might cause "inflated" richness values due to varying field names for the same taxon in different years (see Part II). (Cumulative) family richness was positively correlated with cumulative species richness ($r = 0.713$) as well as with all other richness values.

Biodiversity patterns along the transects

The number of observed vascular plant families ranged from 1 in the Namib Desert (S34 Kleinberg) to 62 for two of the Fynbos Observatories (S31 Riverlands, and S32 Elandsberg; see Electronic Appendix 1). Generally, the family richness was highest in the Woodland Savanna and the Fynbos, lowest in the Namib Desert, and intermediate in the three other biomes (Fig. 1). For species richness, the differences between the biomes were even more pronounced at the analysed spatial scales of 100 m², 1000 m², 1 ha, and 1 km² (Fig. 1 and Electronic Appendix 1). The Observatories in the Fynbos Biome were the richest at all spatial scales except 1 km², where the Observatories in the Succulent Karoo were equally species rich (Figs. 1 & 2). The mean species density along the transects on 100 m² was 23.9 species, with an absolute minimum of 0 (at various Observatories, mainly in the Namib Desert) and an absolute maximum of 128 (S32 Elandsberg) (Fig. 2). The mean species density for 1000-m² plots was 40 species (maximum: 169 in S32 Elandsberg), 53.6 species for 1-ha plots (maximum: 183 in S32 Elandsberg; note that this scale was probably undersampled at various Observatories), and 159 species at the 1-km² scale (minimum: 1 in S34 Kleinberg; maximum: 385 in S32 Elandsberg) (Fig. 2).

Drivers of biodiversity

The 30 abiotic parameters used to explain the biodiversity patterns showed a clear correlation pattern, with each of the parameters being significantly correlated with several other parameters (see Electronic Appendix 2). Apart from trivial relationships such as those between decreasing mean annual temperature and increasing winter precipitation with increasing latitude, differently transformed variants of the same variable, or different measures of similar parameters (e.g. annual precipitation, length of dry season, and De Martonne's aridity index, or among the various pedodiversity measures), the matrix also showed some more subtle connections between various aspects of the environment that need to be considered when interpreting correlations between biodiversity parameters and environmental predictors. The strong negative correlation ($|r| > 0.75$) of soil pH with mean annual precipitation and with the two aridity indices was one of the more interesting relationships. Furthermore, mean annual temperature was strongly positively correlated to diurnal temperature range and strongly negatively correlated to annual temperature range in the study region. Finally, relative humidity was strongly negatively correlated to diurnal temperature range. Many further, less strong, but still significant correlations can be found in the Electronic Appendix 2.

Regarding species richness (density) as the most important measure of plant diversity, we found clear and consistent relationships for the spatial scales 100 m² to 1 ha (see Electronic Appendix 3). The strongest predictors were the precipitation-related parameters, given here in decreasing order of importance: length of dry season (negative, Fig. 6c), De Martonne's aridity index (positive), mean annual precipitation (positive, Fig. 6b), and percentage winter precipitation (positive), while the UNEP aridity index was only correlated at the hectare scale. The second most important predictor group were the soil chemical parameters, organic content (positive) and pH (negative, Fig. 5d). At the 1000-m² scale, mean annual temperature was also a weak negative predictor (Fig. 5a). Species richness at the 1-km² scale showed similar patterns as at the three smaller scales, but with lower r-values in all cases. Additionally, species richness
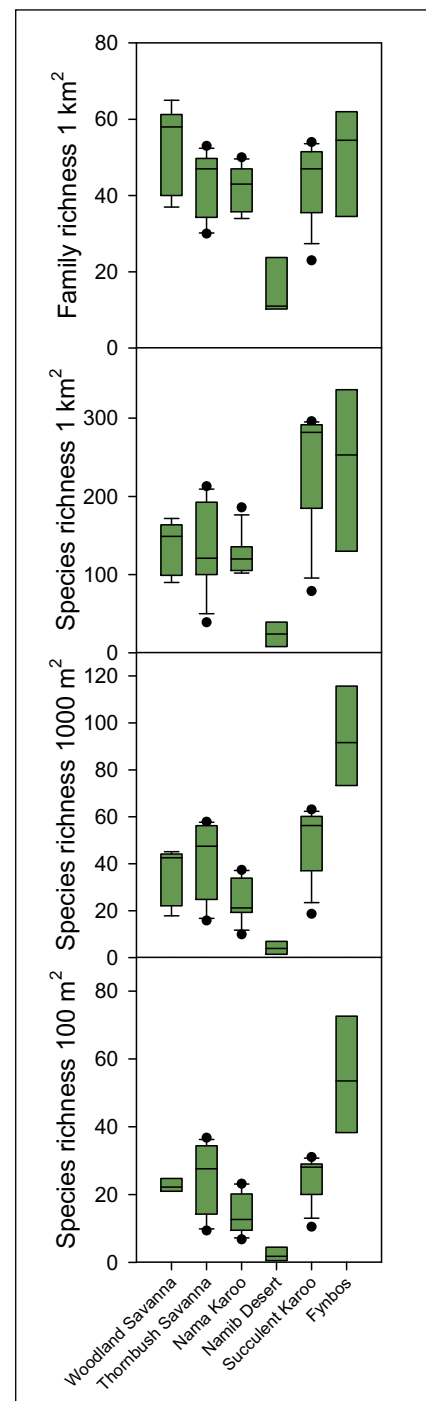
Fig. 1: Variability of the mean vascular plant taxon richness at different spatial scales compared between the Observatories of the six analysed biomes. Family richness is given as a cumulative value over all study years for the entire square kilometre. Species richness values at 1 km² are for a selected year with particularly high recorded species richness (mostly 2008; see Electronic Appendix 1), while the species richness data at the two smaller spatial scales are based on means over all years and all sampled hectare plots. The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots). The differences between the biomes were significant in all cases (tested with ANOVAs; $p = 0.004$ for family richness and $p < 0.001$ for all other parameters).
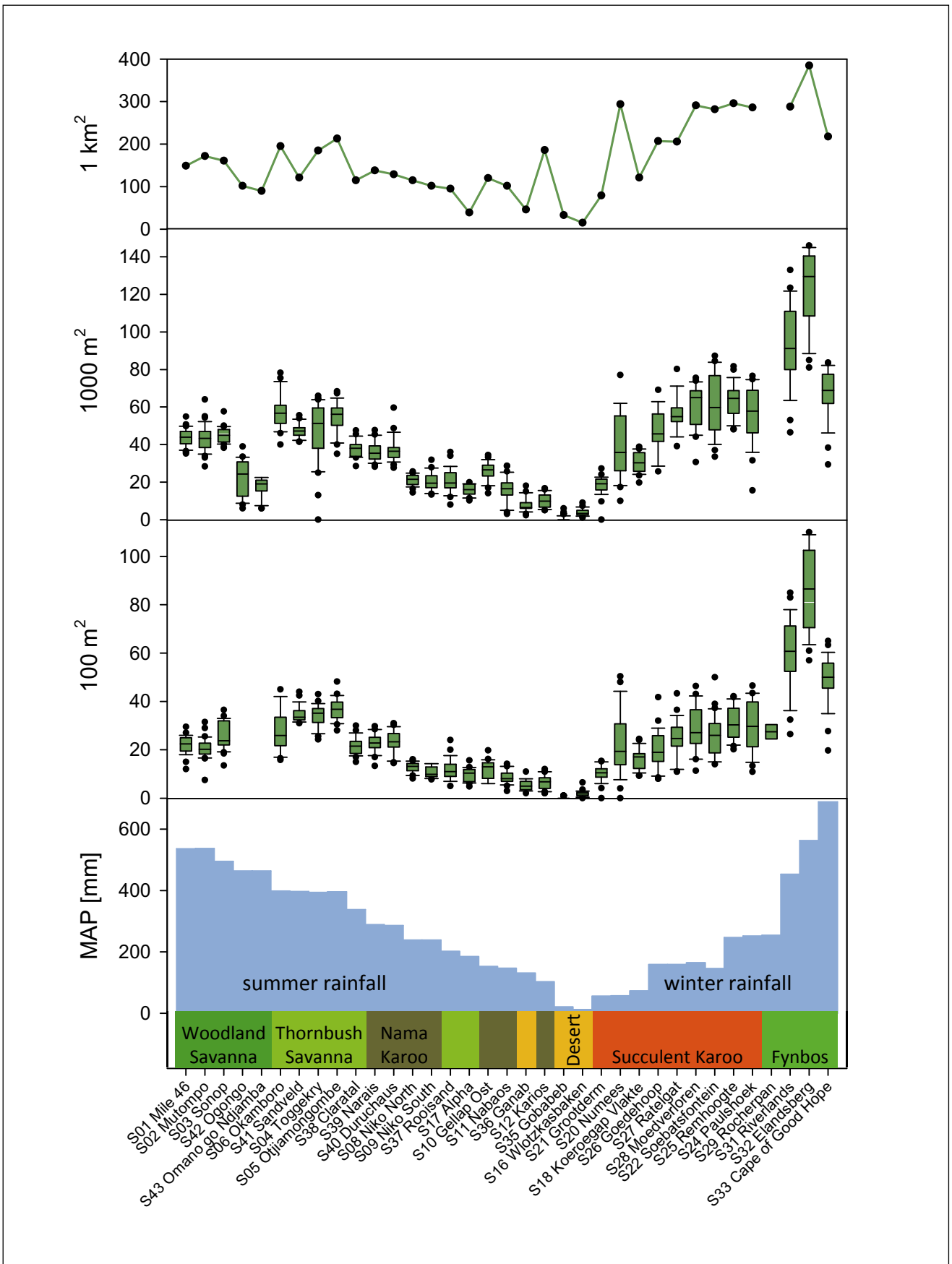
Fig. 2: Variability of vascular plant species richness along the BIOTA transects in southern Africa at three different spatial scales and compared to mean annual precipitation (MAP). The species richness values at the 1-km^2 scale are those for a selected year with particularly good recording quality (mostly 2008; see Electronic Appendix 1). For the graphs at the two smaller spatial scales, mean richness values of the individual hectare plots were used (i.e. averaged over all years). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots).
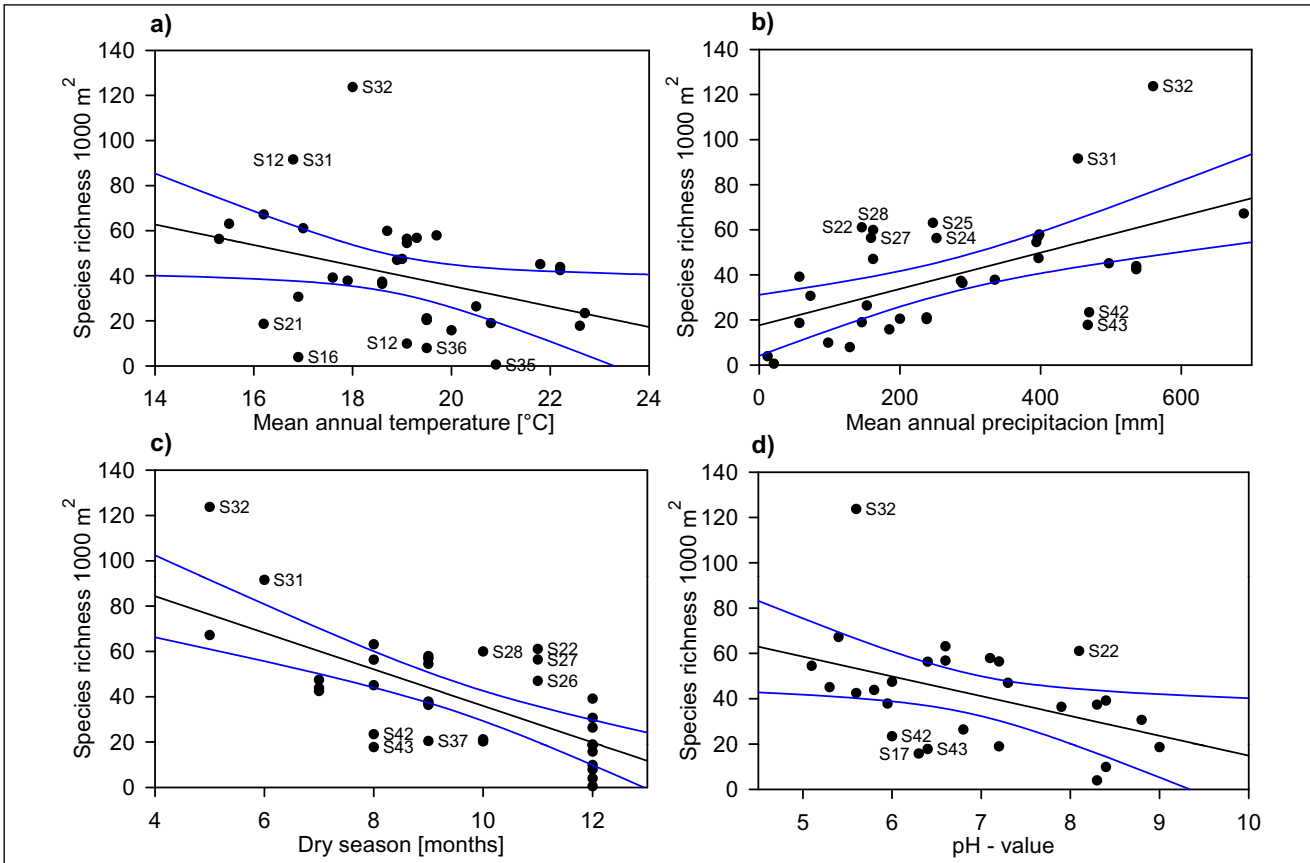
Fig. 5: Regressions of vascular plant species richness at 1000 m^2 vs. four strong environmental predictors. The graphs show the linear regression lines with their 95% confidence intervals. Dots for Observatories with unusually high or low richness values are labelled with their number (for meaning, see caption of Fig. 2). The regression functions for the predictors (*x*) are: (a) mean annual temperature [°C]: $S = 126.4 - 4.5\ x$, $r^2 = 0.1241$, $p = 0.041$; (b) mean annual precipitation [mm]: $S = 17.64 + 0.08\ x$, $r^2 = 0.5553$, $p < 0.001$; (c) Length of dry season [months]: $S = 116.6 - 8.1\ x$, $r^2 = 0.4622$, $p < 0.001$; (d) median soil pH: $S = 102.3 - 8.7\ x$, $r^2 = 0.1822$, $p = 0.026$.
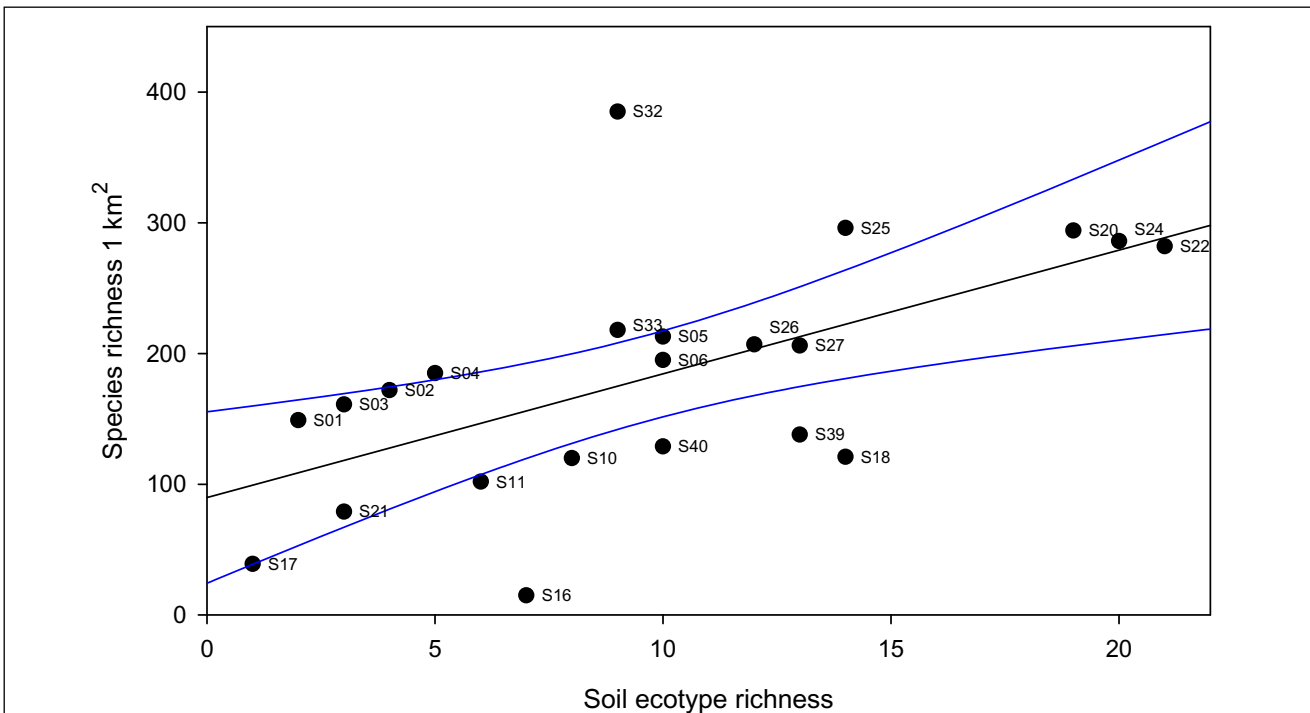

Fig. 6: Linear regression of vascular plant species richness (*S*) dependent on soil ecotype richness (a measure of pedodiversity) at the Observatory level (*x*). The graph shows the regression line with its 95% confidence interval. The points are labelled with the Observatory numbers (see caption of Fig. 2). The linear regression ($S = 89.9 + 9.5\ x$) was highly significant ($p = 0.003$; $r^2 = 0.3616$).
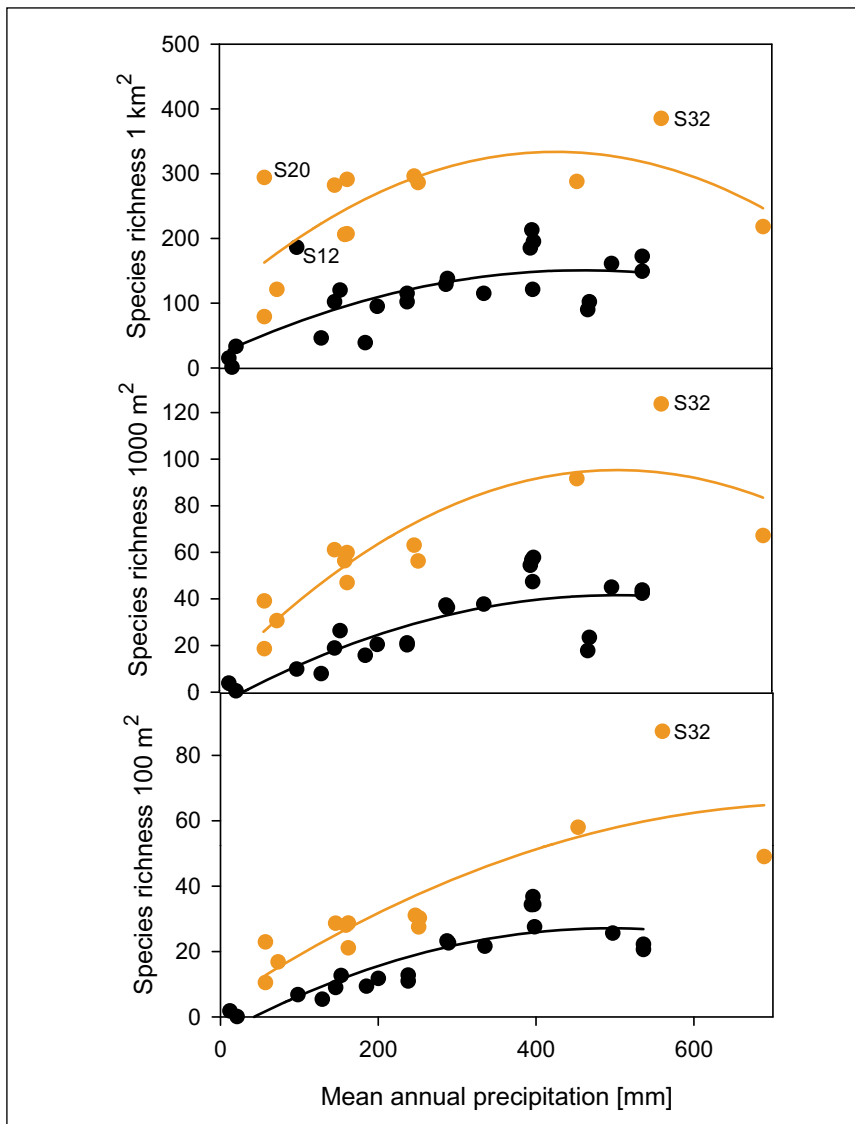
Fig. 7: Second-order polynomial regressions for species richness at three different spatial scales dependent on mean annual precipitation and distinguished between winter rainfall regions (orange; WR) and summer rainfall regions (black; SR). Observatories with unexpectedly high richness values are indicated with their number (for meaning, see caption of Fig. 2). The functions of the regressions of species richness (S) on mean annual precipitation/mm (x) are: 1 km²/WR: $S = 105.64 + 1.07 x - 0.0013 x^2$, $R^2 = 0.4505$, $p = 0.068$; 1 km²/ SR: $S = 20.92 + 0.56 x - 0.0006 x^2$, $R^2 = 0.5003$. $p < 0.001$; 1000 m²/WR: $S = 7.87 + 0.35 x - 0.0003 x^2$, $R^2 = 0.7673$, $p = 0.001$; 1000 m²/SR: $S = -5.70 + 0.20 x - 0.0002 x^2$, $R^2 = 0.6526$, $p < 0.001$; 100 m²/WR: $S = 3.98 + 0.16 x - 0.0001 x^2$, $R^2 = 0.7344$, $p = 0.001$; 100 m²/SR: $-5.33 + 0.13 x - 0.0001 x^2$, $R^2 = 0.7699$, $p < 0.001$.

at this scale was strongly positively correlated to various measures of pedodiversity, in particular to soil ecotype richness (Fig. 6) and to soil parametric space. A closer look at the link between precipitation patterns and species richness at three different spatial scales, revealed that both the total amount of precipitation and the season in which it mainly falls, play a crucial role (Fig. 7). Winter rainfall regions have a consistently two to three times higher species richness than summer rainfall regions with the same total

amount of precipitation. Furthermore, the addition of a second-order polynomial term in all six cases lead to a strong increase in explained variance, while the AIC decreased in four cases compared to a simple linear model (meaning that the quadratic model is more appropriate), remained identical in one case, and slightly decreased in the last case (100 m², winter rainfall). The always negative quadratic term in the polynomial regressions of Fig. 7 indicates that, beyond a certain threshold, additional precipitation did

not further increase richness and could even be associated with lower species richness. Finally, it should be mentioned that some of the Observatories had unexpectedly high or low richness values that could not be explained by any of the analysed predictors. Most notable was the Observatory S32 Elandsberg, with richness values always occurring far above the regression lines (Figs. 5–7). The Observatories Soebatsfontein (S22), Remhoogte (S25), and Riverlands (S31) also showed unexplainably high richness values. Negative deviations from regression lines were much more idiosyncratic, with only the Observatories Ogongo (S42) and Omano go Ndjamba (S43) frequently showing negative deviations.

Family richness responded very similarly to the species richness values of the different scales to mean annual precipitation, aridity indices, soil organic carbon content, and pH (see Electronic Appendix 4). In addition, we found significant influences of landuse intensity (weakly positive), electrical conductivity of the soils (strongly negative), annual temperature range (weakly positive), and solar radiation (weakly negative), while the pedodiversity measures were completely irrelevant for this biodiversity parameter (Electronic Appendix 4).

Interestingly several environmental parameters were of secondary importance and showed no, or only very few, significant (linear) relationships with any of the biodiversity measures. These parameters were altitude, soil-taxonomic richness and evenness of soils, maximum temperature, diurnal temperature range, relative air humidity (only a weak relationship with $S_{100\ m^2}$). Landuse intensity showed a weak positive correlation with family richness at the 1-km² scale and with the β-diversity at the transition from 100 m² to 1000 m².

Scale-dependence of biodiversity

One means of to describing scale-dependency of taxon richness, the fundamental measure of biodiversity, is through the so-called z-values. They represent the slope of the species-area relationship in the log-log representation, and thus describe the relative increase of richness with increasing grain size, but can also
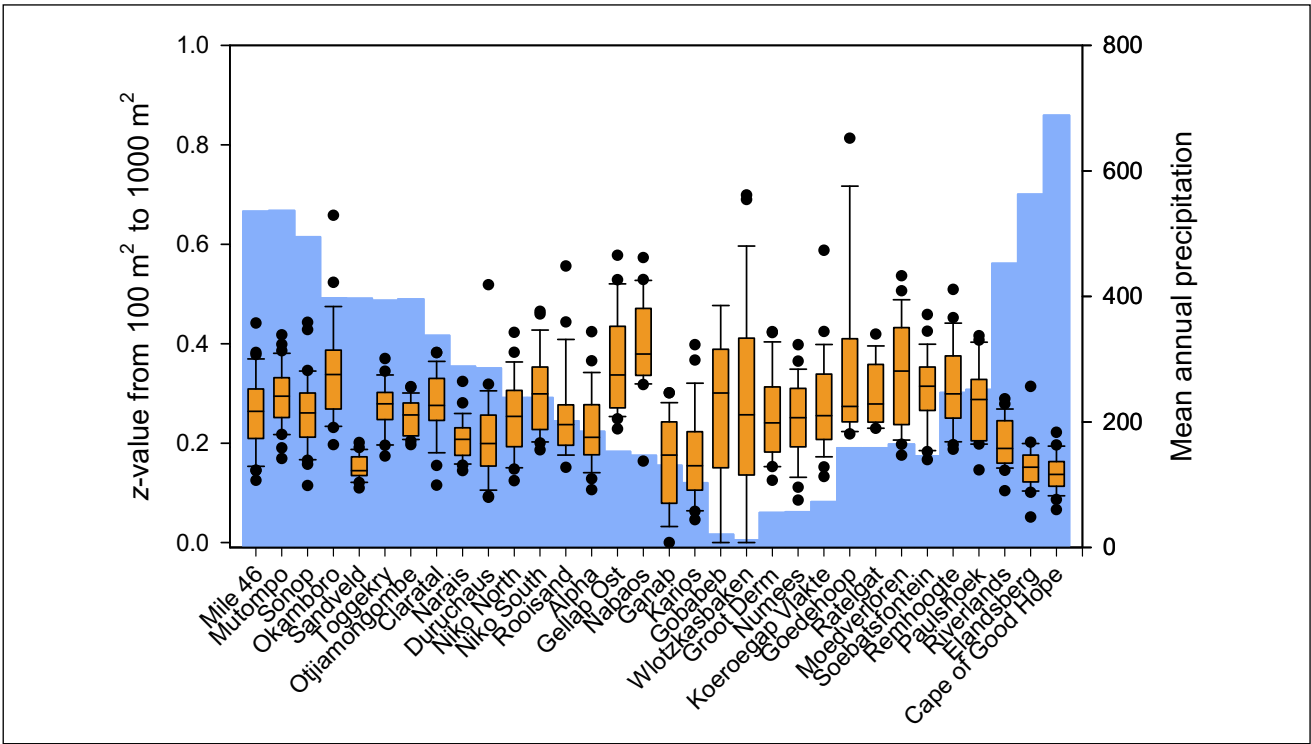
Fig. 3: Variability of the *z*-values within and between Observatories along the BIOTA transects in southern Africa. The *z*-values shown are for the transition from 100 m² to 1000 m² and based on means per hectare plot (i.e. averaged over all years). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots).

be considered as a measure of β-diversity because high *z*-values represent a high spatial turnover in species composition. Furthermore, comparison of *z*-values between spatial scales allows for the investigation of the scale-dependence itself, i.e. how the degree of scale-dependence changes with grain size.

The *z*-values varied widely within most of the Observatories, and this variability was particularly high in the driest parts of the BIOTA transects (Fig. 3). The mean *z*-value of the transition from 100 m² to 1000 m² ("mean-to-mean") for all studied Observatories was 0.2679, with a minimum of 0.1369 at Cape of Good Hope (S33) and a maximum of 0.8373 at Gobabeb (S35) (see Electronic Appendix 1). The mean *z*-value of the transition from 1000 m² to 1 km² was only slightly lower (0.2207) with a minimum of 0.1313 at Alpha (S17) and a maximum of 0.5927 at Gobabeb (S35). In contrast, the mean *z*-value at an intermediate scale (1000 m² to 1 ha) was only 0.1171 (Electronic Appendix 1), indicating that the allocated time did not allow complete censuses of the hectare plots at many Observatories. The 1-ha scale

is therefore not analysed further. The *z*-value for the transition from 1000 m² to 1 km² was higher than that for the transition from 100 m² to 1000 m² for only five out of 32 Observatories, with two out of three of these being Fynbos Observatories. The variation of the *z*-values between Observatories was much lower than the variation within Observatories (Fig. 3), with only slightly significant differences among the six biomes (Fig. 4). The lowest *z*-values at both of the two transitions studied were found in the Fynbos Biome, while above-average *z*-values occurred at the Observatories of the Suc-

Fig. 4: Variability of the mean z-values between the Observatories of the different biomes. The *z*-values are the slopes of a power-law species-area relationship in log-log representation and here based on the comparison of mean richness values for the different spatial scales within the particular square kilometre of the respective Observatory ("mean-to-mean"). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots) within the biomes. The differences between the biomes were significant in all cases (tested with ANOVAs; $p = 0.023$ for $z_{1000\,m^2 - 1\,km^2}$, $p = 0.044$ for $z_{100-1000\,m^2}$).
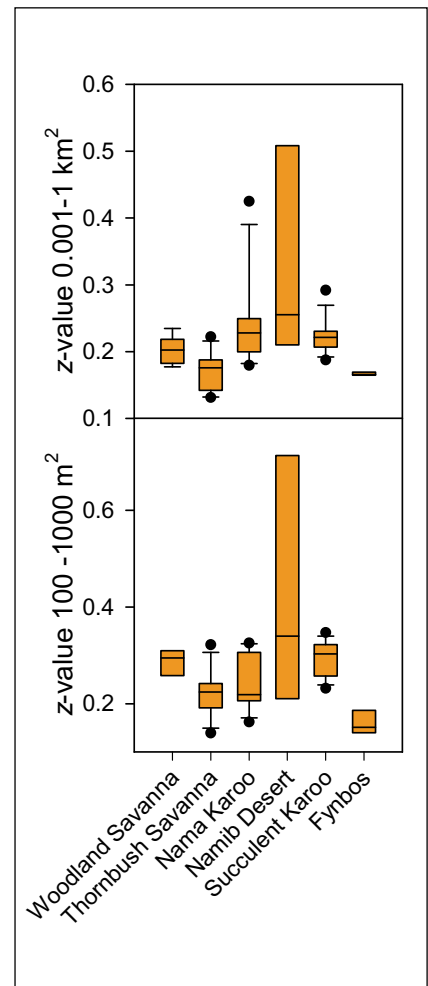
Photo 3: Vegetation at the Observatory Ogongo (S42) in the Oshana system of the Woodland Savanna. Photo: N. Classen.

Photo 4: Thornbush Savanna vegetation at the Observatory Okamboro (S06). Photo: J. Deckert.

Photo 5: Nama Karoo vegetation at the Observatory Gellap Ost (S10). Photo: A. Hoffmann.

Photos 6: *Arthraerua leubnitziae* along a dry river bed at the desert Observatory Kleinberg (S34). Photo: N. Jürgens.

Photos 7: Succulent Karoo vegetation at the Observatory Goede-hoop (S26). Photo: U. Schmiedel.

Photo 8: Fynbos vegetation at the Observatory Elandsberg (S32). Photo: G. Miehlich.
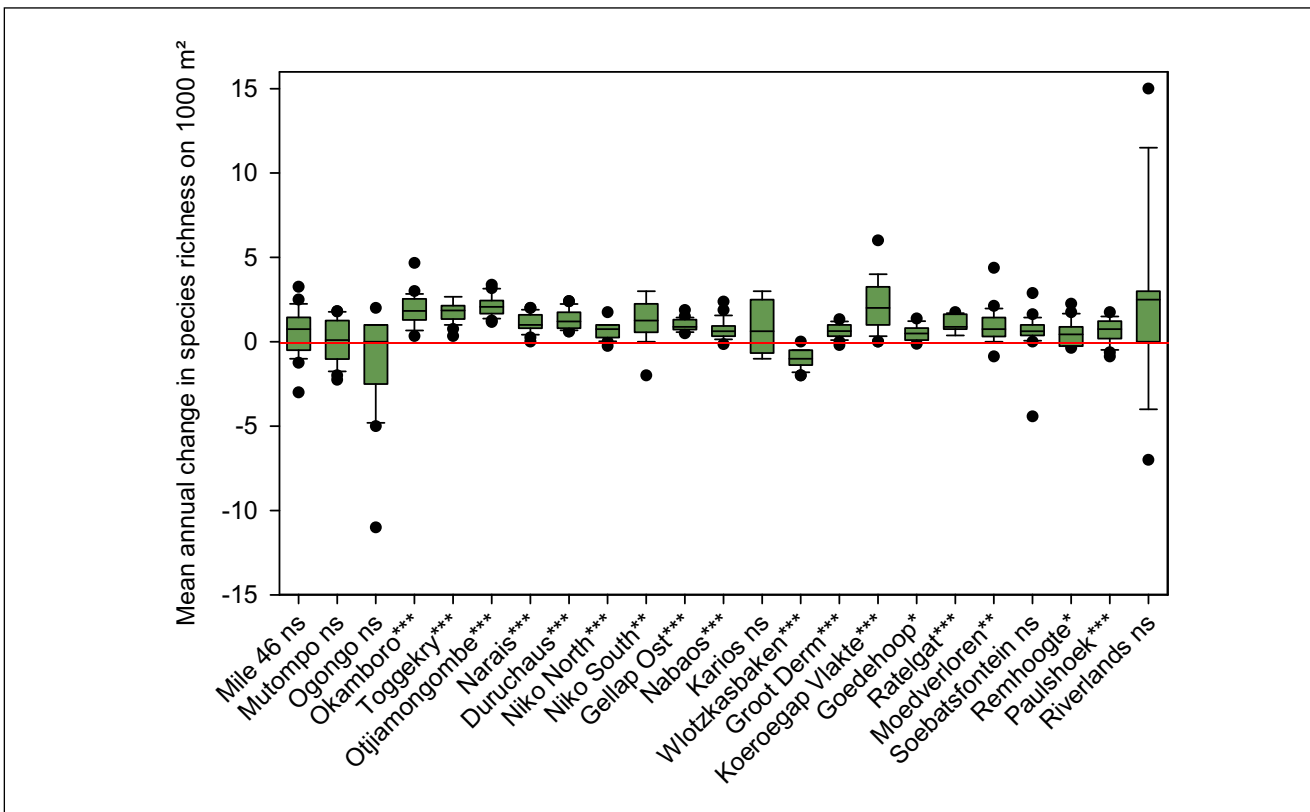
Fig. 8: Mean annual changes in species richness of the major perennial life forms phanerophytes and chamaephytes on 1000-m² plots over the observed period (2–9 years). The graphs depict medians (lines), inter-quartile ranges (boxes), inter-decile ranges (hinges), and extreme values (dots). The symbols after the Observatory names denote the significance of richness changes: ns: $p \geq 0.05$; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

culent Karoo and the Namib Desert, and also in those of the Nama Karoo at the larger scale (Fig. 4).

The z-values for the transitions 100–1000 m² and 1000 m²–1 km² (as measures of β-diversity) were related to quite different environmental variables than the α-diversity measures (see above results on biodiversity patterns along the transects). Most strikingly, the z-values at both scales showed inverse relationships to mean annual precipitation, length of dry season, and De Martonne's aridity index, i.e. they increased with increasing aridity (Electronic Appendix 4). Furthermore, the z-values at the larger scale also showed a positive relationship to soil pH (i.e. they increased with increasing pH). The z-values were positively correlated with minimum temperature and with pedodiversity measures, with significant relationships to soil reference group richness at both spatial scales and additional strong relationships to soil ecotype richness and parametric space at the larger scale.

A final aspect of scale-dependency is the question of whether the ranking of different habitats according to species richness or the relative importance of drivers varies at different spatial scales (i.e. grain sizes). While we found rather consistent patterns at all analysed spatial scales from 100 m² to 1 km² in the majority of cases (see Electronic Appendices 3 and 4), there were some striking exceptions. For example, the Fynbos Biome was by far the most species rich at the 100-m² and 1000-m² scales, but at the 1-km² scale the Succulent Karoo reached the same level of biodiversity (see Fig. 1, Table 2). For species richness, similar predictors played a role at the three spatial scales of 100 m², 1000 m², and 1 km², but their relative importance clearly changed (see Electronic Appendix 4). Soil ecotype richness was only a significant positive predictor at the 1-km² scale, and soil parametric space increased in importance with increasing grain size. The importance of pH-value, mean annual precipitation, De Martonne's aridity index, and the length of dry season for species richness decreased with increasing grain size, while

the importance of mean annual temperature, percentage winter precipitation, and inter-annual precipitation variability increased.

Change of biodiversity in time

During the nine-year study period, most Observatories showed highly consistent diversity changes, i.e. there were only minor variations among the different 1000-m² plots within individual Observatories (Fig. 8). Only the Observatories S31 (Riverlands) and S42 (Ogongo) showed higher within-Observatory variation. Of the 23 Observatories analysed, 16 showed an increase in richness, six no significant change, and only one a decrease (Fig. 8). The highest significant mean annual increases in species richness at the 1000-m² plot level occurred on the Observatories Koeroegap Vlakte S18 (+2.2 species year⁻¹), Otjiamongombe, S05 (+2.1 species year⁻¹), and Okamboro S06 (+1.9 species year⁻¹), while the only significant decrease was at the Observatory Wlotzkasbaken S16 (–1.0 species year⁻¹).

Discussion

Biodiversity patterns along the transect

The species richness at different spatial scales along the BIOTA Southern Africa transects responded positively to the mean annual precipitation, but there were some exceptions. In northern Namibia in the Woodland Savanna, species richness was not higher than for the Thornbush Savanna, regardless of the higher mean annual precipitation there. Species richness in the north-west of Namibia at the two Observatories, Ogongo (S42) and Omano go Ndjamba (S43), was even lower than that of the Thornbush Savanna and had values similar to the much more arid Nama Karoo. These two Observatories fall within the northern Namibian vegetation type Mopaneveld (dominated by mopane, *Colophospermum mopane*), which forms part of the Woodland Savanna and is characterised by dense canopy cover and comparatively sparse understorey vegetation. The Mopaneveld in the more humid northern Namibian is known to be particularly species poor compared to less humid Mopaneveld in other southern African regions (Siebert et al. 2003). Species richness of Mopaneveld has often been found to be dependent on the cover of mopane. High cover of mopane results in low species richness, whereas a higher species richness is noted in areas with low mopane cover (O'Connor 1992, cited in Siebert et al. 2003). Landuse effects on Omano go Ndjamba have an additional negative effect on species richness outside the Agricultural Research Station Ogongo (see Part II, Observatory S43). The two Observatories also represent unusual habitat conditions due to ephemeral, additional water influx from Angola (i.e. Oshana system) as well as the high accumulation of salt in the subsoil layers (compare Part II, Observatory S42 and S43).

The species richness on the Fynbos Observatories was significantly higher than on any other Observatories along the transect. The Fynbos Biome with its Mediterranean climate is renowned for its high species richness, which is described to be particularly high even in terms of global standards (Mutke & Barthlott

2005), at larger spatial scales (> 10 km²) but only moderately so on smaller spatial scales (< 0.1 ha) (Cowling et al. 1996, 1998). According to our data (low z-values), the species richness of the Fynbos Biome shows a lower relative increase with increasing plot sizes than it does in the other biomes. At our largest spatial scale of 1 km², the cumulative species richness of the Succulent Karoo and the Fynbos Biomes were comparable. Cowling et al. (1997) have shown that "local" (i.e. 1000 m² = 0.1 ha) species richness in the Fynbos Biome is similar to, or even lower than, that of the Succulent Karoo and the Savanna. The "regional" species richness (i.e. biome-scale) of the different Fynbos types, however, exceeds that of all other biomes. The differences in species richness between Fynbos and the other biomes as described in the literature (see above) may only become measurable at larger spatial scales that are not covered by the BIOTA Observatory design (i.e. > 10 km²).

The plant diversity at Elandsberg Observatory (S32) was exceptional at all spatial scales and was an outlier in all regressions of species richness with potential soil-related and climatic drivers of plant diversity. With regard to soil features (see Article III.3.3), the Elandsberg Observatory did not show any unique characteristics compared to the less diverse Observatory at Cape of Good Hope (S33), for instance. Most of the vegetation at the Elandsberg Observatory forms part of the Swartland Alluvium Fynbos, but it also borders the Swartland Shale Renosterveld (Rebelo et al. 2006, see also Part II, Observatory S32). The exceptionally high species richness on Elandsberg Observatory may also be caused by its ecotone character between the two vegetation types, Fynbos and Renosterveld. The high species richness could additionally be related to the geomorphologic situation of the Observatory at an alluvial fan, which might have caused and still cause an input of diaspores of mountainous plants into this low-lying area. The species richness of the Elandsberg area has been known to science for some time and this is the reason for its conservation (Part II, Observatory S32) and the various research activities of BIOTA at that site (Chapter III.5).

Beta-diversity within the Observatories along the transect

The very high range in species turnover (β-diversity) on the desert Observatories reflects the huge relative difference between the extremely low species richness (i.e. even completely vegetation-less plots are frequent) at the small and medium plot scale (i.e. 100 m² and 1000 m²) and reasonable totals of 28 (Wlotzkasbaken, S16) and 33 species (Gobabeb, S35) at the 1-km² scale. This high species turnover is driven by micro-topography that influences the run-on and -off of the surface water during scarce rainfall events and exposure to fog, i.e. climatic and soil-related drivers that are not reflected in the parameters included in our analyses.

The comparatively high beta-diversity values for the two Nama Karoo sites, Gellap Ost and Nabaos (S10 and S11), which exceeded that of all other Nama Karoo, Thornbush and Woodland Savanna Observatories, can also be related to small-scale differences in water supply (Petersen 2008). This author describes these differences as being related to soil physical properties such as texture and the available rooting space, i.e. content of coarse fragments and depth to bedrock.

The extraordinarily broad range of z-values at the Succulent Karoo site Goedehoop (S26) and the comparatively high mean values for the Moedverloren Observatory (S28) are to a large extent related to soil heterogeneity that is also reflected in the high diversity of soil ecotypes. These two Observatories are characterised by the dominance of a special habitat type, the quartz fields. High variance in soil chemical features like soil pH and electrical conductivity within a distance of a few meters, which is typical for the quartz fields (Schmiedel & Jürgens 1999, Schmiedel 2002, see also Chapter III.4), drives the extraordinarily high species turnover in this landscape (Schmiedel 2002). The quartz fields at the Ratelgat Observatory (S27) are less pronounced and more strongly mixed with zonal soils within the plots, thus, resulting in relatively higher species richness per 100 m² and 1000 m² plot but also in lower species turnover (lower z-values) between the different sized plots.

The low β-diversity of the Fynbos Observatories at a scale of up to 1 km² reflects the generally high species richness in this biome, which showed a comparatively low relative increase between the spatial scales covered by the Observatories (100 m² to 1 km²). However, a significant increase in species richness can be expected at larger spatial scales (> 10 km²), along topographic and soil-fertility gradients, as described by other studies (Cowling 1990, Cowling et al. 1996).

Drivers of biodiversity
Climatic drivers

Mean annual precipitation and length of dry season showed a significant relationship to species richness at the 1000 m² scale. Length of dry season was negatively correlated whereas mean annual precipitation was positively correlated with species richness. Both variables were strongly negatively correlated to each other as the length of dry season depends on the mean monthly precipitation, which is typically low in the arid regions. This correlation was not unexpected, taking into account the steep rainfall gradient along which the BIOTA Observatories had been arranged. The Fynbos Observatories with the highest species richness were associated with a short dry season, whereas the desert Observatories with the longest dry season had the lowest species richness. Mean annual precipitation was closely related to species richness for the 1000-m² plots, with the Observatories of the Namib Desert having lowest species richness. The Fynbos Observatories, which receive the highest annual precipitation along the transect, possess the highest species richness. However, we cannot exclude with our data that other factors that change collinearly with mean annual precipitation and rainfall season, also play a role in creating and maintaining the exceptional species richness in the Fynbos Biome.

The significant overall difference between species richness in the winter and the summer rainfall regions is not completely new to science. In their comparison of the two arid biomes of the Succulent Karoo and Nama Karoo, Cowling et al. (1994, 1998) identified the much higher diversity in the Succulent Karoo and related this mainly to climatic factors such as the higher predictability of winter rainfall (lower coefficient of variation) in the Succulent Karoo (see also Hoffman & Cowling 1987). In addition to this, our data show that the low winter rainfall regions are characterised by high richness in soil ecotypes (see also Article III.3.3), which has a strong positive relationship with species richness at 1 km² in the Succulent Karoo.

Soil-related drivers

Median soil pH per Observatory was negatively correlated with species richness. As soil pH is typically low in regions with high annual precipitation in the study area due to leaching of the soils, which reduces soil pH (see also Article III.3.3 and discussion on the findings in a global context), this does not necessarily mean a causal relationship, while on the other hand this collinearity does also not exclude that soil pH might affect plant diversity directly. The same negative relationship between single values of soil pH and species richness per plant life form per 100 mm² was found by Medinski et al. (2010) along the same transect. They further showed that the species richness of the five main life forms (i.e. chamaephytes, phanerophytes, hemicryptophytes, therophytes and geophytes) responded differently to the tested soil properties. They concluded that soil infiltration, clay and silt content, electrical conductivity, and soil pH are the most relevant properties to be tested in plant diversity research. However, our analyses using mean values of electrical conductivity per Observatory did not reveal any significant relationship between electrical conductivity and plant species richness. For future analyses we plan to use single values and ranges of electrical conductivity as well as other soil parameters such as clay and silt content.

In the Succulent Karoo, where the majority of the precipitation occurs as low-intensity rainfall from low pressure cells (Desmet & Cowling 1999), the leaching effect of precipitation is typically lower (Article III.3.3). This results in higher overall soil pH-values overall but also a broader range of pH-values due to small-scale patterns of surface water run-on and run-off. These differences in soil acidity drive species turnover and thus species richness at larger spatial scales (Schmiedel & Jürgens 1999).

This important influence of soil and habitat diversity on species richness in southern Africa is revealed by the highly significant regression between vascular plant species richness and soil ecotype richness at 1 km². The complex parameter "soil ecotype richness" reflects the diversity of the combinations of four plant-relevant soil properties recorded at each Observatory. These are soil pH (indicating acidity and alkalinity), electric conductivity as a measure of salt enrichment, amount of fine particles (i.e. clay and silt) as a proxy for water storage ability, and organic carbon content, which is thought to reflect nutrient supply. The spatial distribution of this complex-parameter along the transect revealed highest values for the Succulent Karoo (see Electronic Appendix 3). This high diversity in soils of the Succulent Karoo Biome has been described earlier (Francis et al. 2007, Herpel 2008, Petersen 2008, as well as Article III.3.3) and its role as general driver of the species richness in the Succulent Karoo has been illustrated by various studies (Jürgens 1986, Schmiedel & Jürgens 1999, Herpel 2008, see also Chapter III.4). However, other factors not included in the analysis, such as the predictability of winter rainfall (Hoffman & Cowling 1987), moderate temperature conditions, as well as regular occurrence of droughts, which result in high within-site species turnover (Jürgens et al. 1999) have also been described as potential drivers of the high species richness of the arid Succulent Karoo (Cowling et al. 1998).

Plant diversity in the Fynbos Biome

The Elandsberg Observatory (S32) always and the Riverlands Observatory (S31) frequently were outliers in our regression analyses, for both climatic and soil related predictors (Figs. 5–7). They even exceed the species richness of the Observatory Cape of Good Hope (S33) on the Cape Peninsula, which had been reported as one of the most species-rich phytogeographic centres of the Cape

Floristic Kingdom at larger spatial scales (Goldblatt & Manning 2002). The extraordinarily high species richness on these Observatories can only partly be explained by the analysed variables. Other biotic and abiotic drivers such as topographic diversity, nutrient-poor soils, fire, and floristic and climatic history have been identified as responsible factors driving this exceptional species richness (Cowling 1990, Goldblatt & Manning 2002). Finally, it should be highlighted that our mean species richness for 1000 m^2 on Elandsberg (123.7) already exceeds the highest single species richness count (i.e. 121 species) that has been published for Fynbos vegetation to our knowledge so far (Cowling et al. 1992), while our maximum single-count values for both Observatories Elandsberg (168) and Riverlands (143) are far above.

Landuse as a driver

The impact of landuse along the BIOTA transect, as an important driver of plant species richness at the local- to biome-scale was not the focus of this transect-wide analysis. The absence of significant effects of the simplified landuse intensity classes and species richness along the transect does not mean that landuse intensity does not have an impact on plant diversity. Various aspects of landuse impact on plant diversity are presented elsewhere in this book (e.g. Articles III.5.6, III5.5, III.5.7, and Part IV). Further analysis of landuse impact on plant diversity and species composition based on the botanical data from the BIOTA Observatories will be the focus of separate analyses at the local- to biome scale. However, some of the Observatory pairs with different landuse intensity (i.e. Ogongo – Omano go Ndjamba, Gellap Ost – Nabaos, Remhoogte – Paulshoek) seem to show a trend of lower species richness at both 100-m^2 and 1000-m^2 scales under intensive landuse. However, this trend is not consistent and the effect seems to be strong at a small scale at some sites and at larger scales at other sites. Decline in total species richness does not seem to be the main effect of landuse impact. Studies from different biomes of southern Africa rather showed that unsustainable land management may change the spe-

cies and life form composition of vascular plants (Todd & Hoffman 1999, 2009, Riginos & Hoffman 2003, Anderson & Hoffman 2007, Haarmeyer et al. 2010, Wesuls & Lang 2010, and unpublished results of D. Wesuls & J. Dengler). The main change is often described as a shift in the ratio woody to non-woody plants. In the Succulent Karoo Biome, species composition changed from vegetation dominated by palatable shrubs to sparser perennial vegetation, with mainly non-palatable shrubs (e.g. *Galenia africana*, kraalbos) and more annuals and geophytes, which cover the open patches after good seasonal rains (Todd & Hoffman 1999, 2009). Vegetation changes in the Thornbush Savanna are characterised by an increase of medium-sized *Acacia* trees (e.g. *Acacia mellifera*) that replace the palatable grass biomass (de Klerk 2004).

Change of biodiversity in time

A clear majority of the Observatories (16 of 23) showed increases in species richness over the years of the BIOTA project. This increase was fairly evenly distributed along the transect, although it was slightly less in the southern parts of the Succulent Karoo and in the Cape region. By contrast, only one Observatory experienced a significant decrease in species density.

The observed increase in species richness could partly be an artefact of improved performance of the collectors of monitoring data and the project as a whole. Particularly in the larger plots, observers would more likely find species whose occurrence they knew from the previous year(s) than detect an unexpected "new" species. In this way, the number of species recorded per plot might have increased over the years more than the actual species number did. However, a similar increase of species richness was also found for the smaller plot sizes (100 m^2, data not shown), where the chance of missing a species were much lower, suggesting that this pattern likely reflects real increase in species richness on the Observatories over the study period. Furthermore, the observation data also indicated repeated phases of species richness decrease (e.g. in drought years) and recovery (e.g. following good rains).

Furthermore, a positive trend (increase in species richness) has also been observed in many extremely meticulous local case studies such as those carried out in the Richtersveld at Numees (S20) (compare Part II, Observatory S20) and in the Knersvlakte of the Succulent Karoo. Despite an increase in inter-annual variability of precipitation and of annual maximum and mean temperatures during the last decades, populations of Knersvlakte endemic, quartz field-dwelling plants showed an increase in species richness over 13 years of monitoring (U. Schmiedel, unpublished data). Overall, we consider the measured increases in species diversity in this study during the last decade to be a robust result. However, this finding does not justify an overoptimistic projection of southern African's biodiversity into the future, as passive warming experiments have shown that projected future climate change may have a detrimental impact on just these species (Musil et al. 2009).

The findings seen in a global context

It is not an easy task to compare our richness values from southern Africa at spatial scales between 100 m^2 and 1 km^2 with data from other regions of the World, because spatially representative, high-quality biodiversity data at that grain size are globally still very scarce. At the 1-km^2 scale, to our knowledge, only the Swiss Biodiversity Monitoring (BDM) has produced similar data representative for the whole of Switzerland, which is still a small area compared to the region covered by BIOTA Southern Africa (see Table 2). As the 1-km^2 data shown in this article, also the Swiss data are not really complete censuses of the square kilometre but are based on a 2.5-km transect systematically arranged within the one square kilometre, with the species at both sides of the transect being recorded (BUFA 2009). However, the degree of completeness might be similar to our case where the 1-km^2 values are usually based on 20 hectare plots that are placed in a stratified-random manner. The values of our Fynbos and Succulent Karoo Observatories exceed the average Swiss biodiversity level,

Table 2: Vascular plant species richness values at 1 km², 1000 m² and 100 m²: reported from various studies worldwide that cover a larger region with a representative sampling

Study area	Biome	Source	Extent [km²]	N	Remarks	1 km² Median	1 km² Range	1000 m² Median	1000 m² Range	100 m² Median	100 m² Range
Southern Africa	All	This book	1,200,000	35*		138	1–385	38.4	0–169	22.6	0–128
Southern Africa	- Woodland Savanna	This book		5*		149	90–172	42.5	0–70	22.2	0–39
Southern Africa	- Thornbush Savanna	This book		7*		121	39–213	47.4	0–113	27.6	3–70
Southern Africa	- Nama Karoo	This book		7*		120	102–186	21.1	0–83	12.6	0–45
Southern Africa	- Namib Desert	This book		4*		24	1–46	3.9	0–20	1.8	0–12
Southern Africa	- Succulent Karoo	This book		9*		282	79–296	56.3	0–106	28.1	0–59
Southern Africa	- Fynbos	This book		3*		288	218–385	91.6	19–169	58.0	12–128
Tropical zones	Tropical forest	Plotkin et al. (2000)	5 plots	5	0.5 km² instead of 1 km² and only woody plants	305	68–1171	–	–	–	–
SE United States	Nemoral and laural zonobiome: mostly natural habitats	Fridley et al. (2005)	485,000	1472		–	–	55.0	6–179	30.3	5–91
United Kingdom: East Berkshire	Nemoral zonobiome: cultural habitats	Crawley & Harral (2001)	465	465 – 67 – 88		140	60–512	32.0	7–90	16.0	1–47
Switzerland	Nemoral zonobiome: natural, semi-natural, and cultural habitats	BAFU (2009)	41,000	390	line-transect of 2.5 km length within the 1 km²	239	15–400	–	–	–	–
Russia: Curonian Spit	Transition nemoral-boreal zonobiome: natural and semi-natural habitats	Dolnik (2003)	100	130	900 m² instead of 1000 m², including approx. 50% non-vascular plants	–	–	88.0	2–168	51.0	1–94

* indicates that the number of smaller-sized plots (1000 m², 100 m²) was approximately 20 times higher than the number of 1-km² plots, but the precise number varies slightly between Observatories and between years.

while the four other biomes lie below (Table 2). The reported values for a relatively small section of a cultural landscape in the United Kingdom (Crawley & Harral 2001) lie far below Switzerland and correspond well to the median value of our complete transects (Table 2). For tropical forests as the most species-rich habitat type at larger spatial scales, we are not aware of any complete censuses of all vascular plants for full square kilometres, but there are various detailed counts of woody plants (which are the absolutely dominating life form there) of 0.5-km^2 areas (Plotkin et al. 2000). While the maximum values there far exceed our data range, the median value is very similar to our two most species rich biomes (Table 2).

For the scales of 1000 m^2 and 100 m^2 slightly more data are available, mostly from the temperate zones. According to an extensive global compilation of published richness maxima at different spatial scales (J. Dengler, unpublished data), the documented maximum value for 1000 m^2 seems to be 179 vascular plant species in an open *Pistacia* shrubland in Israel (Mediterranean zonobiome; Naveh & Whittaker 1979) as well as in one plot in North Carolina, United States (laural zonobiome; vegetation type not reported; Fridley et al. 2005). On average, the values in the temperate zones are much lower and their medians are below the values of our Fynbos and Succulent Karoo Observatories, partly also below the values of the two savanna biomes (Table 2). The highest species densities at 100 m^2 are known from semi-natural dry grasslands in the temperate zone of Europe with a maximum of 133 (M. Chytrý, Brno, pers. comm.) and 127 (Dengler et al. 2009) vascular plants species in managed semi-dry grasslands of Czechia and Romania, respectively, and 140 species when including also non-vascular plants (cryptogam-rich dry grassland in Estonia; Dengler & Boch 2008). At the 100-m^2 and 1000-m^2 scales, tropical rain forests are typically less species-rich (see Williamson 2003). Thus, we can conclude our recorded maxima (169 vascular plant species on 1000 m^2 and 128 on 100 m^2, both on Observatory Elandsberg, S32) as well as our median values (see Table 2)

place the Fynbos among the biomes and habitats with the highest species density at that scale worldwide.

The z-values are a widely used and readily interpretable way to measure scale dependency and spatial turnover of biodiversity (e.g. Drakare et al. 2006, Dengler 2009). The range of values recorded in our study, with a mean of 0.268 for the transition 100–1000 m^2 and 0.221 for the transition 1000 m^2–1 km^2, is similar to values reported worldwide (Crawley & Harral 2001, Dolnik 2003, Fridley et al. 2005, Drakare et al. 2006). Given the fact that for most Observatories the richness values at the 1-km^2 scale are probably underestimations (see above), we found on average hardly any scale-dependency of z-values. This contrasts to the findings of Drakare et al. (2006) who in their meta-analysis found a systematic increase of z-values between 1 m^2 and 1 km^2 for nested sampling designs, while Crawley & Harral (2001) in their single study found an increase up to approximately 1 ha followed by a decrease thereafter. The fact that we found much more variation in z-values within rather than between Observatories is similar to the higher variation within rather than between European dry grassland vegetation types (Jeschke et al. 2007), and indicates that z-values are obviously not a property specific to vegetation types but more determined by small-scale variation patterns in abiotic conditions or disturbance. Finally, we could not confirm in our dataset the pole-ward decrease of z-values found by Drakare et al. (2006) in their meta-analysis.

Regarding the drivers of biodiversity patterns, a recent comprehensive meta-analysis by Field et al. (2009) compared six non-exclusive types of hypotheses: (i) climate/productivity; (ii) environmental heterogeneity; (iii) edaphics/nutrients; (iv) area; (v) biotic interactions; and (vi) dispersal/history. They found that, for plants, generally climate/productivity and edaphics/nutrients are the most important diversity drivers and that edaphics/nutrients are particularly important at scales below 1 km^2, while measures of environmental heterogeneity (such as our pedodiversity parameters) do not play a particularly important role. Our results

are in line with these general findings as we found the strongest relationship of species richness at 100 m^2–1 km^2 with factors related to climate-driven water availability, and the second strongest to soil chemical parameters, while soil heterogeneity only played a role at the 1-km^2 scale.

However, when considering the individual parameters, our findings show clear deviations from patterns found elsewhere or at a global scale. Generally, a positive relationship between energy, measured for example as mean annual temperature or potential evapotranspiration (PET), is assumed (Gaston & Spicer 2004), and has been proven at a global scale for many taxa, including vascular plants (Mutke & Barthlott 2005, Kreft & Jetz 2007). We found no effect of PET and even a negative correlation of species richness with mean annual temperature, which deviates from these widely accepted macroecological patterns. This variation could be attributed to peculiarities of our study region, e.g. the widely acknowledged, yet not fully understood unique position of the Cape Floristic Kingdom among the Floristic Kingdoms of the world (Kreft & Jetz 2007). However, we also assume that the very different grain sizes analysed contribute to the differences in the results from those global-scale studies. Mutke & Barthlott (2005) and Kreft & Jetz (2007) based their analyses on species richness counts standardised to 10,000 km^2, while we analysed grain sizes of 0.0001–1 km^2. It is generally accepted though rarely tested directly that different processes shape diversity patterns at different spatial scales (e.g. Willis & Whittaker 2002, Field et al. 2009).

While decreasing species richness with altitude or a mid-altitudinal peak in species richness are among the most frequently reported macroecological patterns for many taxa at practically any grain size (e.g. Gaston & Spicer 2004, Wohlgemuth et al. 2008), we did not find such a pattern in our data. One explanation could be that collinearity of altitude with other, stronger predictors masked the altitudinal pattern. For example, our summer-rainfall Observatories were located at a mean altitude of 1124 m a.s.l.,

while the mean altitude of the winter-rainfall Observatories was only 383 m a.s.l. (see Electronic Appendix 1) which together with the strong positive effects of winter rainfall (see Results) could explain our failure to detect an altitudinal pattern.

Soil reaction (pH or calcium content) is typically highly important for plant species richness at the plot scale (e.g. Schuster & Diekmann 2003, Pärtel 2002, Chytrý et al. 2007) but also at the 1-km^2 scale (e.g. Wohlgemuth et al. 2008). In temperate and boreal regions, usually positive or unimodal relationships are found, whereas in most tropical or subtropical regions the relationship is negative, which is explained historically by the predominating soil pH in the evolutionary centres of the floras (Pärtel 2002, Ewald 2003, but see Medinski et al. 2010 for a unimodal relationship for individual 100 m^2-plots along BIOTA transect). According to the global meta-analysis of Pärtel (2002), the correlation coefficient between richness and soil pH shows a strong latitudinal pattern, with the mean r-value ranging from –0.5 at the equator to approx. +0.8 in the boreal zone. The expected value for our study region should thus range from –0.20 in northern Namibia to +0.05 at the Cape, while our observed correlation values for the whole transects were between –0.15 (1 km^2) and –0.51 (100 m^2), depending on the spatial scale analysed. However, in the study region as in all arid regions, soil pH is strongly negatively correlated with mean annual precipitation (e.g. Chytrý et al. 2007 and discussion above) and due to this collinearity it is not possible to disentangle the effects of both environmental variables on species richness. Still it is remarkable that we found the very opposite pattern to what Chytrý et al. (2007) found in the forest-steppe transition zone of southern Siberia, despite both regions being considered to have evolutionary centres with high soil-pH values (Pärtel 2002).

Finally, it is worth comparing the bio-diversity patterns we found at small grain sizes with those shown in coarse-grain maps of vascular plant diversity (Kier et al. 2005, Mutke & Barthlott 2005). The diversity gradients depicted in the map of Mutke & Barthlott (2005), with a grain size of 10,000 km^2, are very similar to our findings, with the Fynbos Biome being rated in density zone 9 (4,000–5,000 species per 10,000 km^2) and the Succulent Karoo in density zone 8 (3,000–4,000 species per 10,000 km^2). Such a coincidence of diversity patterns across such widely differing spatial scales is not a general finding (see Dengler 2009). Only the very species-poor Namib Desert is not depicted as such in the map of Mutke & Barthlott (2005), but this is likely a modelling artefact rather than a real pattern. Our finding that small-scale species densities in the Fynbos Biome are amongst the highest values worldwide correspond well with the strong positive deviation of the Cape Floristic Kingdom from the global vascular plant diversity model at the 10,000-km^2 scale with contemporary environmental variables as predictors (Kreft & Jetz 2007). However, our results contradict the literature on the diversity of the Fynbos (e.g. Cowling et al. 1996, Goldblatt 1997, Goldblatt & Manning 2002), according to which this biome is not unusually rich at small grain sizes (1000 m^2) but becomes exceptional on a global standard only at larger grain size (> 10 km^2).

Conclusions

The observed plant diversity measures show great variability within the geographical areas studied. Many parameters change gradually along the transects. Our analysis showed that there is not a single predictor for plant species richness along the transect. Mean annual precipitation was among the most important drivers for species richness at small grain sizes, however, other parameters which are strongly correlated with mean annual precipitation (aridity index, length of dry season, median soil pH) were also important. The importance of soil diversity (e.g. richness in soil ecotypes per Observatory) increased with increasing grain size. Future analyses of the same datasets will further reveal the relationships between plant species and life-form diversity in southern Africa and soil and climatic parameters at different spatial scales.

The discussion of the data in the global context revealed that the botanical diversity data along the major climatic gradient and across six biomes in southern Africa is unique not only in terms of regional but also global standards. Comparable data assessed at different spatial scales and with a standardised approach are scarce. Our data thus support, amend, and refine existing comparative analyses on the diversity patterns of biomes in southern Africa. They also provide the basis for further analyses of local to regional plant diversity patterns and their abiotic and biotic drivers. Particularly unique in our study is the combination of large spatial extent with small to medium spatial grain, as most ecological studies are either "small extent/small grain" or "large extent/large grain". The study of small-scale phenomena over huge spatial extents likely will bring us closer to a real understanding of the processes that shape biodiversity patterns on Earth.

During the decade of monitored for the BIOTA project, no major declines of botanical diversity were observed except for a slight increase in perennial species (dwarf shrub, shrubs and trees). These data provides critical benchmark information on the current state of diversity of vascular plants along the transect. The annual monitoring of plant diversity on these plots have the potential to provide evidence for changes that may occur due to climate change and human landuse.

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