1 **Tree phylogenetic diversity supports nature’s contributions to people,** 2 **but is at risk from human population growth**

3 T. Jonathan Davies^{a,b,1}, Olivier Maurin^c, Kowiyou Yessoufou^d, Barnabas H. Daru^e,
4 Bezeng S. Bezeng^d, Hanno Schaefer^f, Wilfried Thuiller^g & Michelle van der Bank^b

5

6 ^aBiodiversity Research Centre, University of British Columbia, 2212 Main Mall,
7 Vancouver, BC, CANADA V6T 1Z4; ^bAfrican Centre for DNA Barcoding, Department
8 of Botany & Plant Biotechnology, University of Johannesburg, PO Box 524, APK
9 Campus, 2006, Johannesburg, South Africa; ^cHerbarium, Royal Botanic Gardens KEW,
10 Richmond, TW93AE, United Kingdom; ^dDepartment of Geography, Environmental
11 Management and Energy Studies, University of Johannesburg, POBox 524, APK
12 Campus, 2006, Johannesburg, South Africa; ^eDepartment of Life Sciences, Texas A&M
13 University, Corpus Christi, United States of America; ^fTechnische Universitaet
14 Muenchen, Plant Biodiversity Research, Emil-Ramann Str. 2, 85354 Freising, Germany;
15 ^gUniversité Grenoble Alpes, Université Savoie Mont Blanc, CNRS, LECA, Laboratoire
16 d’Écologie Alpine, F-38000 Grenoble, France

17

18 ¹To whom correspondence should be addressed. E-mail: j.davies@ubc.ca

19

20 **Keywords:** Africa, ecosystem services, phylogenetic diversity, species richness, human
21 population

ABSTRACT

There is growing evidence for a link between biodiversity and ecosystem function, and for a correlation between human population and the species diversity of plants and animals in a region. Here, we suggest these relationships might not be independent. Using a comprehensive phylogeny of southern African trees and structural equation modelling, we show that human population density correlates with tree phylogenetic diversity and show that this relationship is stronger than the correlation with species richness alone. Further, we demonstrate that areas high in phylogenetic diversity support a greater diversity of ecosystem goods and services, indicating that the evolutionary processes responsible for generating variation among living organisms are also key to the provisioning of nature's contributions to people. Our results raise the intriguing possibility that the history of human settlement in southern Africa may have been shaped, in part, by the evolutionary history of its tree flora. However, the correlation between human population and tree diversity generates a conflict between people and nature. Our study suggests that future human population growth may threaten the contributions to people provided by intact and phylogenetically diverse ecosystems.

Human population has increased dramatically over the last 200 years, and is predicted to approach 9 billion by 2050 (United Nations 2004). The distribution of people, however, is highly uneven. In 2008, the urban population outnumbered the rural population for the first time (United Nations 2011), and in much of the developed world the human population is stable or decreasing (Murray *et al.* 2018). In contrast, although urbanizing rapidly, the human population in sub-Saharan Africa is still increasing (Murray *et al.* 2018), and remains predominantly rural (UNICEF 2012), reflecting a closer relationship between the natural environment and people. Much of the human population in sub-Saharan Africa depends directly or indirectly on the goods and services provided by biodiversity (Shackleton *et al.* 2008; Egoh *et al.* 2012), including clean water, soil productivity, firewood/charcoal, game animals, and medicinal plants (Daily & others 1997; Postel *et al.* 2012) – nature’s contributions to people (Díaz *et al.* 2018; Brondizio *et al.* 2019). However, many of these services are being degraded through habitat loss and transformation, exacerbated by rapid urbanization, agricultural expansion, ‘land grabbing’ by foreign nations for food and biofuel production, and climate change (Egoh *et al.* 2012; Malherbe *et al.* 2019). The poor, and rural communities, tend to be most impacted by losses of ecosystem services as they frequently lack alternatives (Hope Sr 2007; United Nation Economic Commission for Africa 2010; Egoh *et al.* 2012; Kumar & Yashiro 2014), while poverty is a major underlying contributor to environmental degradation (World Commission on Environment and Development 1987; Olanipekun *et al.* 2019), although the relationship is complex (Barbier & Hochard 2018).

Quantifying the value of ecosystem services is challenging because many such services are difficult to measure and different value systems do not necessarily align

closely (Costanza *et al.* 2017; Díaz *et al.* 2018; Brondizio *et al.* 2019), although estimates suggest their crude economic worth might be large (Costanza *et al.* 1998). Species richness provides one surrogate measure of ecosystem services that is easily quantifiable. The link between species richness and ecosystem function has been the focus of much attention (Hooper *et al.* 2005; Cardinale *et al.* 2012; Hooper *et al.* 2012), and experimental manipulations suggest that, in some systems, high species richness might confer both greater ecosystem productivity and stability (Tilman *et al.* 2012; Isbell *et al.* 2015), and also support a greater diversity of services (Hector & Bagchi 2007, see also Gamfeldt *et al.*, 2013, for an ecosystem example). However, the correlation between ecosystem services and species richness at the landscape scale is often mixed (Egoh *et al.* 2009; O’Farrell *et al.* 2010; Manhães *et al.* 2016, see also Anderson *et al.* 2009). This discrepancy may be explained by the mechanisms underlying biodiversity-ecosystem function relationships. Species richness is thought to enhance ecosystem function and stability, at least in part, via species complementarity (Loreau & Hector 2001), which assumes that different species fulfil different functions and occupy separate ecological niches. However, simple measures of species richness may not accurately capture the ecological variation among species.

Phylogenetic diversity – the summed branch lengths that connect species on a phylogenetic tree – provides a more inclusive metric for quantifying species differences (Faith 1992). Because we expect species to diverge over time in their ecological and physiological traits, the set of species with higher phylogenetic diversity is predicted to capture greater feature diversity (Faith 1992, but see Tucker *et al.* 2018; Mazel *et al.* 2018). Experimental data have demonstrated a link between phylogenetic diversity and

ecosystem properties (e.g. productivity and stability), which can be stronger than observed for species richness alone (Cadotte *et al.* 2008, but see Venail *et al.* 2015). There is also evidence that phylogenetic diversity contributes to forest productivity (Hao *et al.* 2018, see also Paquette & Messier 2011). Forest *et al.* (2007) additionally demonstrated that a greater phylogenetic diversity might translates into a greater diversity of ecosystem services, using data on medicinal plants within the Cape of South Africa biodiversity hotspot.

Here, we evaluate the relationship between tree phylogenetic diversity, provisioning of ecosystem services – nature’s contributions to people – and human population density in southern Africa. In Africa and globally, trees have supported and sustained human life through provisioning of various regulating (e.g. carbon sequestration, soil preservation and clean air), provisioning (e.g. food, firewood and charcoal and medicine) and cultural services (Daily & others 1997; Millennium Ecosystem Assessment 2005), worth many millions of dollars (see Commonwealth Science Council and Food and Agriculture Organization 1993). Some of these services provide global benefits (e.g. many regulating services), but others have more local benefits (especially provisioning and cultural services). If such services are linked to species functional traits (Cadotte *et al.* 2011; Huang *et al.* 2019), we would predict that the diversity of ecosystem services within a region would be a product of not only species number, but also of how different species are from one another – i.e. their phylogenetic diversity (Forest *et al.* 2007; Faith *et al.* 2010). We explore this hypothesis here, using a comprehensive phylogeny for the trees of southern Africa (Fig. 1) – a regional flora well known for its incredible plant diversity.

108

109 **RESULTS AND DISCUSSION**

110 We first evaluated the statistical linkages between human population density and the
 111 natural distribution of native woody plant (tree) richness and phylogenetic diversity
 112 across southern Africa. We used a phylogenetic tree encompassing 2,486 tree species in
 113 the region, spanning 115 families and 541 genera, and reconstructed using DNA barcode
 114 sequences for the core plant barcodes (*rbcLa* and *matK*) (CBOL Plant Working Group
 115 2009) generated by the authors as part of a six year-long data collection effort (for
 116 additional details see Maurin *et al.* 2014 and Charles-Dominique *et al.* 2016). Hotspots of
 117 tree species diversity are distributed along the coastal regions of eastern South Africa
 118 through to south Mozambique and Zimbabwe (Fig. 2A, B), and differ notably from
 119 richness maps of total plant diversity for the region (> 20,000 species), which emphasize
 120 the high species richness of the Cape Floristic Kingdom (Cowling & Hilton-Taylor 1994)
 121 with its extraordinary radiations in a few (non-tree) clades (e.g. *Erica*, Restionaceae and
 122 Iridaceae).

123 **A covariation between people and tree phylogenetic diversity**

124 We reveal a significant and strong positive correlation between human population density
 125 and tree phylogenetic diversity (Pearson's $r = 0.76$, $p < 0.01$ on 7.73 adjusted degrees of
 126 freedom to correct for spatial non-independence, Dutilleul *et al.* 1993; Figs. 2A - D), and
 127 show that this relationship is stronger than the correlation with species richness alone ($r =$
 128 0.62 and $p < 0.01$ on 16.74 adjusted degrees of freedom). A positive covariation between
 129 wildlife species richness and human population has been noted previously (Balmford *et*
 130 *al.* 2001; Chown *et al.* 2003; Evans *et al.* 2006; Luck 2007) but, to the best of our

knowledge, we are the first to show that the correlation with phylogenetic diversity is stronger. Our results thus indicate that human population density co-varies not only with the number of tree species but also with how different they are from each other, as reflected in their evolutionary history.

One explanation for the association between human population density and the phylogenetic diversity of trees is that both covary with correlated environmental variables (Chown *et al.* 2003; Evans *et al.* 2006; Luck 2007). For example, tree diversity might correlate with environmental productivity and regions suitable for agriculture and subsistence. We therefore used Structural Equation Models (SEMs) to describe the direct and indirect effect of environmental energy (here, modeled as actual evapotranspiration, AET), topographic heterogeneity (indexed by elevation), and tree species diversity (i.e. richness and phylogenetic diversity) on human population density. While topographic heterogeneity was not a significant predictor in our models, environmental energy had a direct effect on both human population density and PD. However, the effect of AET on human population density was mediated by an indirect effect via phylogenetic diversity, and the direct effect of tree phylogenetic diversity on human density ($\beta=0.43$) was greater than the direct effect of AET ($\beta=0.34$) (Fig. 3A).

To separate out the importance of number of species versus species evolutionary disparity, we calculated a measure of evolutionary dispersion independent of richness, PSV, and a separate measure of richness discounted for species phylogenetic relatedness, PSR (see Helmus *et al.* 2007). The direct effect of PSR (the richness component) on human density was weaker than observed for total phylogenetic diversity, with the missing variation explained by PSV (the phylogenetic component) (Fig. 3B). However,

we note that the SEM including phylogenetic diversity is favored overall (BIC = 1129.78 and 1275.75 for the SEMs with phylogenetic diversity and PSR plus PSV, respectively), as it captures both richness and evolutionary disparity in a single unifying metric. The independent contribution of phylogenetic diversity is further demonstrated when we include in our SEM both species richness and the residual variation in phylogenetic diversity from the regression of phylogenetic diversity against richness (Fig. S1).

There are, of course, many additional predictor variables that we did not explore in our models. For example, in southern Africa, edaphic factors might be particularly important for plant diversity (Goldblatt 1997; Goldblatt & Manning 2002). However, high regional plant species diversity is often associated with nutrient poor soils, such as in the fynbos biome (Cowling *et al.* 1996), presumably poor for agriculture, and which may have limited early human settlement of the Cape peninsular (Cowling *et al.* 1996). In addition, it is not obvious how environmental or climatic factors could drive the correlation between human population and tree phylogenetic diversity independent of tree species richness.

Tree phylogenetic diversity supports nature's contributions to people

We evaluated the relationship between tree phylogenetic diversity and the provisioning of ecosystem goods and services – nature's contributions to people. We examined the diversity of ecosystem services using data on 11 classes of recorded uses, including cultural, medicinal, forage, and food. Because limited availability of data on species' uses precluded the use of traditional metrics for capturing functional diversity (e.g. Petchey & Gaston 2002 and Laliberté & Legendre 2010), we used a simulation approach. Our method quantified the median number of species required to represent at least once each

of the different uses identified for the species within a given 0.5° grid cell when drawing species at random from the species set. Overall, more species had to be sampled to represent the same number of uses in more species-rich cells, suggesting functional redundancy across species; however, after correcting for variation in species richness, new uses were encountered at an increased rate in more phylogenetically dispersed communities (Table 1). More phylogenetically diverse tree communities therefore tend to represent a greater number of ecosystem services than tree communities of equal richness but lower phylogenetic diversity.

It is tempting to speculate on the causal linkages between the provisioning of nature's contributions to people, tree phylogenetic diversity and human population. For example, it is possible that the correlations we reveal reflect in some part the settlement of people in Africa historically, which may have been influenced by the ecosystem services that more phylogenetically diverse tree communities provided, perhaps as part of a shift toward more settled agriculture. However, it is also likely that over the history of human settlement in Africa, humans have shaped the local environment to their needs, including the planting of some species outside their natural range. Our range maps were for native distributions, and at the regional scale of our analysis it thus seems improbable that humans have shaped floristic biodiversity gradients across sub-Saharan Africa. Nonetheless, we cannot exclude this possibility, and the SEM for either direction of causality is equally as well-supported (BIC = 1129.78 for both modeled pathways).

A conflict between trees and people

Irrespective of the underlying drivers, the correlation between human population density and tree diversity presents a potential conflict between people and nature (Balmford *et al.*

2001), especially, as demand for energy and land for agriculture intensifies. Using information on the extinction risk status from the Red List for South African plants (<http://redlist.sanbi.org/>), we show that not only does the total number of tree species correlate positively with human population, but so too does the number of threatened species ($r = 0.54$, $p < 0.001$). It is likely that as human population in Africa becomes more urbanized, and as species diversity decreases through local and global extinctions, the relationship between human population density and species diversity will be eroded (Fjelds & Burgess 2008).

There has been increasing emphasis on the preservation of phylogenetic diversity in the conservation literature (Purvis *et al.* 2005; Forest *et al.* 2007; Pollock *et al.* 2017; Davis *et al.* 2018). Our study suggests how the failure to protect phylogenetic diversity might reduce the provisioning of natural goods and services, likely with disproportion impact on the rural poor – those least able to afford alternatives.

METHODS

Over a six year-long data collection effort, we sampled 1,306 tree species (defined as woody plants with stems or pseudostems > 0.5 m in height) representing 115 families and 541 genera, across southern Africa (Appendix S1). This region encompasses an area of over 4 million km² located between 15°38' S and 34°50' S, and 11°45' E and 36°29' E, and includes Botswana, Lesotho, Mozambique (south of the Zambezi river), Namibia, South Africa, Swaziland, and Zimbabwe. We sequenced the core plant barcodes (*rbcLa* and *matK*) (CBOL Plant Working Group 2009) from sampled material, and merged these data with matching barcode sequence data in GenBank from tree species native to the

region. Voucher specimen information and GenBank accession numbers are listed in Appendix S2 and on the BOLD DataSystem (www.boldsystems.org).

Phylogenetic reconstruction followed the protocol detailed in Maurin *et al.* (2014). Branch lengths were calibrated in millions of years using Bayesian MCMC implemented in BEAST v.1.4.8 (Drummond & Rambaut 2007) and 28 fossil calibrations from Bell *et al.* (2010) (Table S1) as minimum age constraints, except for the root of the Eudicots, which was set at 124 myr.

Species distribution data were extracted from Coates Palgrave *et al.* (2002) and Van Wyk *et al.* (2011), and overlaid on a $0.5^\circ \times 0.5^\circ$ grid (approximately 50 km $\times$ 50 km). For each species, we then collated data on 11 separate uses: firewood and charcoal, carving, building and structural, spiritual, cultural, food, ornamental, forage and fodder, shade, chemical compounds, and medicinal, plus threat category from the IUCN Red Data List of Threatened Species (<http://redlist.sanbi.org/>). All data and source references are listed in Appendix S3. Geographical information system (GIS) data were obtained for actual evapotranspiration, AET (dataset GNV183; <http://www.grid.unep.ch/data/>), as a proxy for productivity, elevation (dataset GTOPO30; <http://www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html>), and human population density (dataset GPWv3 <http://sedac.ciesin.columbia.edu/data/collection/gpw-v3>). Data processing was performed in ArcMap v.10.0 and R (v. 3.5.0) using the libraries *ape*, *picante*, *sf*, *raster*, *rgdal*, *maptools*, *maps*, *sp*, and *ggplot2*. Because human population density can be dramatically elevated in urban centres, we excluded outliers, classified as cells with z-scores >3 , prior to estimating average population densities. Our population outliers identified cells with human population density >489 people/km²,

matching closely accepted criteria for urban areas in South Africa (≥ 500 people/km²) (Statistics South Africa 2001).

To evaluate the relationships between human population and tree diversity, we first correlated tree species richness and phylogenetic diversity (PD – sum of the phylogenetic branch lengths excluding the root branch; Faith 1992) against human population density, adjusting degrees of freedom to correct for spatial non-independence (Dutilleul *et al.* 1993). We report results using half-degree cells because this represents the native coordinate system of the climate and human population density layers; however, correlations using equal-area grid cells were highly similar (slope = 0.39 ± 0.01 and 0.36 ± 0.01 , $t = 42.75$ and 45.22 for the regression of log tree species richness against human population density across $0.5^\circ \times 0.5^\circ$ grid cells and on an equal area $50 \text{ km} \times 50 \text{ km}$ grid, respectively).

We excluded urban areas with high human population density from our analysis (see above) because other factors, such as economic development, industrialisation and global trade have likely influenced the geography of urban population densities. However, we note that cities in Africa predate European colonialization (Mboup 2019), and the correlations with phylogenetic diversity are largely unchanged when centres of high population density were included; Fig. S2).

We used structural equation modelling (SEM) to describe the direct and indirect effects of environment and tree diversity on human population. Before model fitting, we first quantified the pairwise correlations strengths between human population density, AET, tree species richness and PD, variance in elevation, latitude and longitude, respectively (Fig. S3). We then used the *sem* r-library (Fox 2006) to model structural

relationships, including only pathways with pairwise correlation strengths >0.5 to avoid issues of colinearity. To account for spatial structure in the model, we additionally considered the direct effects of longitude and latitude. All variables except latitude and longitude were log-transformed prior to analysis. The inclusion of additional pathways, such as the direct and indirect effects of elevation and latitude (Fig. S4), were not supported by model comparison statistics ($BIC = 1411.17$ versus 1129.78 for the more complex model and the reduced model described above). To separate out the importance of number of species versus species evolutionary disparity, we additionally jointly modelled a richness independent component of evolutionary disparity, PSV, equivalent to the mean pairwise distance between taxa in the assemblage, and a separate measure of richness discounted for species relatedness, PSR. Last, to evaluate model sensitivity, we constructed matching SEMs but included species richness and the residual variation in PD from the regression of PD against richness in place of PSR and PSV, respectively.

We used a simulation approach to test whether more phylogenetically diverse sets of species tended to capture a greater diversity of uses (ecosystem services/nature's contributions to people). Because we had comprehensive data on only a limited number of uses (Appendix S3), it was not possible to simply correlate diversity of services against diversity of species (all uses were represented by at least one tree in the majority of cells). Therefore, for each cell, we randomly re-sampled species without replacement, and recorded the median number of species required to represent at least once all uses listed for the entire species set in the cell (1000 randomizations). We then regressed the median richness required for capturing diversity of recorded uses against per-cell PSV plus PSR, and in a second model per-cell species richness plus residual PD.

292

293 **Acknowledgements** We thank the Government of Canada through Genome Canada and
 294 the Ontario Genomics Institute (2008-OGI-ICI-03), the University of Johannesburg, the
 295 South African National Research Foundation, the Royal Society (U.K.), Toyota South
 296 Africa through the Toyota Enviro Outreach Programme for financial support and various
 297 local and international authorities granting us plant collections permits. KY is supported
 298 by NRF grant #112113.

299

300 **Author Contributions** M.vd.B., O.M. and T.J.D. conceived and designed the
 301 experiments. O.M., B.H.D., B.S.B. and M.vd.B. performed the experiments. T.J.D., O.M.
 302 and H.S. analyzed the data. M.vd.B., H.S. and W.T. contributed
 303 reagents/materials/analysis tools. T.J.D., K.Y., B.H.D., W.T., O.M. and M.vd.B. wrote
 304 the paper.

305

306 **Conflict of interest statement:** The authors declare no competing financial interest.

307

REFERENCES

- Anderson, B.J., Armsworth, P.R., Eigenbrod, F., Thomas, C.D., Gillings, S., Heinemeyer, A., *et al.* (2009). Spatial covariance between biodiversity and other ecosystem service priorities. *J. Appl. Ecol.*, 46, 888–896.
- Balmford, A., Moore, J.L., Brooks, T., Burgess, N., Hansen, L.A., Williams, P., *et al.* (2001). Conservation conflicts across Africa. *Science*, 291, 2616–2619.
- Barbier, E.B. & Hochard, J.P. (2018). Land degradation and poverty. *Nat. Sustain.*, 1, 623–631.
- Bell, C.D., Soltis, D.E. & Soltis, P.S. (2010). The age and diversification of the angiosperms re-revisited. *Am. J. Bot.*, 97, 1296–1303.
- Brondizio, E.S., Settele, J., Díaz, S. & Ngo, H.T. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *IPBES Secr. Bonn, Ger.*
- Cadotte, M.W., Cardinale, B.J. & Oakley, T.H. (2008). Evolutionary history and the effect of biodiversity on plant productivity. *Proc. Natl. Acad. Sci.*, 105, 17012–17017.
- Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011). Beyond species: functional diversity and the maintenance of ecological processes and services. *J. Appl. Ecol.*, 48, 1079–1087.
- Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., *et al.* (2012). Biodiversity loss and its impact on humanity. *Nature*, 486, 59–67.
- CBOL Plant Working Group. (2009). A DNA barcode for land plants. *Proc. Natl. Acad.*

331 *Sci. USA*, 106, 12794–12797.

332 Charles-Dominique, T., Davies, T.J., Hempson, G.P., Bezeng, B.S., Daru, B.H.,

333 Kabongo, R.M., *et al.* (2016). Spiny plants, mammal browsers, and the origin of

334 African savannas. *Proc. Natl. Acad. Sci.*, 113, E5572–E5579.

335 Chown, S.L., Van Rensburg, B.J., Gaston, K.J., Rodrigues, A.S.L. & Van Jaarsveld, A.S.

336 (2003). Energy, species richness, and human population size: conservation

337 implications at a national scale. *Ecol. Appl.*, 13, 1233–1241.

338 Coates Palgrave, K., Drummond, R.B., Moll, E.J. & Palgrave, M.C. (2002). Trees of

339 southern Africa. Cape Town.

340 Commonwealth Science Council and Food and Agriculture Organization. (1993). *Non-*

341 *wood forest products - A regional expert consultation for English-speaking African*

342 *countries.*

343 Costanza, R., d’Arge, R., De Groot, R., Farber, S., Grasso, M., Hannon, B., *et al.* (1998).

344 The value of the world’s ecosystem services and natural capital. *Ecol. Econ.*, 25, 3–

345 15.

346 Costanza, R., De Groot, R., Braat, L., Kubiszewski, I., Fioramonti, L., Sutton, P., *et al.*

347 (2017). Twenty years of ecosystem services: how far have we come and how far do

348 we still need to go? *Ecosyst. Serv.*, 28, 1–16.

349 Cowling, R.M. & Hilton-Taylor, C. (1994). Patterns of plant diversity and endemism in

350 southern Africa: an overview. *Strelitzia*, 1, 31–52.

351 Cowling, R.M., MacDonald, I.A.W. & Simmons, M.T. (1996). The Cape Peninsula,

352 South Africa: physiographical, biological and historical background to an

353 extraordinary hot-spot of biodiversity. *Biodivers. Conserv.*, 5, 527–550.

354 Daily, G.C. & others. (1997). *Nature's services*. Island Press, Washington, DC.

355 Davis, M., Faurby, S. & Svenning, J.-C. (2018). Mammal diversity will take millions of
356 years to recover from the current biodiversity crisis. *Proc. Natl. Acad. Sci.*, 115,
357 11262–11267.

358 Díaz, S., Pascual, U., Stenseke, M., Martín-López, B., Watson, R.T., Molnár, Z., *et al.*
359 (2018). Assessing nature's contributions to people. *Science*, 359, 270–272.

360 Drummond, A.J. & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by
361 sampling trees. *BMC Evol. Biol.*, 7, 1–8.

362 Dutilleul, P., Clifford, P., Richardson, S. & Hemon, D. (1993). Modifying the t test for
363 assessing the correlation between two spatial processes. *Biometrics*, 305–314.

364 Egoh, B., Reyers, B., Rouget, M., Bode, M. & Richardson, D.M. (2009). Spatial
365 congruence between biodiversity and ecosystem services in South Africa. *Biol.*
366 *Conserv.*, 142, 553–562.

367 Egoh, B.N., O'Farrell, P.J., Charef, A., Gurney, L.J., Koellner, T., Abi, H.N., *et al.*
368 (2012). An African account of ecosystem service provision: use, threats and policy
369 options for sustainable livelihoods. *Ecosyst. Serv.*, 2, 71–81.

370 Evans, K.L., Van Rensburg, B.J., Gaston, K.J. & Chown, S.L. (2006). People, species
371 richness and human population growth. *Glob. Ecol. Biogeogr.*, 15, 625–636.

372 Faith, D.P. (1992). Conservation evaluation and phylogenetic diversity. *Biol. Conserv.*,
373 61, 1–10.

374 Faith, D.P., Magallón, S., Hendry, A.P., Conti, E., Yahara, T. & Donoghue, M.J. (2010).
375 Ecosystem services: an evolutionary perspective on the links between biodiversity
376 and human well-being. *Curr. Opin. Environ. Sustain.*, 2, 66–74.

377 Fjeldså, J. & Burgess, N.D. (2008). The coincidence of biodiversity patterns and human
378 settlement in Africa. *Afr. J. Ecol.*, 46, 33–42.

379 Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., *et al.*
380 (2007). Preserving the evolutionary potential of floras in biodiversity hotspots.
381 *Nature*, 445, 757–760.

382 Fox, J. (2006). Structural Equation Models, 11, 1–20.

383 Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., *et al.*
384 (2013). Higher levels of multiple ecosystem services are found in forests with more
385 tree species. *Nat. Commun.*, 4, 1–8.

386 Goldblatt, P. (1997). Floristic diversity in the Cape flora of South Africa. *Biodivers.*
387 *Conserv.*, 6, 359–377.

388 Goldblatt, P. & Manning, J.C. (2002). Plant diversity of the Cape region of southern
389 Africa. *Ann. Missouri Bot. Gard.*, 281–302.

390 Hao, M., Zhang, C., Zhao, X. & Von Gadow, K. (2018). Functional and phylogenetic
391 diversity determine woody productivity in a temperate forest. *Ecol. Evol.*, 8, 2395–
392 2406.

393 Hector, A. & Bagchi, R. (2007). Biodiversity and ecosystem multifunctionality. *Nature*,
394 448, 188–191.

395 Helmus, M.R., Bland, T.J., Williams, C.K. & Ives, A.R. (2007). Phylogenetic measures
396 of biodiversity. *Am. Nat.*, 169, E68–E83.

397 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich,
398 K.L., *et al.* (2012). A global synthesis reveals biodiversity loss as a major driver of
399 ecosystem change. *Nature*, 486, 105–108.

400 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.* (2005).
401 Effects of biodiversity on ecosystem functioning: a consensus of current knowledge.
402 *Ecol. Monogr.*, 75, 3–35.

403 Hope Sr, K.R. (2007). Poverty and environmental degradation in Africa: towards
404 sustainable policy for reversing the spiral. *Int. J. Environ. Sustain. Dev.*, 6, 451–472.

405 Huang, X., Su, J., Li, S., Liu, W. & Lang, X. (2019). Functional diversity drives
406 ecosystem multifunctionality in a *Pinus yunnanensis* natural secondary forest. *Sci.*
407 *Rep.*, 9, 1–8.

408 Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., *et al.*
409 (2015). Biodiversity increases the resistance of ecosystem productivity to climate
410 extremes. *Nature*, 526, 574–577.

411 Kumar, P. & Yashiro, M. (2014). The marginal poor and their dependence on ecosystem
412 services: evidence from South Asia and Sub-Saharan Africa. In: *Marginality*.
413 Springer, Dordrecht, pp. 169–180.

414 Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring
415 functional diversity from multiple traits. *Ecology*, 91, 299–305.

416 Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in
417 biodiversity experiments. *Nature*, 412, 72–76.

418 Luck, G.W. (2007). A review of the relationships between human population density and
419 biodiversity. *Biol. Rev.*, 82, 607–645.

420 Malherbe, H., Pauleit, S. & Lorz, C. (2019). Mapping the loss of ecosystem services in a
421 region under intensive land use along the southern coast of South Africa. *Land*, 8,
422 51.

Manhães, A.P., Mazzochini, G.G., Oliveira-Filho, A.T., Ganade, G. & Carvalho, A.R.
(2016). Spatial associations of ecosystem services and biodiversity as a baseline for
systematic conservation planning. *Divers. Distrib.*, 22, 932–943.

Maurin, O., Davies, T.J., Burrows, J.E., Daru, B.H., Yessoufou, K., Muasya, A.M., *et al.*
(2014). Savanna fire and the origins of the ‘underground forests’ of Africa. *New
Phytol.*, 204, 201–214.

Mazel, F., Pennell, M.W., Cadotte, M.W., Diaz, S., Dalla Riva, G.V., Grenyer, R., *et al.*
(2018). Prioritizing phylogenetic diversity captures functional diversity unreliably.
Nat. Commun., 9, 1–9.

Mboup, G. (2019). African Cities in Time and Space: Past, Emerging Trends and
Perspectives. In: *Smart Economy in Smart African Cities*. Springer, pp. 51–93.

Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being:
Synthesis*. Island Press, Washington DC.

Murray, C.J.L., Callender, C.S.K.H., Kulikoff, X.R., Srinivasan, V., Abate, D., Abate,
K.H., *et al.* (2018). Population and fertility by age and sex for 195 countries and
territories, 1950–2017: a systematic analysis for the Global Burden of Disease
Study 2017. *Lancet*, 392, 1995–2051.

O’Farrell, P.J., Reyers, B., Le Maitre, D.C., Milton, S.J., Egoh, B., Maherry, A., *et al.*
(2010). Multi-functional landscapes in semi arid environments: implications for
biodiversity and ecosystem services. *Landsc. Ecol.*, 25, 1231–1246.

Olanipekun, I.O., Olasehinde-Williams, G.O. & Alao, R.O. (2019). Agriculture and
environmental degradation in Africa: The role of income. *Sci. Total Environ.*, 692,
60–67.

446 Paquette, A. & Messier, C. (2011). The effect of biodiversity on tree productivity: from
447 temperate to boreal forests. *Glob. Ecol. Biogeogr.*, 20, 170–180.

448 Petchey, O.L. & Gaston, K.J. (2002). Functional diversity (FD), species richness and
449 community composition. *Ecol. Lett.*, 5, 402–411.

450 Pollock, L.J., Thuiller, W. & Jetz, W. (2017). Large conservation gains possible for
451 global biodiversity facets. *Nature*, 546, 141–144.

452 Postel, S., Bawa, K., Kaufman, L., Peterson, C.H., Carpenter, S., Tillman, D., *et al.*
453 (2012). *Nature's services: Societal dependence on natural ecosystems*. Island Press.

454 Purvis, A., Gittleman, J.L. & Brooks, T. (2005). *Phylogeny and conservation*. Cambridge
455 University Press.

456 Shackleton, C., Shackleton, S., Gambiza, J., Nel, E., Rowntree, K. & Urquhart, P. (2008).
457 *Links between ecosystem services and poverty alleviation: situation analysis for arid*
458 *and semi-arid lands in southern Africa*. Cape Town.

459 Statistics South Africa. (2001). *Investigation into appropriate definitions of urban and*
460 *rural areas for South Africa: Discussion document. Report No. 03-02-20*. Pretoria.

461 Tilman, D., Reich, P.B. & Isbell, F. (2012). Biodiversity impacts ecosystem productivity
462 as much as resources, disturbance, or herbivory. *Proc. Natl. Acad. Sci.*, 109, 10394–
463 10397.

464 Tucker, C.M., Davies, T.J., Cadotte, M.W. & Pearse, W.D. (2018). On the relationship
465 between phylogenetic diversity and trait diversity. *Ecology*, 99, 1473–1479.

466 UNICEF. (2012). *An urban world*.

467 United Nation Economic Commission for Africa. (2010). *Climate Change and the Rural*
468 *Economy in Southern Africa: Issues, Challenges and Opportunities. Report ref.*

469 *ECA-SA/TPUB/CLIMATE2012/2. 88p.*

470 United Nations. (2004). *World Population to 2300. United Nations Department of*

471 *Economic and Social Affairs. Publ. ESA/P/WP.187/Rev.1.*

472 United Nations. (2011). *Population distribution, urbanization, internal migration and*

473 *development: an international perspective.* New York.

474 Venail, P., Gross, K., Oakley, T.H., Narwani, A., Allan, E., Flombaum, P., *et al.* (2015).

475 Species richness, but not phylogenetic diversity, influences community biomass

476 production and temporal stability in a re-examination of 16 grassland biodiversity

477 studies. *Funct. Ecol.*, 29, 615–626.

478 World Commission on Environment and Development. (1987). *Our common future.*

479 *World Commission on Environment and Development.* Oxford University Press.

480 Van Wyk, A.E., den Berg, E., Coates Palgrave, M. & Jordaan, M. (2011). Dictionary of

481 names for southern African trees. Scientific names of indigenous trees, shrubs and

482 climbers with common names from 30 languages.

483

Table 1. Regression of median number of species required to capture the uses represented within each grid cell.

Model	r^2_{adjusted}	DF	P-value	Coefficient	Estimate (s.e.)	t-value
1	0.77	1204	<0.001	Log(PSR)*	4.97 (0.97)	59.43
				PSV*	-29.71 (2.73)	-10.90
2	0.78	1204	<0.001	Log(Richness)*	4.75 (0.07)	65.16
				PD _{residuals} *	-0.002 (<0.01)	-11.59

*significant at P<0.001

FIGURES

Figure 1. Phylogeny of 1,308 southern African tree species. Reconstruction based on DNA barcodes for land plants using maximum likelihood and transforming branch lengths to millions of years by enforcing a relaxed molecular clock and multiple fossil calibrations. Colours indicate higher-level taxonomic groupings.

Figure 2. Geographical distribution of tree diversity and human population density.

Tree phylogenetic diversity (myr) (a), total tree species richness (b), mean human population density (persons/km²) excluding urban areas (c), and richness of threatened trees (d). Data were divided into 32 quantiles and plotted on a 0.5° × 0.5° grid.

Figure 3. Structural Equation Models. Illustration of the direct and indirect effects of actual evapotranspiration (AET), phylogenetic diversity (PD) and longitude on human population density (**a**), and an equivalent model decomposing phylogenetic diversity into a richness independent measure of evolutionary disparity (PSV) and a measure of richness discounted for species relatedness (PSR) (**b**). Model A is favored by model fit statistics (BIC = 1129.78 and 1275.75 for model A and B respectively), although model B explains more of the total variation in human population density ($r^2 = 0.56$ and 0.59 for human density, model A and B respectively). Arrows indicate inferred direction of causation and numbers relative path strengths (standardized coefficients). The inclusion of additional pathways, such as the direct and indirect effects of elevation and latitude (Fig. S4), was not supported by model comparison statistics.

a

522

523 b