

Identifying the determinants of tree distributions along a large ephemeral river

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Citation: Douglas, C. M. S., G. Cowlishaw, X. A. Harrison, J. R. Henschel, N. Pettorelli, and M. Mulligan. 2018. Identifying the determinants of tree distributions along a large ephemeral river. *Ecosphere* 9(6):e02223. 10.1002/ecs2.2223

Abstract. Although ephemeral rivers act as linear oases and play a fundamental role in sustaining regional biodiversity in dryland regions, little is known about these systems or their sensitivity to human impacts. Without such knowledge, it is difficult to manage or conserve them. Here, we conduct the first systematic investigation into the determinants of riparian tree distributions along a large ephemeral river. Adopting a macroecological approach, we test four hypotheses relating to the effects of topography, river flow, climate, and land tenure on three indices of tree distribution: species richness, occupancy, and recruitment. We also consider the effect of upstream damming. Our study site is the Swakop River in Namibia. The most common trees along the river were the invasive *Prosopis* spp., followed by native *Faidherbia albida*, *Vachellia erioloba*, *Euclea pseudebenus*, and *Vachellia tortilis*. We found a gradient in tree distributions along the river, with a drier climate westward associated with lower native tree species richness and increased scarcity of the dominant native species (*F. albida*). These patterns were seen in both pre- and post-dam samples. We also found *F. albida* was more likely to recruit immediately downstream of tributaries. Our results suggest that water availability (climate and river flow) is a more important determination of tree distribution along this ephemeral river than topography or land tenure and that ephemeral rivers may show a nodal organization.

Key words: dams; drylands; ecohydrology; *Euclea pseudebenus*; *Faidherbia albida*; intermittent rivers; Namib Desert; Namibia; *Prosopis*; Swakop River; *Vachellia erioloba*; *Vachellia tortilis*.

Received 29 September 2017; revised 15 February 2018; accepted 27 March 2018. Corresponding Editor: Sujith Ravi.

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INTRODUCTION

In drylands, ephemeral rivers act as linear oases and play an important role in supporting regional biodiversity (Jacobson et al. 1995). A wide variety of animals, such as insects, birds, reptiles, and mammals, use the river as habitat and/or as dispersal corridors (Steward et al. 2012, Jacobson and Jacobson 2013, Williams et al. 2014). The woody vegetation along ephemeral rivers also provides important services for

people such as food, fodder, shelter, construction materials, and medicine (Jacobson et al. 1995). Ephemeral rivers are a type of intermittent river that are usually dry, only flowing for all or part of their length during and after precipitation (Tooth and Nanson 2011). Intermittent rivers comprise over half the length of the global river network, and an improved understanding of their ecology has been highlighted as a priority for scientists, policy makers, and managers (Datry et al. 2014). Ephemeral rivers can also be

detrimentally affected by human activities, which impact the vegetation and its associated benefits (Steward et al. 2012). Unfortunately, the natural determinants of tree occurrence in ephemeral rivers and their sensitivity to anthropogenic impacts are poorly understood. Although information is available on the drivers of vegetation distributions in smaller ephemeral rivers (catchment area <100 km²), such rivers are significantly different to larger ephemeral rivers that have sufficient groundwater and sediment accumulation to allow for the growth of obligate riparian trees and shrubs (Shaw and Cooper 2008). The purpose of this study is to explore the determinants of tree species distributions along a large ephemeral river (>30,000 km²).

Several factors are expected to play a role in the occurrence of trees in dryland ephemeral river systems. The most important of these tends to be water availability (Jacobson et al. 2000, Renöfält and Nilsson 2007). In ephemeral rivers with large catchments, water availability is primarily driven by flow events generated by climatic patterns in the upper watershed (Shaw and Cooper 2008). Flows decrease in discharge downstream, primarily because of infiltration but with further losses arising from evaporation and transpiration (Reid and Frostick 2011). The flows recharge the riparian ecosystem's groundwater reserves (Dahan et al. 2008). To a certain extent, the river's groundwater buffers trees from the local climate (Friedman and Lee 2002). However, local climate still has an influence through solar radiation and the associated potential evapotranspiration demand placed on vegetation (Niklas 1992). In addition, drier climates naturally have elevated salt concentrations in the soil and groundwater due to reduced runoff and increased evaporation leading to dominantly upward fluxes of water and the accumulation of salts at and near the surface (Raheja 1966). As salinity reduces the ability of plants to take up water, it causes a similar response to water stress (Munns 2002). Therefore, local climate may not only influence tree distributions directly but also indirectly through increases in groundwater/soil salinity: As a result, the relative roles of climate and salinity on tree distributions can be difficult to differentiate.

Not only do flows recharge groundwater, they also provide a variety of benefits to the

ecosystem: Flows scour the river channel and distribute and deposit nutrients, sediment, woody debris, and propagules (Jacobson et al. 1995). However, flows are not always beneficial as they can cause mortality by washing individual trees away or by depleting oxygen in the root zone (Friedman and Auble 1999, Friedman and Lee 2002). There is, therefore, a local trade-off between the benefits and disadvantages of river flow. As a result, trees are limited to locations where perennial groundwater is available and there is protection from erosive flows (Shaw and Cooper 2008). Occurrence can be especially limited in narrow reaches of rivers, where the flow occupies a greater proportion of the riverbed's width and often travels with higher velocity; broader river reaches provide more space that is safe for establishment and growth (Seely et al. 1981, Jacobson and Jacobson 2013). Tree occurrence is therefore influenced by a combination of spatial patterns of water availability and flow disturbance (Jacobson and Jacobson 2013). As species often exhibit differences in their tolerances and preferences regarding both water availability and frequency of disturbance, zonation typically occurs with those species requiring, or tolerating, frequent inundation located closer to the river channel (Seely et al. 1981, O'Connor 2001).

Along ephemeral rivers and their tributaries, flow is typically localized due to variable and patchy rain events and high transmission losses (Tooth and Nanson 2011). The fact that tributaries can flow independently of the main river channel means that they may have a pronounced localized effect on the occurrence of woody species downstream of their confluence. Surprisingly, there do not appear to have been any previous studies on the importance of tributaries on tree species richness and occupancy in any river system, but such patterns have been explored in a riparian animal. Specifically, along the main stem of perennial rivers, the richness and abundance of fish species has been found to peak below tributaries due to the additional nutrients, organic matter, and increased habitat heterogeneity in these areas (Fernandes et al. 2004, Kiffney et al. 2006).

People can also influence tree occurrence. For example, dams built along perennial rivers alter species composition and cover downstream

(Johnson 1994, Stromberg et al. 2007). However, the impacts of dams on tree distributions along ephemeral rivers are unknown. Two other anthropogenic activities likely to impact tree occurrence are livestock browsing and water abstraction. In the case of livestock, positive effects can be experienced for some species at lower livestock densities (e.g., through scarification of seeds in the gut facilitating germination), but negative effects are experienced for most at higher densities (e.g., through consumption of saplings; Skarpe 1991, Oba 1998). However, while saplings are particularly vulnerable to intense browsing, there is little evidence to suggest that browsing seriously damages mature individuals (Bergström 1992). In the case of water abstraction, recruitment and survival can be affected as both young and mature riparian plants are sensitive to sudden drops in groundwater (Scott et al. 1999, Shafroth et al. 2000). Finally, people can influence tree occurrence simply by planting or removing trees.

In this study, we explore the potential determinants of riparian tree species occurrence along a large ephemeral river, the Swakop River, in Namibia. The riparian trees play an important role in supporting wildlife and livestock populations as well as acting as a source of fuel and construction material (Curtis and Mannheimer 2005, Moser 2006, Williams et al. 2014). Like other large ephemeral rivers, only very sparse data are available for the Swakop on the frequency and volume of river flow, groundwater depth and groundwater salinity, and how these have varied along the river over the lifetimes of the riparian trees of interest. Consequently, we focus on alternative landscape-level variables that should nevertheless reflect the influence of these parameters. Specifically, we test the following four hypotheses: first, that there will be more trees in wider parts of the river where there are more suitable locations for trees to grow (topography, hypothesis 1, H1); second, that there will be more trees immediately downstream of tributary confluences due to the associated benefits of additional water, scouring, and/or nutrient and sediment distribution and deposition (tributary, H2); third, that there will be fewer trees in drier areas where water availability is diminished (local climate, H3); and fourth, that different land tenures will influence tree distributions,

specifically that more trees will occur in protected areas than in communal farmland due to the higher densities of livestock and people in the latter, while private farmlands will exhibit a pattern between the two (land tenure, H4). We also consider, in two ways, the potential impacts of two upstream dams on the tree distributions of the Swakop River: first, by re-testing the above hypotheses in a reconstructed sample of trees (incorporating dead individuals) approximating the original tree populations prior to damming, and second, by quantifying the impact of the dam on river flows using simulation modeling.

METHODS

Study area

The Swakop River is one of Namibia's twelve major westerly-flowing ephemeral rivers: These rivers consist of dry sandy riverbeds for the majority of the year and typically only flow after precipitation events. The duration of flows typically last from a few days to several weeks, although after exceptional rainfall these rivers can flow for a few months (Jacobson et al. 1995). Despite being without flow for much of the year, groundwater is continually contained within their alluvium.

The Swakop catchment is located in the central region of the country with its headwaters in the Khomas Hochland Plateau. The river flows west through the Central-Western Plains to where it meets the Atlantic Ocean near the coastal town of Swakopmund. It is 460 km in length with a catchment area of 30,100 km² (Jacobson et al. 1995). The annual mean temperature of the catchment is 18–22°C, but with large fluctuations at the daily, seasonal, and annual scales (Mendelsohn et al. 2009). Precipitation mainly falls in the wet austral summer (October–March) and ranges from 0 mm/yr in the west to 475 mm/yr in the east of the catchment; however, 80% of the catchment experiences <100 mm of rainfall per year (Jacobson et al. 1995). The longitudinal profile of the river is associated with two environmental gradients: a near-linear decline in precipitation and increase in groundwater salinity from the east of the catchment westward to the coast (Gevers and Westhuyzen 1937, Jacobson et al. 1995, Bittner et al. 2010). Although there is very high inter-annual variability in rainfall (the

coefficient of variation increases from 35% in the east to 100% in the west of the catchment), long-term annual rainfall has remained stable over the last 100 yr (Ward et al. 2000, Mendelsohn et al. 2009).

The riparian tree community of the Swakop River is largely composed of the native ana tree *Faidherbia albida* (Delile) A. Chev., camel thorn *Vachellia erioloba* (E. Mey.) P. J. H. Hurter, umbrella thorn *Vachellia tortilis* (Forssk.) Galasso & Banfi, ebony tree *Euclea pseudebenus* E. Mey., and the invasive mesquite *Prosopis* species L. (Jacobson et al. 1995). Mustard bush *Salvadora persica* L. and wild tamarisk *Tamarix usneoides* E. Mey. are also common but, along this river, both species tend to have a shrub-like growth form and thus were not included in this study. *Prosopis* was first introduced to Namibia around 1912; since then, there has been widespread hybridization between species, particularly between *Prosopis glandulosa* Torr., *Prosopis chilensis* Stuntz, and *Prosopis velutina* Wooton (Smit 2004). As the hybridization makes species identification difficult, this study does not attempt to differentiate between *Prosopis* species.

The Swakop River has two upstream dams: The first to be built was the Sartorius Von Bach Dam, 360 km upstream from the river's mouth, in 1970 (48 Mm³ capacity; 5 km² surface area; 22.02 S, 16.95 E). It was followed by the Swakoppoort Dam in 1978 (63 Mm³ capacity; 8 km² surface area; 22.21 S, 16.53 E), 70 km downstream from the Von Bach Dam. As the Swakoppoort Dam has no sluice gates, the river below this dam is cut off from the flows occurring upstream, except during exceptional flow conditions when the dam overtops. The dams capture approximately 43% of the catchment's rainfall (Douglas 2014). These dams have reduced the frequency and magnitude of flow events downstream (CSIR 1997, Ward et al. 2000, Jacobson and Jacobson 2013). The reduction in flow has in turn caused groundwater declines downstream of the dams (Marx 2009).

Three land tenures occur along the Swakop River: private, communal, and park lands. The dominant land tenure is private land, usually consisting of a homestead with surrounding land. Typical livelihood activities on private land include livestock and game farming, tourism, trophy hunting, and/or small-scale crop

production. The communal land is Otjimbingwe, a 1170-km² reserve which straddles the Swakop River in the center of the catchment. In 2000, as many as 8000 people were estimated to live in the reserve, with between 800 and 2000 people living in Otjimbingwe town and the remainder on the surrounding grazing land (Ward et al. 2000). Livestock farming is the dominant livelihood activity in the reserve although some small-scale crop production occurs (Ward et al. 2000). The main protected area in the catchment is the Namib-Naukluft National Park, which was created in its present form in 1979 and is 49,768 km² in size, located in the southwest of the catchment. There are strict regulations on human activity within the national park.

River surveys

Our 24 survey sites were located between 22°26 S 16°43 E (17 km downriver of the Swakoppoort Dam) and 22°64 S 14°75 E (25 km upstream of the river's mouth), covering more than 250 km of the river's total 460 km length (Douglas 2014). The 24 sites were distributed across the three categories of land tenure as follows: 42% of sites on private land, 21% on communal land, and 37% on park land. The distribution of sampling effort is roughly proportional to the coverage of the land tenures: The land tenures represent the following coverage of the river's borders within the study's extent: 55% private, 15% communal, and 30% park (Fig. 1).

The surveys were conducted between 2 August and 24 October 2010 and were performed in a non-sequential order to minimize any temporal bias along the climate gradient associated with the river's long profile. At each site, multiple 20 m wide transects were placed, oriented perpendicular to the river course; the transects were of variable length as determined by the width of the riverbed at that point. Each site was centered on a borehole; two transects were placed adjacent to each other with their shared boundary running directly through the center of the borehole. Additional transects were also placed 250 m up- and downriver of the central transects, for a total of four transects (except at one site with multiple boreholes, where only transects over the boreholes were placed; for a total of six transects). This design was selected due to the patchy nature of the riparian vegetation and to balance the

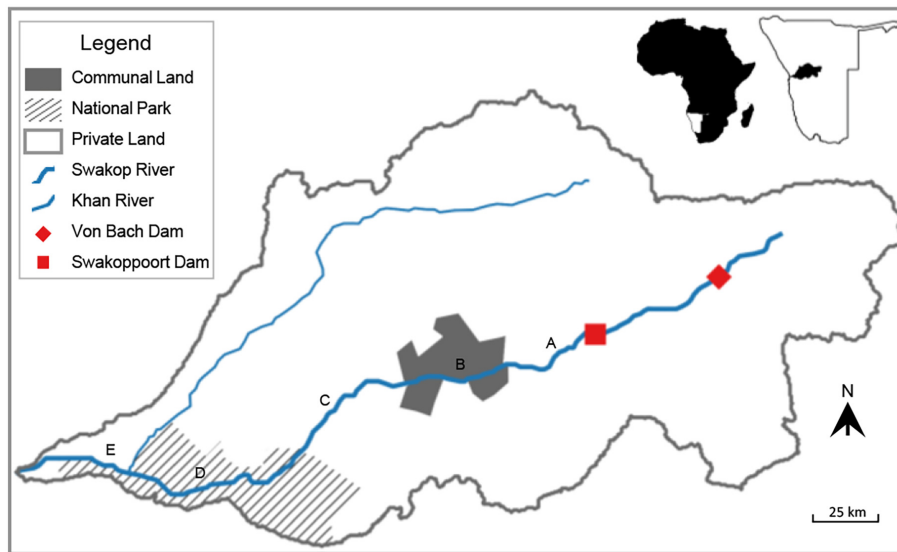


Fig. 1. Inset: (left to right) Namibia in Africa, and the Swakop River catchment in Namibia. Main: simplified map of the river catchment showing the distribution of land tenures and sampling regions. For illustrative purposes, the river below the Swakoppoort Dam has been divided into five sampling areas (from east to west): zone A (private land with one sampling site), zone B (communal land with five sampling sites), zone C (private land with three sampling sites), zone D (park lands with nine sampling sites), and zone E (private lands with six sampling sites).

need for the transects to be close enough to still be considered the same “site” but distant enough to capture any local heterogeneity in the river. Each transect was divided into a series of consecutive 20×20 m quadrats.

During the survey, data were collected at three spatial scales: quadrat, transect, and site. For each tree within each quadrat, data were collected on the species, diameter of trunk above the buttress swelling, and percentage canopy dieback. A diameter tape was used to measure tree diameter, but if the trunk was inaccessible due to impenetrable vegetation, it was estimated with a ruler (10% of cases) or visually (24% of cases). The diameter measurement was used to calculate the basal area of each tree. Trees were assessed as living except in the case of 100% canopy dieback, in which case the trees were recorded as dead. Both standing and fallen dead trees were recorded.

Indices of tree distribution, predictors of those indices, and samples for analysis

We use three indices to quantify tree distributions: species richness, occupancy, and recruitment. Trees larger than 5 cm diameter above the

buttress swelling were used for the species richness and occupancy analyses, while trees with a diameter <5 cm were used for the recruitment analysis. The 5 cm threshold was selected because we wanted to consider only established trees for richness and occupancy. Smaller trees may root in a location even though it may not be suitable for their long-term growth and survival. All three indices were quantified at the transect scale. Analyses were not possible at the quadrat scale due to the patchy distribution of trees, which resulted in large numbers of quadrats without trees. Further details about how these indices were employed during hypothesis testing are given below.

Each of the three indices was explored in relation to four fixed effects (i.e., predictors) representing the four hypotheses under test. These indices were measured at either the transect ($n = 98$) or site ($n = 24$) scale. At the transect scale, we quantified one fixed effect: river width (measured as the length of the transect, which was calculated in quadrat lengths, i.e., rounded to the nearest 20 m). At the site scale, we quantified three fixed effects: (1) dryness, the ratio of local potential evapotranspiration to local

precipitation, representing the near-linear decline of precipitation which coincides with the longitudinal profile of the river (Pearson's R correlation 0.9 between longitudinal position along the river and dryness; Appendix S1; see Appendix S2 for further details on how the metric is calculated); (2) land tenure, a categorical variable with three levels: private ($n = 9$ sites), communal ($n = 5$ sites), and park ($n = 8$ sites); and (3) tributary, a binomial variable (tributary [1], no tributary [0]; $n = 12$ sites in each case), where the presence of tributaries was based on modeled runoff from \geq third Strahler stream-order tributaries located within 5 km upstream of each sampling site (see Appendix S2 for further details). To compare differences in effect size between variables in the same model, all continuous fixed effects were standardized to have a mean of zero and a standard deviation of one. All possible combinations of these fixed effects were tested as separate models (see *Hypothesis testing and statistical analysis*).

Our primary analysis focused on the contemporary determinants of species richness, occupancy, and recruitment in living trees. However, these contemporary patterns inevitably incorporate any cumulative impact of damming on this ecosystem over the last 40 yr. It is therefore possible that the currently observed patterns may be partially influenced by the dams. As a preliminary investigation into this possibility, we attempted to re-construct the original patterns of tree species prior to the dams by compiling an extended sample of species distributions which differed from the contemporary sample by including trees that were dead as well as alive. Because dead trees can be washed away by the episodic flows in undammed ephemeral rivers, very few dead trees are normally present in such systems (Auala et al. 2013). However, after the cessation of natural flows, dead trees accumulate. This is further assisted by the low rates of woody decomposition characteristic of arid environments (Vogel 2003). Consequently, the dead individuals recorded in this survey should provide an approximation of those trees that have died since dam construction. A small number may represent trees that were already dead prior to the dams, but by chance were not washed away; similarly, a small number of trees may have died since dam construction and gone

undetected in our sample (e.g., because they were removed by people, or lost in small, localized flows). While it is unlikely that these two sources of error are large, the reconstructed extended sample should only be considered a first approximation of a pre-dam assessment, because we were also unable to identify and remove those individuals that have recruited into the population following dam construction (i.e., grown to a size of >5 cm above the buttress swelling), since local growth rates for each species are unknown. Consequently, the results of the extended sample are reported solely as a supplement to the main analysis of the contemporary (hereafter: living) sample. The extended sample is used to analyze species richness and occupancy but not recruitment, while the living sample is used to analyze all three indices.

Hypothesis testing and statistical analysis

Below we discuss each index and its analysis in turn. A summary overview of the statistical analyses is provided in Table 1.

Species richness.—Our analysis of species richness focuses on native tree species characteristic of the Swakop River. Native species in this locality were identified following Curtis and Manheimer (2005). Introduced taxa that were either non-native to Namibia (e.g., mesquite, *Prosopis* spp.) or native to other regions of Namibia (e.g., wild date palm, *Phoenix reclinata* Jacq.) were excluded as the presence of these species may reflect sites of introduction rather than natural distributions. Characteristic species were defined as those that occurred at more than one sampling location (refer to Appendix S3 for the complete species list). Under these criteria, we recorded five native trees characteristic of the Swakop River: *F. albida*, *V. erioloba*, *E. pseudebenus*, *V. tortilis*, and *Dichrostachys cinerea* (L.) Wight & Arn. We examined species richness using general linear mixed models with a Poisson error structure and log link. We used the `glmmadmb` function in the `glmmADMB` package (Fournier et al. 2012, Skaug et al. 2016) implemented in Rv3.3.0 (R Development Core Team 2016). The response variable was the number of characteristic native tree species in each transect. Models were assessed for overdispersion using the functions in Harrison (2014). No overdispersion was detected and there was no evidence that a

Table 1. Summary of analyses.

Analysis and taxa	Model set	Fixed effects for each analysis				
		Conspecifics (T)	River width (T)	Tributary (S)	Dryness (S)	Land tenure (S)
Species richness (<i>n</i>)						
All, including <i>Faidherbia albida</i> , <i>Vachellia erioloba</i> , <i>Euclea pseudobenus</i> , <i>Vachellia tortilis</i> , and <i>Dichrostachys cinerea</i>	15	No	Yes	Yes	Yes	Yes
Occupancy (1/0)						
<i>F. albida</i>	15	No	Yes	Yes	Yes	Yes
<i>V. erioloba</i>	15	No	Yes	Yes	Yes	Yes
<i>E. pseudobenus</i>	15	No	Yes	Yes	Yes	Yes
<i>V. tortilis</i>	15	No	Yes	Yes	Yes	Yes
Recruitment (1/0)						
<i>F. albida</i>	22	Yes	Yes	Yes	Yes	Yes
<i>V. erioloba</i>	22	Yes	Yes	Yes	Yes	Yes
<i>Prosopis</i> spp.	27	Yes	Yes	Yes	Yes	Yes

Notes: The taxa included in each analysis are listed, as well as the number of models in the candidate set and the inclusion of fixed effects (yes/no). All analyses are conducted at the transect level ($n = 98$) over 24 sites. Fixed effects are measured at either the transect (T) or site (S) level.

negative binomial model provided a better fit than the corresponding Poisson model (Poisson model Akaike information criterion [AIC]: 288.6, NB AIC: 290.77). One random effect, site, was included to control for any non-independence resulting from the sampling design of multiple transects ($n = 4$ or 6) within each sampling site ($n = 24$). We assessed the presence of collinearity using variance inflation factors as detailed in Zuur et al. (2009), and no evidence of collinearity was found. Due to the relatively small number of sites relative to fixed effects, we limited our candidate models to a maximum of three fixed effects. With a total of four fixed effects to test, this generated a candidate model set of 15 models: a null model and all possible combinations up to three fixed effects. However, the final model could still contain all four fixed effects through the process of model averaging (see *Model selection*).

Occupancy.—We conducted the occupancy analysis for all tree species along the river, except those that were extremely common (*Prosopis* spp., $n = 23$ of 24 sites) or rare (*P. reclinata* Jacq. $n = 4$ of 24 sites; *Hyphaene petersiana* Klotzsch ex Mart. $n = 3$; *Vachellia luederitzii* Engl. $n = 1$; *Eucalyptus* spp. L'Her. $n = 1$; *Vachellia senegal* Willd. $n = 1$). For these species, there was insufficient variation in their presence/absence across sites to explore their determinants of occupancy. The

final sample therefore comprised four trees, all of which were natives: *F. albida* ($n = 20$ sites), *V. erioloba* ($n = 15$ sites), *E. pseudobenus* ($n = 14$ sites), and *V. tortilis* ($n = 11$ sites; Appendix S3). We examined the presence/absence of each species in each transect using a general linear mixed model with a Binomial error structure and logit link. Models were not assessed for overdispersion because overdispersion cannot be quantified for binary models (Harrison 2015). Binomial models were fitted with the `glmer` function in the R package `lme4` (Bates et al. 2015). The same fixed effects, random effect, and candidate model set were used as with the species richness analysis. We assessed the presence of collinearity using variance inflation factors as detailed in Zuur et al. (2009) as well as inspecting the correlation of the fixed effects in `lme4` fits. No evidence of collinearity was found.

Recruitment.—To explore recent patterns of tree establishment, we examined the presence/absence of young trees (<5 cm diameter). The absence of saplings at a site was extremely common; therefore, we conducted the recruitment analysis for all species except those whose saplings were rare (*E. pseudobenus* $n = 5$ of 24 sites; *V. tortilis* $n = 3$; *H. petersiana* $n = 1$) or absent altogether (*P. reclinata*, *D. cinerea*, *V. luederitzii*, *V. senegal*, *Eucalyptus* spp.) The final sample comprised *F. albida* ($n = 11$ sites), *V. erioloba* ($n = 8$

sites), and the invasive *Prosopis* species ($n = 19$ sites). We examined the presence of young trees using the same statistical approach as the occupancy analysis. An additional fixed effect was included that controlled for the abundance of the local parental population and therefore availability of propagules. This fifth fixed effect, conspecifics, the abundance of nearby living adult trees (i.e., trees >5 cm diameter and $<100\%$ canopy dieback), was calculated by dividing the total adult basal area for each transect by the transect area. We assessed the presence of collinearity using the same techniques as the occupancy analyses. Correlations of >0.7 were detected between dryness and land tenure for both *F. albida* and *V. erioloba* (in the case of *F. albida*, the correlation was between dryness and communal land, and in the case of *V. erioloba*, it was between dryness and park land). As a result, both dryness and land tenure were not included together in the same model. The candidate model sets therefore consisted of 26 models for *Prosopis* (a null model and all possible combinations of up to three fixed effects) and 22 for *F. albida* and *V. erioloba*.

Model selection.—This study uses an information-theoretic approach to model selection (Burnham and Anderson 2002). Specifically, it uses the AIC to evaluate competing candidate models (Johnson and Omland 2004). We used the R package MuMIn (Barton 2016) to rank the models according to corrected AIC (AIC_c). Due to the small sample sizes used in this study, AIC_c is used instead of AIC as the former has been shown to be more robust at small sample sizes (Burnham and Anderson 2002). We considered all models within $\Delta 6$ AIC units of the best-supported model as being competitive (Richards 2008). As AIC can select unnecessarily complex models, we removed models that were more complex versions of simpler models with better AIC support (the nesting rule; Richards 2008, Arnold 2010). If more than one model remained in the top model set after the application of the nesting rule, a model averaging approach was used to calculate the parameter estimates and standard errors of a final composite model using the model.avg function in the MuMIn package. We performed full-coefficient (zeroes) modeling, where parameter estimates were set to zero in the models in the top model set from which they

were absent, to fully propagate uncertainty in parameter effect sizes and standard errors (Gruber et al. 2011).

We used confidence intervals to assess the strength of the fixed effects (du Prel et al. 2009). Therefore, if a fixed effect is included in the composite model but its confidence interval crosses zero, the result is considered inconclusive.

Spatial modeling

In addition to the main statistical analyses, simulation modeling was used to determine the likely decline in river flow as a result of the Swakoppoort Dam. The modeling allows us to assess the extent to which the results from the statistical analyses align with the changes in flow that are likely since damming. The analysis was run using the WaterWorld Policy Support System v.2.92 (Mulligan 2013). WaterWorld is an open-access self-parameterizing, process-based spatial model which uses inbuilt interpolated ground-based and remotely sensed data. It is widely used for modeling the impacts of climate change and management activities. Full details of the model, including calculations and assumptions, are provided in Mulligan (2013). Briefly, precipitation and temperature maps (Hijmans et al. 2005) were used to calculate annual total water balance (rainfall + fog inputs + snowmelt inputs – actual evapotranspiration; although only rainfall and actual evapotranspiration are significant fluxes in the Swakop). This water balance was calculated for 1 km resolution pixels on the basis of mean 1950–2000 climate and 2010 land cover. Positive water balances were then accumulated along a local drainage direction map as runoff (full equation available in Appendix S2).

Two simulations were run: a baseline simulation (i.e., no dam) and another simulation where the Swakoppoort Dam is present (the effect of the Von Bach Dam is irrelevant for this purpose as the water draining into it would in its absence be caught by the Swakoppoort Dam). For each sampling site, WaterWorld's hydrological footprint tool was used to examine the proportion of water that originates upstream of the dam by dividing the runoff generated upstream of the dam by the total runoff at that site. In order to mask the portion of the catchment draining into the Swakoppoort Dam, the dam's upstream

catchment was calculated using the HydroSHEDS stream network (Lehner et al. 2008). HydroSHEDS was also used in the local drainage direction map and the delineation of the entire catchment.

RESULTS

Predictors of riparian tree distributions

Species richness.—The number of native tree species per transect ranged from 0 to 5 (median = 1). The top model set examining factors affecting species richness contained two models: The top model included only dryness, indicating that there were fewer tree species in drier areas

(in support of hypothesis H3; Table 2, Fig. 2), and the other was the null model (Δ 4.81; Appendix S4: Table S1). There was no effect of river width (H1), tributary flow (H2), or land tenure (H4). Dryness was also found to reduce richness in the extended sample that includes dead trees (Appendix S5: Table S1), but its effects seem to be more marked in the contemporary data: A one standard deviation change in dryness causes a 34% greater change in species richness on the link scale for the living compared to the extended sample.

Occupancy.—Along the Swakop River, the invasive *Prosopis* spp. was the most common tree (occurring in 87% of transects sampled),

Table 2. Final composite models for species richness, occupancy, and recruitment analyses ($n = 98$).

Analysis and species	Parameter	Estimate	Standard error	95% confidence intervals	
				Lower	Upper
Species richness†	Intercept	0.19	0.15	−0.11	0.48
	Dryness	−0.39	0.19	−0.76	−0.02
Occupancy‡					
	<i>Faidherbia albida</i>				
<i>Vachellia tortilis</i>	Intercept	0.07	0.58	−1.07	1.20
	Tributary§	0.90	1.01	−1.08	2.88
	Dryness	−1.56	0.50	−2.49	−0.53
	Intercept	−2.27	0.57	−3.37	−1.17
	Dryness	−1.72	0.89	−3.46	0.02
	Land tenure:¶ communal	0.26	0.82	−1.36	1.88
Recruitment#	Land tenure:¶ park	−0.08	0.39	−0.84	0.68
	River width	0.04	0.18	−0.32	0.40
	<i>Faidherbia albida</i>				
<i>Vachellia erioloba</i> †	Intercept	−3.75	1.48	−6.62	−0.84
	Tributary §	2.62	1.28	0.121	5.12
	Conspecifics	0.72	0.96	−1.14	2.59
	Dryness	−4.37	1.78	−7.86	−0.88
	Intercept	−3.62	1.17	−5.91	−1.32
<i>Prosopis</i>	River width	0.17	0.38	−0.58	0.92
	Dryness	−0.86	0.98	−2.78	1.07
	Tributary§	0.67	0.99	−1.27	2.61
	Conspecifics	0.17	0.33	−0.47	0.82
	Land tenure:¶ communal	0.91	1.52	−2.08	3.90
	Land tenure:¶ park	0.92	1.46	−1.95	3.79
<i>Prosopis</i>	Intercept	−0.28	0.46	−1.35	0.65
	Land tenure:¶ communal	1.95	0.91	0.28	4.16
	Land tenure:¶ park	−0.99	0.70	−2.56	0.43

Notes: Conclusive effects are highlighted in bold; inconclusive effects (where the confidence intervals cross zero) are not emboldened. The null model was the top-ranked model for the occupancy of both *V. erioloba* and *E. pseudebenus*. Refer to Appendix S4: Tables S1–S8 for rankings and further details of individual models. All continuous fixed effects were standardized (mean of zero, standard deviation of one).

† The null model also received support.

‡ *Faidherbia albida* and *V. tortilis* are composite models averaged from two and three models, respectively.

§ Reference category for tributary is no tributary.

¶ Reference category for land tenure is private.

Faidherbia albida and *V. erioloba* are composite models averaged from three and five models, respectively.

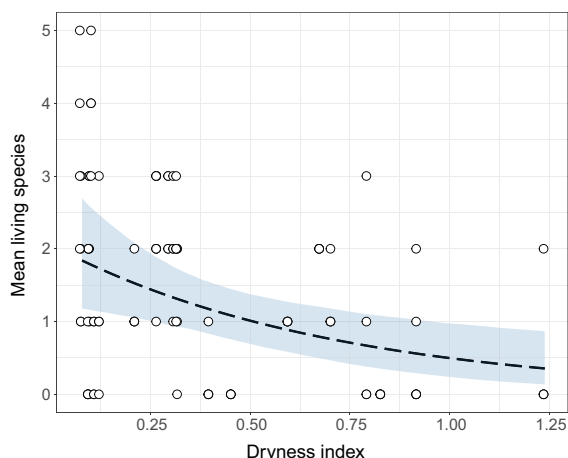


Fig. 2. Native tree species richness in relation to local climate (i.e., dryness). The dryness index is calculated by dividing potential evapotranspiration by precipitation; higher values are drier. The fitted line is the mean predicted probability from a Poisson mixed-effects model, where the shaded area represents 95% credible intervals. The points are the raw data. The dryness index also relates to increased groundwater salinity and the distance downstream along the longitudinal profile of the river. A figure showing the relationship between species richness and the longitudinal profile of the river is provided in Appendix S1: Fig. S1.

followed by *Faidherbia albida* (56%), *Vachellia erioloba* (40%), *Euclea pseudobenus* (28%), and *Vachellia tortilis* (19%). In the extended sample, the order of species was the same, but all species were present in more transects (Appendix S5). This indicates that for all species, there were now transects which contained only dead individuals. Comparing occupancy between the extended and living samples, *F. albida* declined the most (20% of transects), followed by *V. tortilis* (4%), *V. erioloba* and *E. pseudobenus* (both 3%), and *Prosopis* (1%).

Following the application of the nesting rule, the top model sets examining occupancy for *F. albida*, *V. tortilis*, *V. erioloba*, and *E. pseudobenus* contained two, three, one, and one model, respectively (Appendix S4: Tables S2–S5).

In the analysis of the predictors of occupancy, across the four species tested, the only clear result was that *F. albida* was less likely to occur in drier areas (H3; Table 2, Fig. 3). *Faidherbia albida* was also more likely to occur downstream of

tributary flows (H2), but this pattern was inconclusive. In the case of *V. tortilis*, there was inconclusive support for lower occupancy in drier areas (H3), in wider stretches of the river (H1), and for differences across land tenure types (H4). There was no evidence to support any of the hypotheses tested for *V. erioloba* and *E. pseudobenus* occupancy: The null model was the top model ($\Delta 0.00$) in both cases.

In the analysis of the predictors of occupancy in the extended sample, similar models were obtained for all four species (Appendix S5: Table S1). Once again, the effect of dryness tended to be stronger in the contemporary data. For example, a one standard deviation change in dryness causes a 73% greater change in *F. albida* occupancy on the link scale for the living sample compared to the extended sample.

Recruitment.—Recruitment of *Prosopis* spp. (presence of young trees with a diameter of <5 cm) was recorded in 45% of all transects, followed by *F. albida* and *V. erioloba* in 33% and 13% of all transects, respectively. Of the transects where adults were present, there was no recruitment in 52%, 58%, and 81% of

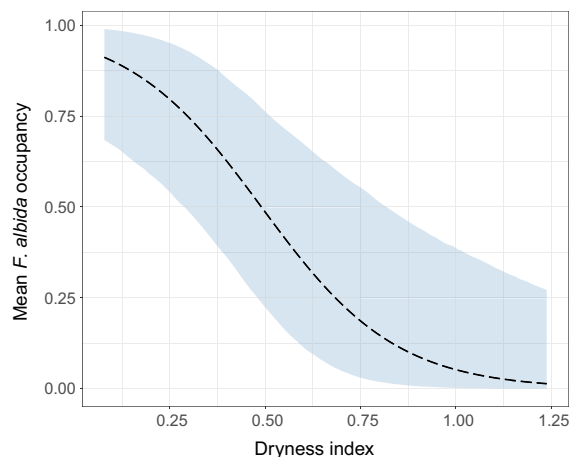


Fig. 3. *Faidherbia albida* occupancy in relation to local climate (i.e., dryness). The dryness index is calculated by dividing potential evapotranspiration by precipitation; higher values are drier. The fitted line is the mean predicted probability from a logistic mixed-effects model, where the shaded area represents 95% credible intervals. The dryness index also relates to increased groundwater salinity and the distance downstream along the longitudinal profile of the river.

transects for *Prosopis*, *F. albida*, and *V. erioloba*, respectively.

Following the application of the nesting rule, the top model sets examining occupancy for *F. albida*, *V. erioloba*, and *Prosopis* contained three, six, and one model, respectively (Appendix S4: Tables S6–S8).

Analysis of the predictors of recruitment for *Prosopis* spp. revealed that recruitment was highest in communal lands (compared to private lands; H4; Table 2). In contrast, recruitment for *F. albida* was highest immediately downstream of tributaries (H2) and lower in drier areas (H3) (Fig. 4). Additionally in the case of *F. albida*, recruitment was more likely in the presence of conspecifics (our control variable), although this pattern was inconclusive. In the case of *V. erioloba*, there was mixed support for all the predictors (and control variable), but all of these effects were inconclusive. The null model also emerged in the top model set for *V. erioloba* (Δ 2.94).

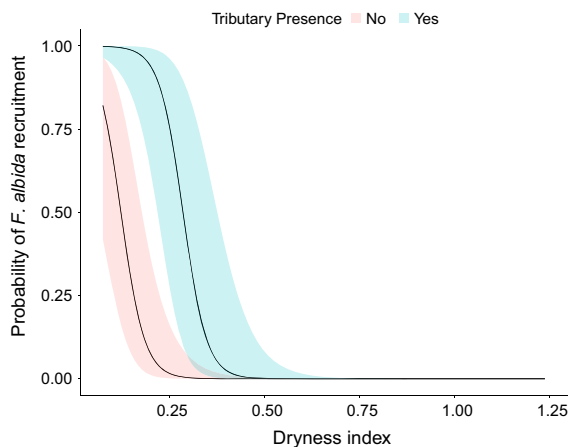


Fig. 4. *Faidherbia albida* recruitment in relation to local climate (i.e., dryness) and upstream tributary presence. The dryness index is calculated by dividing potential evapotranspiration by precipitation; higher values are drier. Tributary presence is based on modeled runoff from tributaries within 5 km upstream of each sampling site. The fitted line is the mean predicted probability from a logistic mixed-effects model, where the shaded area represents \pm the standard error. The dryness index also relates to increased groundwater salinity and the distance downstream along the longitudinal profile of the river.

Summary.—A summary of the results of the statistical analyses for the living sample is provided in Table 3. A comparison of the results between the “living” and “extended” samples is provided in Appendix S5: Table S2.

Spatial modeling

The Swakoppoort Dam has resulted in an estimated median 43% reduction in downstream river flow across the 24 survey sites (min: 32%, max: 68%; Fig. 5), with the greatest declines at sites closest to the dam. A major tributary (the Khan River; Fig. 1) joins the Swakop 45 km upstream of the river’s mouth; as a result of this tributary’s considerable flows, the four sampling sites below its confluence show a much smaller proportional decline in annual flow following the damming of the river.

DISCUSSION

This study has explored the processes that drive patterns of tree species richness, occupancy, and recruitment along an ephemeral river that is dammed. The native trees frequently observed along the Swakop River, *Faidherbia albida*, *Vachellia erioloba*, *Euclea pseudebenus*, and *Vachellia tortilis* (in order of abundance), are typical of the twelve westerly-flowing ephemeral rivers of Namibia, although the relative abundance of these species can vary between rivers (Seely et al. 1981, Jacobson et al. 1995, Schachtschneider 2010). Among these twelve rivers, the Swakop River is the only one along which the invasive *Prosopis* was considered as common riparian vegetation over twenty years ago (Jacobson et al. 1995). *Prosopis* is indeed a common species along the Swakop River; it was the most frequently surveyed taxon, with its presence recorded at 87% of all sampling locations. Why *Prosopis* should be so common along the Swakop but not on the other major ephemeral rivers is unknown, but it may be related to the relatively high proportion of farmland in the Swakop River catchment, and thus higher number of potential sites of introduction, compared to the other ephemeral rivers. In this discussion, we will consider the three predictors of tree distributions: dryness, tributary presence, and land tenure type, before discussing what other factors may be influencing distributions and the implications of our findings for the

Table 3. Summary of results.

Analyses	Transect		Site		
	Conspecifics [control]	River width H1	Tributary H2	Dryness H3	Land tenure H4
Species richness†		0	0	–	0
Occupancy					
<i>Faidherbia albida</i>		0	(+)	–	0
<i>Vachellia erioloba</i>		0	0	0	0
<i>Euclea pseudobenus</i>		0	0	0	0
<i>Vachellia tortilis</i>		(+)	0	(–)	(*)
Recruitment					
<i>F. albida</i>	(+)	0	+	–	0
<i>V. erioloba</i> †	(+)	(+)	(+)	(–)	(*)
<i>Prosopis</i> spp.	0	0	0	0	* ‡

Notes: The outcomes are summarized in relation to each hypothesis: 0 indicates no effect (variable did not enter the best model); + and – indicate conclusive positive and negative effects with continuous variables; and * indicates an effect for the categorical variable, land tenure (conclusive results explained). Parentheses indicate inconclusive results where confidence intervals crossed zero.

† The null model also received support.

‡ Less *Prosopis* recruitment on private than communal lands.

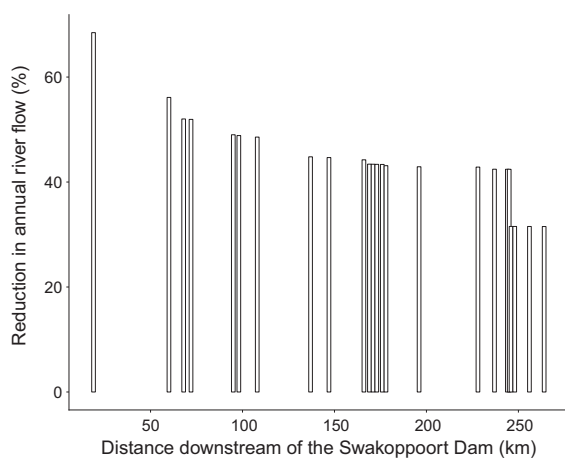


Fig. 5. Modeled reductions in river flow as a result of the Swakoppoort Dam in relation to distance below the dam. Measurements represent modeled flow at each sampling site. The dam has the greatest impact on river flow on those locations closest to the dam. This impact declines with distance downstream because of the greater contribution of tributary flows. The last four sites are downstream of a large tributary (the Khan River). Modeling conducted in WaterWorld Policy Support System v2.92 (Mulligan 2013).

Swakop River specifically and for ephemeral rivers in general.

Local climate, specifically dryness, emerged as an important predictor of native tree distributions along the Swakop River. Drier areas were

associated with lower species richness together with the reduced occupancy and recruitment of *F. albida*, the most common native tree. In addition, dryness was also associated with lower occupancy in *V. tortilis* and lower recruitment in *V. erioloba*, although these patterns were inconclusive.

The dryness effects were manifested as a longitudinal decline. Longitudinal declines in species richness have similarly been observed along both natural and dammed perennial rivers, in alpine as well as subtropical environments, and have been attributed to correlated altitudinal or climatic gradients (Karrenberg et al. 2003, Stave et al. 2005). In the case of the Swakop River, the evidence clearly suggests a climatic gradient, but it is difficult to tell whether the influence of dryness reflects a direct effect of local climate and/or indirect effects of groundwater salinity or river flow. In the latter case, because the discharge of ephemeral rivers declines in the downstream direction (Reid and Frostick 2011), the dryness gradient may relate to water availability via river flow and by extension groundwater levels. Unfortunately, groundwater depth data for the Swakop are not available at a sufficient spatial or temporal resolution to evaluate the relationships between groundwater depth and tree occurrence. Nevertheless, the fact that both *F. albida* recruitment and occupancy decline as the climate becomes drier, and that the effect becomes more

marked after the dam was built, suggests that this species is particularly responsive to changes in water availability. This conclusion is consistent with previous reports of *F. albida*'s vulnerability to drought and hydrological change (O'Connor 2001, Schachtschneider 2010, Douglas et al. 2016).

Tributary flows also may play a role in riparian tree distributions. The recruitment of *F. albida* was higher downstream of tributaries. *Faidherbia albida* occupancy and *V. erioloba* recruitment also showed a similar pattern, although these results were inconclusive. In a previous study, tributaries were likewise found to reduce the extent of dieback in *F. albida* on the Swakop River (Douglas et al. 2016). Taken together, these findings not only underscore the water sensitivity of *F. albida*, but also highlight the potentially important role that tributaries play in shaping tree distributions along this river. Although the effects of tributaries may have accentuated since damming, it seems probable that they would also have influenced the ecology of the Swakop River prior to this. Tributaries are likely to play a beneficial role in the ecology of undammed ephemeral rivers, given their contribution of additional water, sediment, and nutrients. This interpretation is supported by the presence of tributary in the *F. albida* occupancy model (albeit with an inconclusive effect) in the extended sample which may approximate pre-dam conditions. This study therefore supports research undertaken on perennial rivers which suggests that there is a nodal rather than linear organization to rivers and that tributary confluences can act as biological hotspots (Benda et al. 2004, Kiffney et al. 2006).

Land tenure was a predictor of tree recruitment for the invasive *Prosopis* species. Recruitment was higher in communal land than in private land (Table 2), which is counter to the hypothesis that human habitation would decrease recruitment. Communal lands have the highest livestock and human densities (Ward et al. 2000) as well as the greatest occurrence of water abstraction (recent/current abstraction observed on 100% of communal sites [5/5], 78% of private sites [7/9], and 13% of park sites [1/8]). The high recruitment of *Prosopis* in communal lands is not driven by high adult biomass as private land tenure had considerably higher

biomass levels (basal area: private 1.1 m²/quad, communal 0.5, and park 0.3). It is unclear why *Prosopis* recruitment is highest on communal land, but one plausible explanation is that in the case of this species, the high livestock levels are beneficial through promoting germination and seed dispersal (Schachtschneider 2010).

Among our remaining predictors, we found little support for the hypothesis that tree distributions might be related to river width: Only *V. tortilis* occupancy and *V. erioloba* recruitment showed a width effect, and both were inconclusive. The reasons for this are uncertain, but may reflect long-term dynamics in river width that we were unable to capture with our single-season survey. Similarly, the anticipated influence of conspecific presence on recruitment was unclear: Although recruitment was associated with conspecifics for the recruitment of the two native tree species tested (i.e., for *F. albida* and *V. erioloba*), the results were inconclusive in both cases. This might reflect the way in which this variable was quantified, as it was measured across the transect rather than within a given radius of each individual. The uncertainty of this effect may also reflect the importance of seed dispersal, either by livestock/wildlife or by localized river flow, in recruitment.

Across species, we were unable to identify reliable predictors for the occupancy of either *V. erioloba* or *E. pseudebenus*. This is perhaps unsurprising as it is consistent with the known biology of these two species. *Euclea pseudebenus* does not fix nitrogen, in contrast to the other species (Schulze et al. 1991). Therefore, its distribution may be the result of its high soil nitrogen dependency overriding the effects of all other environmental factors. *Vachellia erioloba* is well known for its wide environmental tolerances including that of brackish water (Barnes 2001, Burke 2006) which may explain why no predictors described its presence. In the case of *V. erioloba* recruitment, all predictors received inconclusive support and the null model was within the top model set. This ambiguous result is likely a consequence of a general lack of *V. erioloba* recruitment along the Swakop River (only 13 of 98 transects) and the high correlation between land tenure and dryness which meant that half of the top models contained land tenure and the other half dryness (Appendix S4:

Table S7). As a result of using the full-coefficient method to model average (see *Methods*), the parameter estimates of both land tenure and dryness were cut in half, so neither received conclusive support when in fact one or both variables might play a role. Consequently, the relative roles of land tenure and dryness in the recruitment of *V. erioloba* cannot currently be disentangled.

Overall, our findings suggest that water availability (dryness, tributary flow) is a more important determinant of tree distribution along this ephemeral river than either land tenure or river width. The similar patterns observed in our extended sample suggest that these are unlikely to be simply an artifact of the dam. Our results also indicate that ephemeral rivers may show a nodal organization. Assuming a nodal organization to rivers, the ecological functioning of tributaries becomes particularly important to the biological integrity of the main channel. In the case of ephemeral rivers, the notion of a nodal organization is particularly important given the variable and isolated nature of flow events. This interpretation also has implications for the impacts of damming. After an ephemeral river has been dammed, it may potentially transition from a linear oasis to a series of disjointed oases located immediately downstream of tributary confluences.

Implications of tree decline and the roles of dams and invasive species

This study suggests that the dams along the Swakop River have had a detrimental effect on the riparian community. This is evidenced by the declines in occupancy (between the living sample and the extended sample), that the effect of dryness became more accentuated in the living sample, and that recruitment is low. Although recruitment of desert trees tends to be episodic and rare (Ward 2009) and saplings experience high mortality (Moser 2006), the size of trees considered as recent recruits in this study is up to 5 cm in diameter and thus represents not just saplings but also woody individuals. The spatial simulation modeling also supports the interpretation that the dams have had a detrimental effect on the river ecosystem; the Swakoppoort Dam has reduced the river's flow by nearly half. Although the model indicates that flow reductions relative to total runoff are lower further

from the dam, these areas are naturally much more water-stressed and hence more susceptible to small changes in flow. Therefore, the effect of reduced flow, and associated declines in water table, will be felt most severely where the climate is drier and the groundwater more saline.

Another factor that might be involved in tree declines in the Swakop River is the invasive *Prosopis* species. *Vachellia erioloba* growing near *Prosopis* along an ephemeral river in South Africa showed greater water stress and increased dieback (Schachtschneider and February 2013). Similarly, along the Swakop River, greater *Prosopis* abundance is associated with increased dieback in *F. albida* (Douglas et al. 2016). However, it is possible that *Prosopis* is primarily a passenger rather than a driver of change (sensu MacDougall and Turkington 2005) in the Swakop River ecosystem. Either way, its extensive dieback where it still remains (Douglas et al. 2016) suggests that *Prosopis* is also suffering from the impacts of the dam.

The reduction in living native tree species, the prevalence of the invasive *Prosopis* spp., and the few young trees along the Swakop River have important implications for regional biodiversity and also for the livelihoods of people using the river. *Faidherbia albida* is the most common native species along the Swakop and uniquely provides pods during the dry austral winter, upon which both wildlife and people rely during this period (Barnes and Fagg 2003, Moser 2006). Similarly, *V. erioloba*, the second most common native species, is experiencing declines in occupancy and low recruitment and is also an important tree that is highly regarded, among other things, for its nutritious pods and shade provision (Moser 2006). The decline of the riparian trees thus has important ramifications, jeopardizing the ability of the Swakop River to act as a linear oasis across the Namib Desert. The findings of this study suggest that the future of the riparian tree community along the Swakop River is uncertain.

ACKNOWLEDGMENTS

We would like to thank Tamsin Burbidge, Justus Kauatjirue, and Thomas Sloan for help with data collection, and Mike Chadwick and Richard Mundy for advice during the development of this research. We are also grateful to two anonymous reviewers for the constructive comments that improved the manuscript. Thank you to the many people in Namibia who helped

to make the project a success and who provided access to their land. We also thank the Ministry of Environment and Tourism and the Namib-Naukluft National Park for research permissions and the Gobabeb Research and Training Centre for affiliation. Financial support was provided by an Economic and Social Research Council and Natural Environment Research Council Joint Studentship (ES/I902872/1), Ambiotek Community Interest Company, and King's College London Department of Geography Small Grants Fund (to C.M.S.D.). This paper is a contribution to the Zoological Society of London (ZSL) Institute of Zoology's "Tsaobis Baboon Project."

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