

Land-Use Is More Important Predictor of Native Abundance and Diversity Than Invasive *Tithonia Diversifolia* - Evidence From a Tropical Savanna

Quadri Agbolade Anibaba (✉ qanibaba@man.poznan.pl)

Institute of Dendrology Polish Academy of Sciences <https://orcid.org/0000-0002-5195-2920>

Rahila M Yilangai

A. P. Leventis Ornithological Research Institute University of Jos Biological Conservatory, Jos, Plateau State, Nigeria

Zingfa W Wala

Sol Plaatje University

Sonali Saha

Miami Dade College

Research Article

Keywords: vegetation, natives, invasive species, tropical savanna, sub-Saharan Africa

Posted Date: May 17th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-486697/v1>

License:   This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

**Land-use is more important predictor of native abundance and diversity than invasive
Tithonia diversifolia - evidence from a tropical savanna**

Quadri A. Anibaba^{1, 2*}, Rahila M. Yilangai², Zingfa W. Wala^{2, 3}, Sonali Saha^{2, 4}

¹ Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland

² A.P. Leventis Ornithological Research Institute (APLORI), University of Jos Biological Conservatory Laminga, Jos, Plateau State, Nigeria

³ Biological and Agricultural Science Department, School of Natural and Applied Sciences, Sol Plaatje University, Kimberley, South Africa

⁴ Biology, Health, and Wellness Department, Miami Dade College, Miami, United States

*Correspondence: Quadri A. Anibaba, Institute of Dendrology, Polish Academy of Sciences, Kórnik, Poland.

ORCID: <https://orcid.org/0000-0002-5195-2920>

E-mail: qanibaba@man.poznan.pl

Abstract

Invasive alien species (IAS) and land-use represent major threats to native plant communities around the globe. However, studies on IAS and potential ecological impacts in the context of land-use are limited in sub-Saharan Africa. Using a set of 45 plots in Jos metropolis in central Nigeria, we assessed the abundance of invasive *Tithonia diversifolia* (Hemsls.) A. Gray, and its relationship with abundance and diversity of native plant species among land-use types. Abundance of *T. diversifolia* was the highest in farmland when compared to riparian and roadside land-use types. Also, the abundance and diversity of native species were lowest in farmland when compared to the roadside and riparian plant communities with increased *T. diversifolia* abundance. We showed that while *T. diversifolia* has low impact on native species, land-use type is an important predictor of native abundance and diversity. Although *T. diversifolia* has benefitted from the disturbances across land-use types, we found a very weak negative estimate of *T. diversifolia* effects on native species. These results consolidate existing evidence that land-use transformation in sub-Saharan Africa provides opportunities for alien plant invasion and native species decline. More important is the preservation of land-use types, which will result in a synergy of conservation effort - both reducing *T. diversifolia* abundance and preserving native plant abundance and diversity in central Nigeria.

Keywords: vegetation; natives; invasive species; tropical savanna; sub-Sahara Africa

Introduction

Human-mediated landscape modifications have created disjointed patches of native habitats interspaced with land-use types such as roads, dams, farmlands, riparian, and recreational gardens (Saunders et al., 2002). Land-use modifications favor plant invasions and provide a channel for propagule entrance including suitable conditions (i.e. higher light and nutrient availability and reduced competition) for invasive seedling establishment (Hobbs & Huenneke, 1992). For instance, roadsides create corridors for alien plant colonization and propagule dispersal (Safford & Harrison, 2001; Gelbard & Belnap, 2003; Godefroid & Koedam, 2004). Soils along roadsides tend to be nutrient-rich relative to surrounding soils, thus providing opportunities for fast-growing invasive alien species (IAS) (Tyser & Worley, 1992; Greenberg et al., 1997; Ullmann et al., 1998; Parendes & Jones, 2000; Williamson & Harrison, 2002). Agriculture also promotes the spread of IAS due to seed trade (Rejmanek & Richardson, 1996; Chen, 2012). Additionally, farm management practices (e.g., herbicide application and land-clearing) that involve a greater number of people and vehicles increase the spread of IAS (Chen et al., 2013; Perrings & Halkos, 2015). Anthropogenic activities along riparian ecosystems in urban areas make urban vegetation vulnerable to invasion by IAS (Cao & Natuhara, 2020). Moreover, the mesic condition of riparian habitats in disturbed landscapes increases their vulnerability to invasion by IAS (Pyšek & Prach, 1994). Thus, riparian habitat could serve as a corridor for dispersal of IAS to surrounding native ecosystems. For example, the spread and impact of Crofton weed (*Eupatorium adenophorum*) along riparian habitats in Southwest China has reduced native species cover (Lu & Ma, 2006). Riparian habitats have been reported to support both indigenous and alien woody species (Dyderski et al., 2015). These disturbances influence plant communities by increasing their invisibility and facilitation by alien species (Hobbs & Huenneke, 1992).

Invasion ecologists across the globe acknowledge that Africa has scant information available in the literature on biological invasions, with most studies emanating from South Africa (van Wilgen et al., 2020). Besides, some studies have proposed that tropical ecosystems may be less susceptible to invasion than temperate ecosystems (Sax, 2001; Freestone et al., 2013). However, its low invasibility (the relatively low tendency of an intact ecosystem to acquire and retain IAS) is rapidly changing due to natural resource exploitation and related disturbances, which create available niches for IAS to thrive (Anning & Yeboah-Gyan, 2007; Ansong et al., 2019).

While our understanding of invasion ecology has expanded substantially over the last decades, research has been firmly biased towards certain geographical regions and ecosystems (Pyšek et al., 2008; Bellard & Jeschke, 2016). Our greatest knowledge about the patterns and processes of invasion comes from research conducted in temperate terrestrial ecosystems, however, tropical regions which have larger and more diverse habitats remain amazingly understudied (Rodríguez, 2001; Nuñez & Pauchard, 2010; Barlow et al., 2018). This scarcity of data is particularly problematic because tropical ecosystems are among the most threatened globally (Sala et al., 2000; Lövei et al., 2012). Henderson, (2007) highlighted 48 species as “flamboyant invaders” in the savanna biome of South Africa, while recently 291 species of naturalized alien plants were recorded in Ghana (Ansong et al., 2019). Therefore, knowledge of IAS is scarce and requires special attention in tropical and subtropical Africa.

Tithonia diversifolia (Hemsl) A. Gray is one of the most widespread IAS in tropical and subtropical Africa (Obiakara & Fourcade, 2018; Witt et al., 2019). The plant is an annual shrub or perennial herb under favorable conditions, and it has large alternate lobed leaves and bright yellow capitula (Olorode et al., 2011). *T. diversifolia* requires high temperatures and light intensities for optimal growth, but does not tolerate water stress (Chukwuka, et al., 2007; Wen, 2015). It thrives in open, sunny and ruderal habitats, along river courses and road verges (Ayeni et al., 1997). Life-history traits that explain the high invasiveness of *T. diversifolia* include fast vegetative growth, prolific seed production, and allelopathic potential (Muoghalu, 2008; Otusanya & Ilori, 2012). The invasiveness of *T. diversifolia* could be linked to its aggressive colonization resulting in dense monocultures, thereby contributing to the decline of local valued native species, including medicinal flora (Sun et al., 2007; Borokini, 2011; Witt et al., 2019). For example, *T. diversifolia* invades farmland and competes with crops, thereby reducing crop yield. Further, *T. diversifolia* is an important agricultural weed by competing with crops and reducing yield due to its allelopathic properties (Otusanya & Ilori, 2012). Therefore, *T. diversifolia* as an IAS could be recognized as a significant conservation and agricultural problem in the tropics.

Despite the apparent significance of *T. diversifolia*, its impact on native plant communities in the context of land-use types in tropical savannah remains unknown. Few studies have focused on *T. diversifolia* distribution (Ayeni et al., 1997; Chukwuka, Ogunyemi, & Fawole, 2007; Obiakara & Fourcade, 2018; Witt et al., 2019) or its impact on species composition (Agboola & Joseph, 2014)

without attention to natives and land-use types. Our study aims to assess the abundance of *T. diversifolia* and its relationship with native plant species across roadside, riparian, and farmland - typical land-use types in a tropical savannah. Jos metropolis provides a perfect study area, as it represents various types of land-use typical of an African tropical savannah landscape. We hypothesized that: (1) Land-use types will support a comparable abundance of invasive *T. diversifolia*. Disturbances will impact land-use types homogeneously from the perspective of creating suitable habitats for *T. diversifolia* to form a self-sustaining population (Ayeni et al., 1997; Adebawale & Olorode, 2005); (2) abundance of *T. diversifolia* will be negatively correlated with native species abundance and diversity across land-use types. We expect that *T. diversifolia* will have a competitive advantage over native species, thereby affecting them negatively across land-use types (Agboola & Joseph, 2014).

Methods

Site description

Our study was conducted in Jos metropolis, Plateau State, North-central Nigeria (09°52'N, 08°58'E) (Fig. 1). The Plateau is the largest landmass above 1,000 m in Nigeria and is approximately 250 km by 150 km in area. It comprises high plains with scattered rock outcrops ranging from 1,220 to 1,450 m above sea level and some granite hill ranges that rise to 1,781 m. Total annual precipitation is 1,400 mm which falls during a period of 6 - 8 months (Payne, 1998). The savanna vegetation is dominated by interspersed shrubs and grasses, grazed by livestock, with riparian forest fragments and extensive agricultural cultivation. The most important native species of economic significance are *Parkia biglobosa* (Leguminosae), *Daniella oliveri* (Caesalpiniaceae), *Dichrostachys cinerea* (Leguminosae), and *Vitex doniana* (Lamiaceae).

We distinguished three land-use types: farmland, roadside, and riparian, based on land-use features and human activities. The sampled farmlands were active and used for maize, beans, cucumber, and Irish potato cultivation, farm practices included pesticides and fertilizer applications. The sampled roadsides are major roads with vegetation dominated by herbaceous and shrub plant species and sparse trees. Land-clearing, road and building construction are common human activities along the roadside. The riparian sites are also disturbed by land clearing, sand excavation, and illegal dumping. Riparian vegetation is dominated by shrub and tree species.

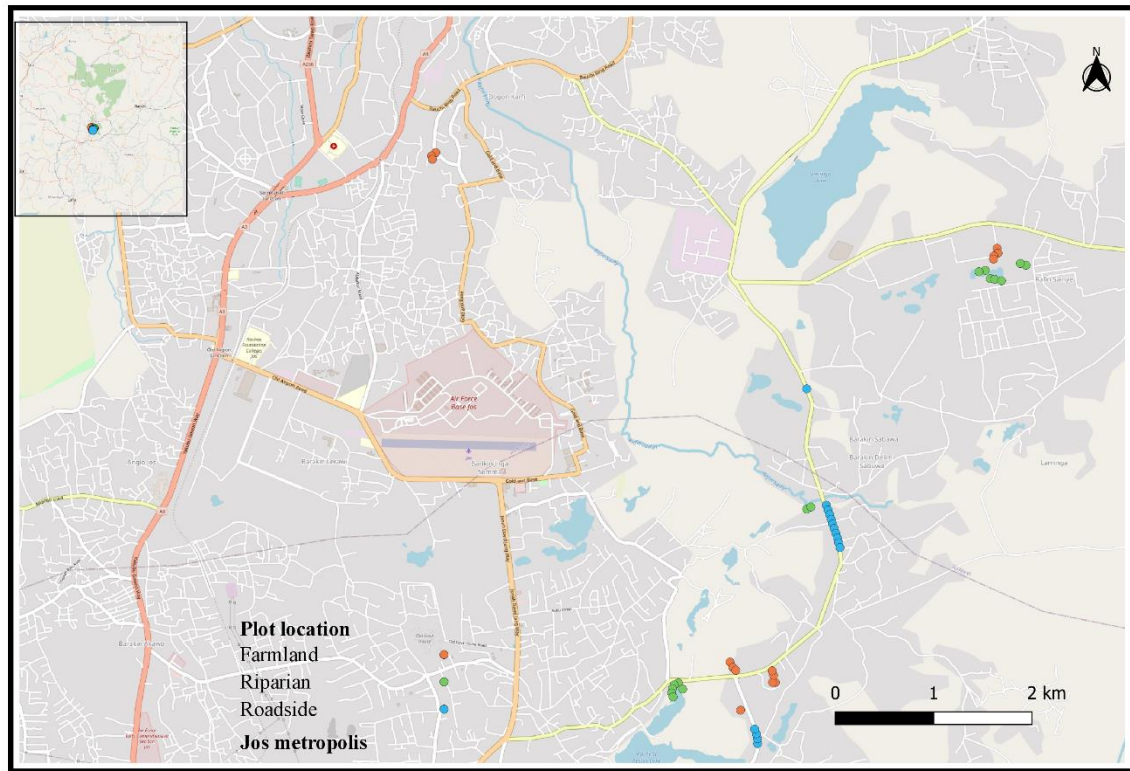


Fig: 1 Map of Jos metropolis with distributions of the study plots

Data collection

We set 15 sample transects 450 m long across the land-use types. In each transect, we established three 10 m × 10 m plots within vegetation patches occupied by *T. diversifolia*. Plots were at least 150 m from other plots. Within each plot, we identified and counted the individuals of all vascular plant species. Species were identified following nomenclatures by (Hutchinson & Dalziel, 1954; Akobundu & Agyarkwa, 1998; Arbonnier, 2004). Specimens of unknown species were collected and identified at the A. P. Leventis Ornithological Research Institute (APLORI) herbarium. The growth habits of the plants encountered were grouped into herbaceous annuals, herbaceous perennials, and woody perennials. The origin of the plant species was determined from online flora databases including the Plant list (<http://www.theplantlist.org/>); Plants of the World Online (POWO) (<http://www.plantsoftheworldonline.org/>); Global Biodiversity Information Facility (GBIF) (<https://www.gbif.org/>); and CABI Invasive Species Compendium

(<https://www.cabi.org/ISC>). Vegetative sampling was done immediately after the rainy season between October and December 2019.

Data analyses

We computed native species abundance and Shannon's diversity index (H) for each sampling plot. To investigate differences in the abundance of *T. diversifolia* across the three land-use types we fitted a linear mixed-effect model (LMM). In the model, we included land-use type as a fixed effect and transect as a random effect to account for spatial dependence of study plots within transects. Following this, we also performed a post-hoc comparison test on *T. diversifolia* abundance among three land-use types using the 'emmeans' (Lenth, 2020), 'multcomp' (Hothorn et al., 2008), and 'multview' (Graves et al., 2019) R packages.

We also fitted a generalized linear mixed-effect model (GLMM) with a Poisson distribution using the 'lme4' R package (Bates et al., 2015) to evaluate the effect of *T. diversifolia* on abundance of native species across the three land-use types. However, this model showed overdispersion and we developed GLMMs based on negative binomial distribution using the 'glmmTMB' package (Brooks et al., 2017), with the 'family = nbinom' argument. For this model, we considered the abundance of *T. diversifolia* and land-use types as fixed effects and transect as a random effect to account for spatial dependence of study plots within transects.

To determine if *T. diversifolia* explains the Shannon diversity index of native species across land-use types, we fitted an LMM which assumed a Gaussian distribution of the dependent variable. The dependent variable follows a normal distribution with no overdispersion. The abundance of *T. diversifolia* and land-use types serve as fixed effects and transect as a random effect.

We developed a final model by variable selection based on Akaike Information Criterion, corrected for small samples (AICc) from a global model using the dredge function in the 'MuMin' package (Bartoń, 2020). To show how final models are better than the global model and null (intercept-only), we reported AICc of the final model, global model, and null model. The marginal R^2 (R^2_m) explaining the fixed effect component and the conditional R^2 (R^2_c) explaining both the fixed effect and random effects are shown for each model. To visualize the result, we showed the outcome of fixed-effect only, providing values of the random effects in the model table. All mean variables are followed by $\pm$ SE. We ensured a lack of problems with zero-inflation and overdispersion of models using a test provided by the 'DHARMa' package (Hartig, 2020). All

statistical analyses were conducted using the R statistical environment version 4.0.3 (R Core Team, 2020).

Results

We found no significant difference in *T. diversifolia* abundance across land-use types (ANOVA $\chi^2=0.155$, $p=0.926$). However, *T. diversifolia* abundance was the higher in farmlands than in the other two land-use types (Table 1).

Table 1 Multi-comparison of mean *T. diversifolia* abundance across land-use types

Land-use	Marginal mean	S.E.	D.f.	lower.CL	upper.CL	group
Roadside	85.4	23.1	12	35	136	a
Riparian	93.9	22.9	11.5	43.8	144	a
Farmland	98.1	23.4	12.5	47.4	149	a

S.E.: standard error of estimate; D.f.: degree of freedom; lower.CL: lower confidence limit; upper.CL: upper confidence limit; group with the same letter – no significant difference

Across the three land-use types, we counted 1612 individuals belonging to 31 native plant species. The riparian sites had the highest native species abundance (795 individuals), dominated mainly by *Ipomoea asarifolia* (Convolvulaceae; 253 individuals), *Dichrostachys cinerea* (Leguminosae; 127 individuals), and *Acacia ataxacantha* (Leguminosae; 119 individuals). In roadside sites, we found a total of 446 individuals, represented mainly by *Urena lobata* (Malvaceae; 96 individuals), *Acacia ataxacantha* (Leguminosae; 83 individuals), and *Vernonia perrottetii* (Compositae; 57 individuals). The farmland sites had the least abundant native species (371 individuals), most represented by *Aspilia africana* (Compositae; 100 individuals), *Leucas martinicensis* (Lamiaceae; 88 individuals), and *Urena lobata* (Malvaceae; 87 individuals) (see supplemental Table 1).

Our model showed lack of relationships between *T. diversifolia* abundance and native species abundance across the three land-use types (Table 2, Fig. 2). Also, there was the lack of relationships between *T. diversifolia* abundance and native species diversity across land-use types (Table 2, Fig. 3). Thus, we found that *T. diversifolia* may not provide a good explanation of native

species abundance and diversity decline, however, land-use types influenced native species diversity (farmland: 0.686 ± 0.219 ; riparian: 1.290 ± 0.277 ; roadside: 0.997 ± 0.280). The high R^2_m and low R^2_c indicated that the results were strongly site-specific within a particular transect.

1 **Table 2** Generalized Mixed-Effect Model (GLMM) of native species abundance across land-use types

Response	Variable	Estimate	S.E.	z	Pr(> z)	Random Effect and AICc
Native species abundance	(Intercept)	2.4900	0.215	11.554	<0.001	Random effect SD = 0.1323
	<i>T. diversifolia</i> abundance	-0.0009	0.001	-0.675	0.500	AICc = 1059.3
	Land-use = Riparian	-0.0692	0.195	-0.355	0.723	AICc _o = 1061.0, AICc _g = 1066.5
	Land-use = Roadside	-0.1370	0.204	-0.670	0.503	R ² _m = 0.218; R ² _c = 0.96
Native species diversity	(Intercept)	0.6860	0.219	3.134	0.007	Random effect SD = 0.4172
	<i>T. diversifolia</i> abundance	0.0001	0.001	0.158	0.875	AICc = 185.3
	Land-use = Riparian	0.6040	0.277	2.178	0.053	AICc _o = 186.8, AICc _g = 224.6
	Land-use = Roadside	0.3110	0.280	1.112	0.289	R ² _m = 0.0066; R ² _c = 0.71

2 S.E.: standard error of estimate; AICc: Akaike's Information Criterion, with correction for small sample size; AICc_o: AICc of the null model (intercept-only); AICc_g: AICc of the global model (covering
3 all hypothesized variables); R²_m: marginal R²; R²_c: conditional R²; SD: standard deviation

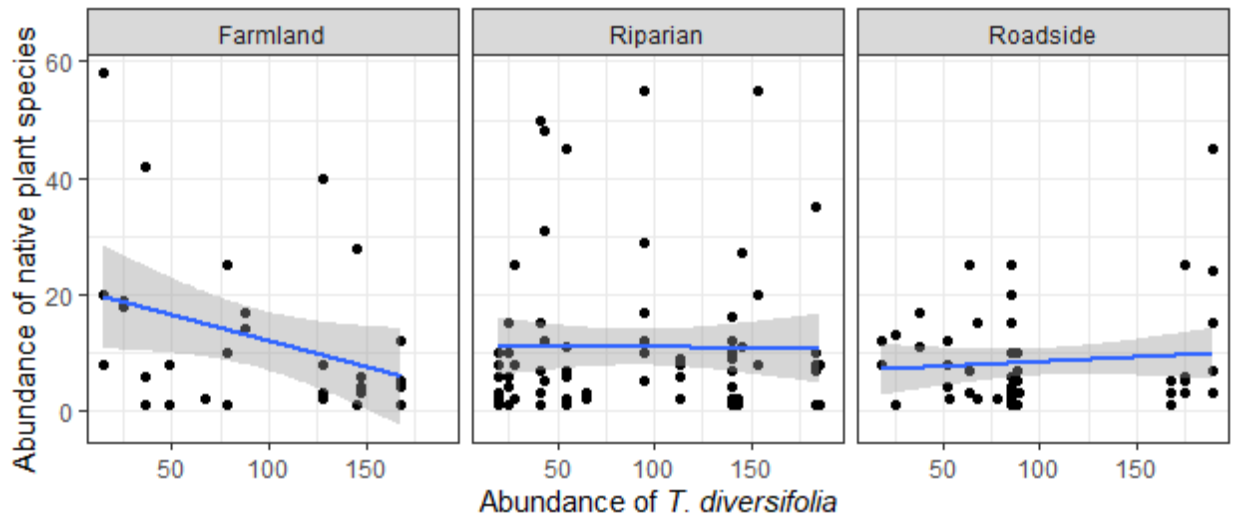


Fig. 2 Relationships between the abundance of native species and *T. diversifolia* abundance across land-use types. The figure shows linear relationships of the response variable (abundance of native plant species) depending on the predictor variable (abundance of *T. diversifolia*) on farmland, riparian, and roadside. Blue lines represent linear regressions, and grey shading shows the 95% confidence interval of the fit

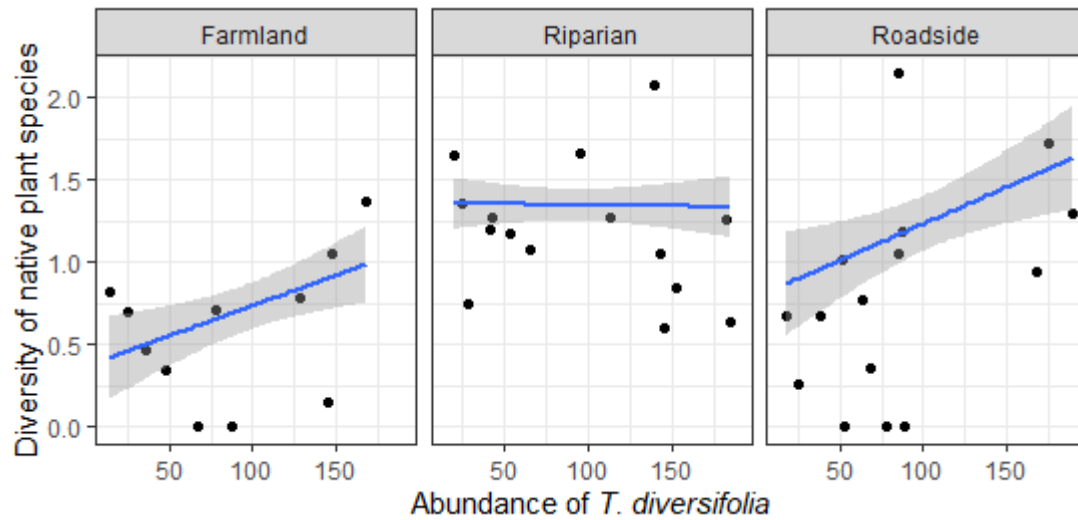


Fig. 3 Relationships between the diversity of native species and *T. diversifolia* abundance across land-use types. The figure shows linear relationships of the response variable (diversity of native plant species) depending on the predictor variable (abundance of *T. diversifolia*) on farmland, riparian, and roadside. Blue lines represent linear regression lines and grey shading shows the 95% confidence interval of the fit

Discussion

*The abundance of invasive *T. diversifolia* across land-use types.*

Our study showed that *T. diversifolia* abundance did not differ significantly across land-use types. Spatial connectedness and microsite conditions such as soil moisture and light availability across the three land-use types could have influenced the similarity in the overall abundance of *T. diversifolia*. Besides, Chukwuka et al., (2007) revealed that *T. diversifolia* seeds grow better in sites with moist soil and full light which are characteristics of our studied land-use types. Our results are consistent with other studies which revealed an equal abundance of *T. diversifolia* in these land-use types (Ayeni et al., 1997; Adebowale & Olorode, 2005; Chukwuka, Ogunyemi, & Fawole, 2007; Olorode et al., 2011; Okach & Amuka, 2015).

Ruderal life-history traits of *T. diversifolia* such as high seed production (Muoghalu, 2008) could allow for its establishment in habitats with high disturbance and low stress. The high mean abundance of *T. diversifolia* in farmland could be attributed to disturbances such as land-clearing and intense fertilizer application. Besides, the cultural methods of weed control such as hand weeding and hoeing could promote continuous establishment *T. diversifolia* in farmland since the plant can proliferate by vegetative means when fully established. Our finding agrees with Chukwuka, Ogunyemi, & Fawole (2007) who reported that most farmers had abandoned their farmland due to aggressive colonization by *T. diversifolia* in Southwest Nigeria. In general, it could be inferred that *T. diversifolia* can establish a small population of individuals which could spread to other areas if the habitat is adaptable.

*Relationship between *T. diversifolia* abundance and native abundance and diversity.*

Our models showed lack of relationships between native species abundance and diversity with *T. diversifolia* abundance across land-use types. Thus, we inferred that *T. diversifolia* might not be the reason for the paucity of native species, however, land-use types influenced native species diversity. Our results were highly dependent within transects, showing that other site-specific factors are more important than the presence of *T. diversifolia*, which supports context-dependence. Besides, many studies have highlighted the context-dependence of biological invasions (Pauchard & Alaback, 2004; González-Moreno et al., 2014; Vieira et al., 2014; Sapsford et al., 2020).

We found a very low abundance and diversity of natives with increased *T. diversifolia* abundance in farmland. We inferred that native plant communities in farmland experience severe anthropogenic disturbance and high resource availability which continuously support the establishment and proliferation of IAS such as *T. diversifolia* (Davis et al., 2000; Colautti et al., 2006). Our finding reaffirms the report by (Aleman et al., 2016; Hubert et al., 2020), where the decline in native species abundance and diversity were attributed to agricultural land-use in sub-Saharan Africa. Also, Ibrahim & Balzter, (2018) reported that the diversity of native plants has continued to decline in the Nigeria-Niger border area, despite regreening as a result of land degradation.

On the roadside, we recorded a diverse but low abundance of natives with increased *T. diversifolia* abundance. Abiotic factors such as high light availability (Christen & Matlack, 2009), increased water runoff and altered soil texture (Okach & Amuka, 2015) along roadsides could promote the continuous establishment of *T. diversifolia*. In contrast, roadsides had a varied impact on native plant species, which could be species-specific and favor ruderal species (Lázaro-Lobo & Ervin, 2019). For example, roadside could affect native climbers such as *Strophanthus sarmentosus* DC. due to its habitat specificity, but benefit native weedy species which are disturbance-and stress-tolerant such as *Urena lobata* L. (Okach & Amuka, 2015)

In the riparian land-use type, we found a high abundance and diversity of natives with increased *T. diversifolia* abundance. A possible reason for the abundant and diverse native community in riparian habitats is regular exposure to flooding which reduces the potency of competitive interactions, thereby returning riparian plant communities to the early successional stage after flooding (Pollock et al., 1998). A similar explanation that supports high native species abundance and diversity in riparian habitats could also increase its susceptibility to IAS such as *T. diversifolia* (Pyšek & Prach, 1994). For instance, anthropogenic disturbance such as land-clearing could promote plant species establishment in riparian habitats, while natural disturbances such as flooding may enhance their continuous spread along the watercourse (Säumel & Kowarik, 2013; McShane et al., 2015; Nobis & Skórka, 2016). Also, the availability of moisture and dispersal of *T. diversifolia* seeds by water could enhance the invasibility of the riparian land-use type. In general, dominant native vegetation in the riparian land-use type could represent a more invasion-resistant community and conservation priority. Thus, sustaining dominant native vegetation at high

abundance and diversity is critical to preventing the establishment of large monospecific *T. diversifolia* stands.

Conclusions

Our study demonstrated how *T. diversifolia* is distributed across land-use types and its relationship with native abundance and diversity. We provided the first assessment of the relationship between *T. diversifolia* and native abundance and diversity for the study area, thus, broadening our understanding of invasive species and natives in the context of land-use. We proved that land-use type is an important predictor of native species status. Additionally, we showed that riparian habitats still hold high native species abundance and diversity. This is essential in setting a conservation priority aimed at promoting the natural regeneration of native plant species.

Acknowledgement

We would like to thank the A. P. Leventis Foundation for the funding, Assistant Professor Sara Kuebbing (University of Pittsburgh) for her honest review, and Marcin K. Dyderski PhD for his advice on statistical analysis.

Authors' contributions

AQA: Conceptualization, formal analysis, methodology, writing, discussion, review, and editing.

RMY: Conceptualization, discussion, and supervision.

ZWW: Conceptualization, discussion, and supervision.

SS: Conceptualization, discussion, review, editing and supervision.

Declarations

Conflicts of interest: The authors declare no conflict of interest

References

- Adebowale, A., & Olorode, O. (2005). An overview of the invasive potential of *Tithonia* species (Asteraceae) in Nigeria. *Science Focus*, 10(3), 65–69.
- Agboola, O., & Joseph, I. M. (2014). Impact of *Tithonia diversifolia* (Hemsl) A. Gray on the soil, species diversity and composition of vegetation in Ile-Ife (Southwestern Nigeria), Nigeria. *International Journal of Biodiversity and Conservation*, 6(7), 555–562. <https://doi.org/10.5897/ijbc2013.0634>
- Akobundu, I. O., & Agyarkwa, C. W. (1998). *A handbook of West African weeds* (2nd Edition). Ibadan, International Institute of Tropical Agriculture.
- Aleman, J. C., Blarquez, O., & Staver, C. A. (2016). Land-use change outweighs projected effects of changing rainfall on tree cover in sub-Saharan Africa. *Global Change Biology*, 22(9), 3013–3025. <https://doi.org/10.1111/gcb.13299>
- Anning, A. K., & Yeboah-Gyan, K. (2007). Diversity and distribution of invasive weeds in Ashanti Region, Ghana. *African Journal of Ecology*, 45(3), 355–360. <https://doi.org/https://doi.org/10.1111/j.1365-2028.2007.00719.x>
- Ansong, M., Pergl, J., Randall, R., Pyšek, P., Essl, F., Hejda, M., & Kleunen, M. Van. (2019). Naturalized and invasive alien flora of Ghana. *Biological Invasions*, 21, 669–683. <https://doi.org/10.1007/s10530-018-1860-7>
- Arbonnier, M. (2004). *Trees, shrubs, and lianas of West African dry zones*. Paris, CIRAD.
- Ayeni, A. O., Lordbanjou, D. T., & Majek, B. A. (1997). *Tithonia diversifolia* (Mexican Sunflower) in South-Western Nigeria: Occurrence and growth habit. *Weed Research*, 37(6), 443–449. <https://doi.org/10.1046/j.1365-3180.1997.d01-72.x>
- Barlow, J., França, F., Gardner, T. A., Hicks, C. C., Lennox, G. D., Berenguer, E., Castello, L., Economo, E. P., Ferreira, J., & Guénard, B. (2018). The future of hyperdiverse tropical ecosystems. *Nature*, 559(7715), 517–526.
- Bartoń, K. (2020). *MuMIn: Multi-Model Inference*. (R package version 1.43.17.). <https://cran.r-project.org/package=MuMIn>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/https://doi.org/10.18637/jss.v067.i01>
- Bellard, C., & Jeschke, J. M. (2016). A spatial mismatch between invader impacts and research publications. *Conservation Biology*, 30(1), 230–232.
- Borokini, T. I. (2011). Invasive alien plant species in Nigeria and their effects on biodiversity conservation. *Tropical Conservation Science*, 4(1), 103–110. <https://doi.org/10.1177/194008291100400110>
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9(2),

- Cao, Y., & Natuhara, Y. (2020). Effect of urbanization on vegetation in riparian area: Plant communities in artificial and semi-natural habitats. *Sustainability*, 12(1), 204.
- Chen, G.-Q., He, Y.-H., & Qiang, S. (2013). Increasing seriousness of plant invasions in croplands of Eastern China in relation to changing farming practices: A case study. *PLoS ONE*, 8(9), e74136. <https://doi.org/10.1371/journal.pone.0074136>
- Chen, X. (2012). Distribution patterns of invasive alien species in Alabama, USA. *Management of Biological Invasions*, 3(1), 25–36. <https://doi.org/10.3391/mbi.2012.3.1.03>
- Christen, D. C., & Matlack, G. R. (2009). The habitat and conduit functions of roads in the spread of three invasive plant species. *Biological Invasions*, 11(2), 453–465. <https://doi.org/10.1007/s10530-008-9262-x>
- Chukwuka, K. S., Ogunyemi, S., & Fawole, I. (2007). Ecological distribution of *Tithonia diversifolia* (Hemsl.) A. Gray-A new exotic weed in Nigeria. *Journal of Biological Sciences*, 7(5), 709–719. <https://doi.org/10.3923/jbs.2007.709.719>
- Chukwuka, K. S., Ogunyemi, S., Osho, J. S. A., Atiri, G. I., & Moughalu, J. I. (2007). Eco-physiological responses of *Tithonia diversifolia* (Hemsl.) A. Gray in nursery and field conditions. *Journal of Biological Sciences*, 7(5), 771–775. <https://doi.org/10.3923/jbs.2007.771.775>
- Colautti, R. I., Grigorovich, I. A., & MacIsaac, H. J. (2006). Propagule pressure: a null model for biological invasions. *Biological Invasions*, 8(5), 1023–1037.
- Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, 88(3), 528–534. <https://doi.org/10.1046/j.1365-2745.2000.00473.x>
- Dyderski, M. K., Gdula, A. K., & Jagodziński, A. M. (2015). “The rich get richer” concept in riparian woody species – A case study of the Warta River Valley (Poznań, Poland). *Urban Forestry & Urban Greening*, 14(1), 107–114. <https://doi.org/10.1016/j.ufug.2014.12.003>
- Freestone, A. L., Ruiz, G. M., & Torchin, M. E. (2013). Stronger biotic resistance in tropics relative to temperate zone: effects of predation on marine invasion dynamics. *Ecology*, 94(6), 1370–1377.
- Gelbard, J. L., & Belnap, J. (2003). Roads as conduits for exotic plant invasions in a semiarid landscape. *Conservation Biology*, 17(2), 420–432. <https://doi.org/10.1046/j.1523-1739.2003.01408.x>
- Godefroid, S., & Koedam, N. (2004). The impact of forest paths upon adjacent vegetation: Effects of the path surfacing material on the species composition and soil compaction. *Biological Conservation*, 119(3), 405–419. <https://doi.org/10.1016/j.biocon.2004.01.003>
- González-Moreno, P., Diez, J. M., Ibáñez, I., Font, X., & Vilà, M. (2014). Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat. *Diversity and Distributions*, 20(6), 720–731.

- Graves, S., Piepho, H.-P., Selzer, L., & Dorai-Raj, S. (2019). *multcompView: Visualizations of Paired Comparisons*. (R package version 0.1-8.). <https://cran.r-project.org/package=multcompView>
- Greenberg, C. H., Crownover, S. H., & Gordon, D. R. (1997). Roadside soils: A corridor for invasion of xeric scrub by nonindigenous plants. *Natural Areas Journal*, 17(2), 99–109.
- Hartig, F. (2020). *DHARMA: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models*. (R package version 0.3.3.0.). <https://cran.r-project.org/package=DHARMA>
- Henderson, L. (2007). Invasive, naturalized and casual alien plants in southern Africa: A summary based on the Southern African Plant Invaders Atlas (SAPIA). *Bothalia*, 37(2), 215–248. <https://doi.org/10.4102/abc.v37i2.322>
- Hobbs, R. J., & Huenneke, L. F. (1992). Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology*, 6(3), 324–337. <https://doi.org/10.1046/j.1523-1739.1992.06030324.x>
- Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical Journal: Journal of Mathematical Methods in Biosciences*, 50(3), 346–363.
- Hubert, L., Marie, B., Nacoulma, I., & Bayen, P. (2020). Agricultural land use reduces plant biodiversity and carbon storage in tropical West African savanna ecosystems: Implications for sustainability. *Global Ecology and Conservation*, 21(3), 1–15. <https://doi.org/10.1016/j.gecco.2019.e00875>
- Hutchinson, J., & Dalziel, J. M. E. (1954). *Flora of West Tropical Africa*. Kew, London, Royal Botanic Gardens.
- Ibrahim, Y. Z., & Balzter, H. (2018). Land degradation continues despite greening in the Nigeria-Niger border region. *Global Ecology and Conservation*, 16(10), 1–12. <https://doi.org/10.1016/j.gecco.2018.e00505>
- Lázaro-Lobo, A., & Ervin, G. N. (2019). A global examination on the differential impacts of roadsides on native vs. exotic and weedy plant species. *Global Ecology and Conservation*, 17(1), 1–13. <https://doi.org/10.1016/j.gecco.2019.e00555>
- Lenth, R. (2020). *emmeans: Estimated Marginal Means, aka Least-Squares Means* (R package version 1.5.2-1.). <https://cran.r-project.org/package=emmean>
- Lövei, G. L., Lewinsohn, T. M., Dirzo, R., Elhassan, E. F., Ezcurra, E., Freire, C. A., Gui, F.-R., Halley, J. M., Tibazarwa, J. M., & Jiang, M.-X. (2012). Megadiverse developing countries face huge risks from invasives. *Trends in Ecology & Evolution*, 27(1), 2–3.
- Lu, Z., & Ma, K. (2006). Spread of the exotic Crofton weed (*Eupatorium adenophorum*) across Southwest China along roads and streams. *Weed Science*, 54(6), 1068–1072. <https://doi.org/10.1614/ws-06-040r1.1>
- McShane, R. R., Auerbach, D. A., Friedman, J. M., Auble, G. T., Shafroth, P. B., Merigliano, M. F., Scott, M. L., & Poff, N. L. (2015). Distribution of invasive and native riparian woody

- plants across the western USA in relation to climate, river flow, floodplain geometry and patterns of introduction. *Ecography*, 38(12), 1254–1265.
- Muoghalu, J. I. (2008). Growth, reproduction and resource allocation of *Tithonia diversifolia* and *Tithonia rotundifolia*. *Weed Research*, 48(2), 157–162. <https://doi.org/10.1111/j.1365-3180.2007.00613.x>
- Nobis, A., & Skórka, P. (2016). River corridor plants revisited: What drives their unique distribution patterns? *Plant Biosystems-An International Journal Dealing with All Aspects of Plant Biology*, 150(2), 244–253.
- Núñez, M. A., & Pauchard, A. (2010). Biological invasions in developing and developed countries: does one model fit all? *Biological Invasions*, 12(4), 707–714.
- Obiakara, M. C., & Fourcade, Y. (2018). Climatic niche and potential distribution of *Tithonia diversifolia* (Hemsl) A. Gray in Africa. *PLoS ONE*, 13(9), 1–18. <https://doi.org/10.1371/journal.pone.0202421>
- Okach, D. O., & Amuka, O. (2015). Plant species diversity along road reserve in Kisumu County-Kenya. *Ecologia*, 5(1), 8–21. <https://doi.org/10.3923/ecologia.2015.8.21>
- Olorode, O., Sekinat O. Hassan, O. A. O. &, & Raimi, I. O. (2011). *Tithonia* (Asteraceae) in Nigeria. *Ife Journal of Science*, 13(1), 1–10.
- Otusanya, O., & Ilori, O. (2012). Phytochemical screening and the phytotoxic effects of aqueous extracts of *Tithonia diversifolia* (Hemsl) A. Gray. *International Journal of Biology*, 4(3), 97. <https://doi.org/10.5539/ijb.v4n3p97>
- Parendes, L. A., & Jones, J. A. (2000). Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. *Conservation Biology*, 14(1), 64–75. <https://doi.org/10.1046/j.1523-1739.2000.99089.x>
- Pauchard, A., & Alaback, P. B. (2004). Influence of Elevation, Land Use, and Landscape Context on Patterns of Alien Plant Invasions along Roadsides in Protected Areas of South-Central Chile. *Conservation Biology*, 18(1), 238–248. <https://doi.org/10.1111/j.1523-1739.2004.00300.x>
- Pauchard, A., Meyerson, L. A., Bacher, S., Blackburn, T. M., Brundu, G., Cadotte, M. W., Courchamp, F., Essl, F., Genovesi, P., Haider, S., Holmes, N. D., Hulme, P. E., Jeschke, M., Lockwood, J. L., Novoa, A., Núñez, M. A., Peltzer, D. A., Pyšek, P., Richardson, D. M., ... Zenni, R. D. (2018). Biodiversity assessments : Origin matters. *PLoS Biology*, 16(11), 1–4.
- Payne, R. B. (1998). A new species of Firefinch *Lagonosticta* from Northern Nigeria and its association with the Jos Plateau Indigobird *Vidua maryae*. *Ibis*, 3(140), 369–381. <https://doi.org/10.1111/j.1474-919x.1998.tb04598.x>
- Perrings, C., & Halkos, G. (2015). Agriculture and the threat to biodiversity in sub-Saharan Africa. *Environmental Research Letters*, 10(9), 95015.
- Pollock, M. M., Naiman, R. J., & Hanley, T. A. (1998). Plant species richness in riparian wetlands—a test of biodiversity theory. *Ecology*, 79(1), 94–105.

- Pyšek, P., & Prach, K. (1994). How Important are Rivers for Supporting Plant Invasions? In L. de Waal, L. E. Child, P. M. Wade, & J. H. Brock (Eds.), *Ecology and management of invasive riverside plants*. (pp. 21–31). John Wiley & Sons.
- Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtová, Z., & Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution*, 23(5), 237–244. <https://doi.org/10.1016/j.tree.2008.02.002>
- R Core Team. (2020). *R: a language and environment for statistical computing*. (R-4.0.3). R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>
- Rejmanek, M., & Richardson, D. M. (1996). What attributes make some plant species more invasive? *Ecology*, 77(6), 1655–1661.
- Rodríguez, J. P. (2001). Exotic species introductions into South America: an underestimated threat? *Biodiversity & Conservation*, 10(11), 1983–1996.
- Safford, H. D., & Harrison, S. P. (2001). Grazing and substrate interact to affect native vs. exotic diversity in roadside grasslands. *Ecological Applications*, 11(4), 1112–1122. [https://doi.org/10.1890/1051-0761\(2001\)011\[1112:GASITA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1112:GASITA]2.0.CO;2)
- Sala, O. E., Chapin, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., & Kinzig, A. (2000). Global biodiversity scenarios for the year 2100. *Science*, 287(5459), 1770–1774.
- Sapsford, S. J., Brandt, A. J., Davis, K. T., Peralta, G., Dickie, I. A., Gibson, R. D., Green, J. L., Hulme, P. E., Nuñez, M. A., & Orwin, K. H. (2020). Towards a framework for understanding the context dependence of impacts of non-native tree species. *Functional Ecology*, 34(5), 944–955.
- Säumel, I., & Kowarik, I. (2013). Propagule morphology and river characteristics shape secondary water dispersal in tree species. *Plant Ecology*, 214(10), 1257–1272.
- Saunders, S. C., Mislivets, M. R., Chen, J., & Cleland, D. T. (2002). Effects of roads on landscape structure within nested ecological units of the Northern Great Lakes Region, USA. *Biological Conservation*, 103, 209–225. [https://doi.org/10.1016/S0006-3207\(01\)00130-6](https://doi.org/10.1016/S0006-3207(01)00130-6)
- Sax, D. F. (2001). Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography*, 28(1), 139–150.
- Sun, W.-B., Chen, G., & Wang, S.-H. (2007). Characteristics of *Tithonia diversifolia*: an alien invasive plant in Yunnan, South-west China. *3rd Global Botanic Gardens Congress*, 2, 1–7. <http://www.bgci.org/files/Wuhan/PapersConserving/SunTithonia.pdf>
- Tyser, R. W., & Worley, C. A. (1992). Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana (U.S.A.). *Conservation Biology*, 6(2), 253–262. <https://doi.org/10.1046/j.1523-1739.1992.620253.x>
- Ullmann, I., Bannister, P., & Wilson, J. B. (1998). Lateral differentiation and the role of exotic species in roadside vegetation in Southern New Zealand. *Flora*, 193(2), 149–164. [https://doi.org/10.1016/S0367-2530\(17\)30832-0](https://doi.org/10.1016/S0367-2530(17)30832-0)

- Van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Kreft, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L., ... Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, 525(7567), 100–103. <https://doi.org/10.1038/nature14910>
- van Wilgen, B., Measey, J., Richardson, D., Wilson, J., & Zengeya, T. (2020). Biological Invasions in South Africa: An Overview. In B. W. van Wilgen, J. Measey, D. M. Richardson, J. R. Wilson, & T. A. Zengeya (Eds.), *Biological Invasions in South Africa, Invading Nature - Springer Series in Invasion Ecology 14* (pp. 3–31). Springer Nature. https://doi.org/10.1007/978-3-030-32394-3_1
- Vieira, R., Finn, J. T., & Bradley, B. A. (2014). How does the landscape context of occurrence data influence models of invasion risk? A comparison of independent datasets in Massachusetts, USA. *Landscape Ecology*, 29(9), 1601–1612.
- Wen, B. (2015). Effects of high temperature and water stress on seed germination of the invasive species Mexican Sunflower. *PLoS ONE*, 10(10), 1–13. <https://doi.org/10.1371/journal.pone.0141567>
- Williamson, J., & Harrison, S. (2002). Biotic and abiotic limits to the spread of exotic revegetation species. *Ecological Applications*, 12(1), 40–51. [https://doi.org/10.1890/1051-0761\(2002\)012\[0040:BAALTT\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2002)012[0040:BAALTT]2.0.CO;2)
- Witt, A. B. R., Shackleton, R. T., Beale, T., Nunda, W., & van Wilgen, B. W. (2019). Distribution of invasive alien *Tithonia* (Asteraceae) species in Eastern and Southern Africa and the socio-ecological impacts of *T. diversifolia* in Zambia. *Bothalia*, 49(1), 1–11. <https://doi.org/10.4102/abc.v49i1.2356>

Figures

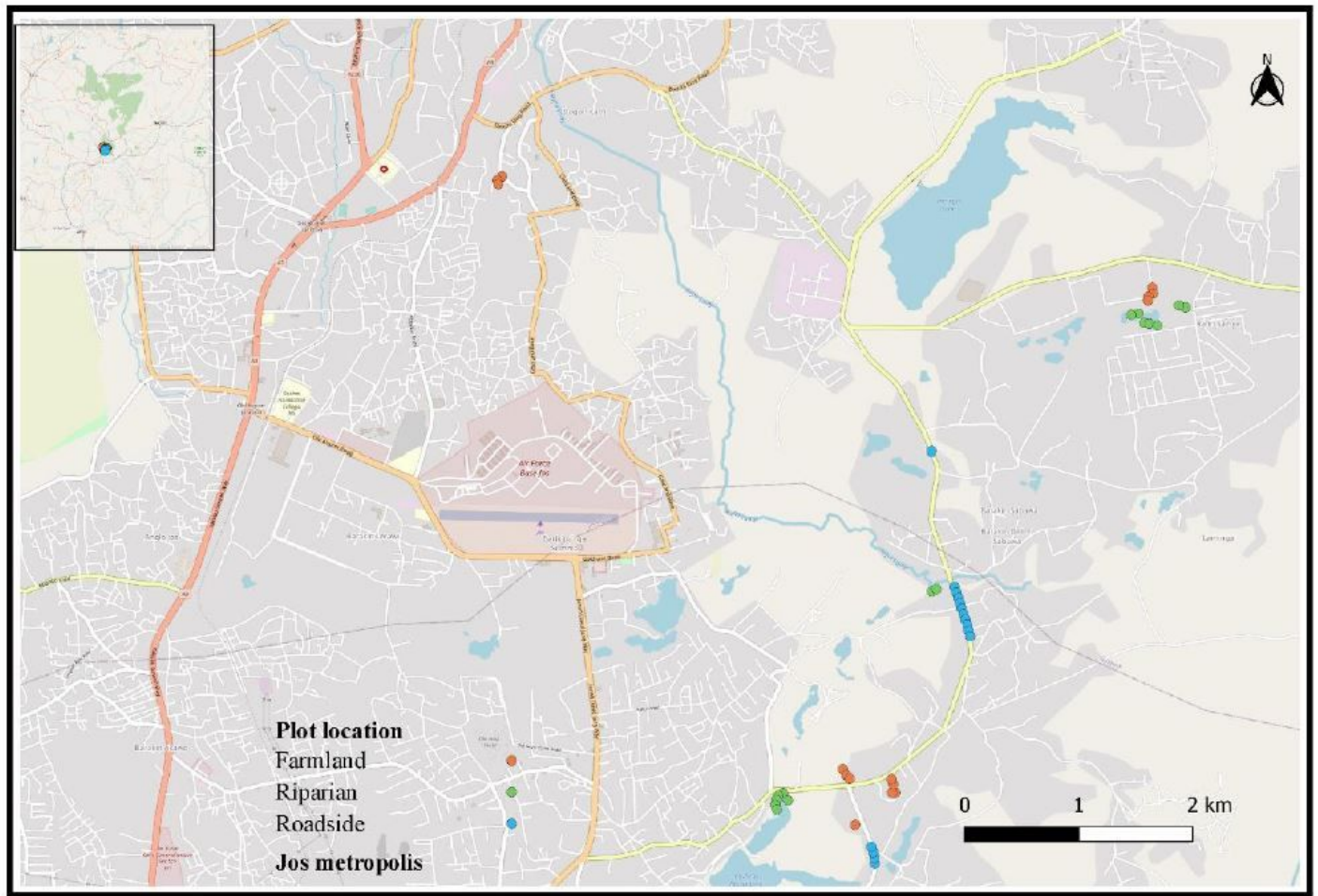


Figure 1

Map of Jos metropolis with distributions of the study plots Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

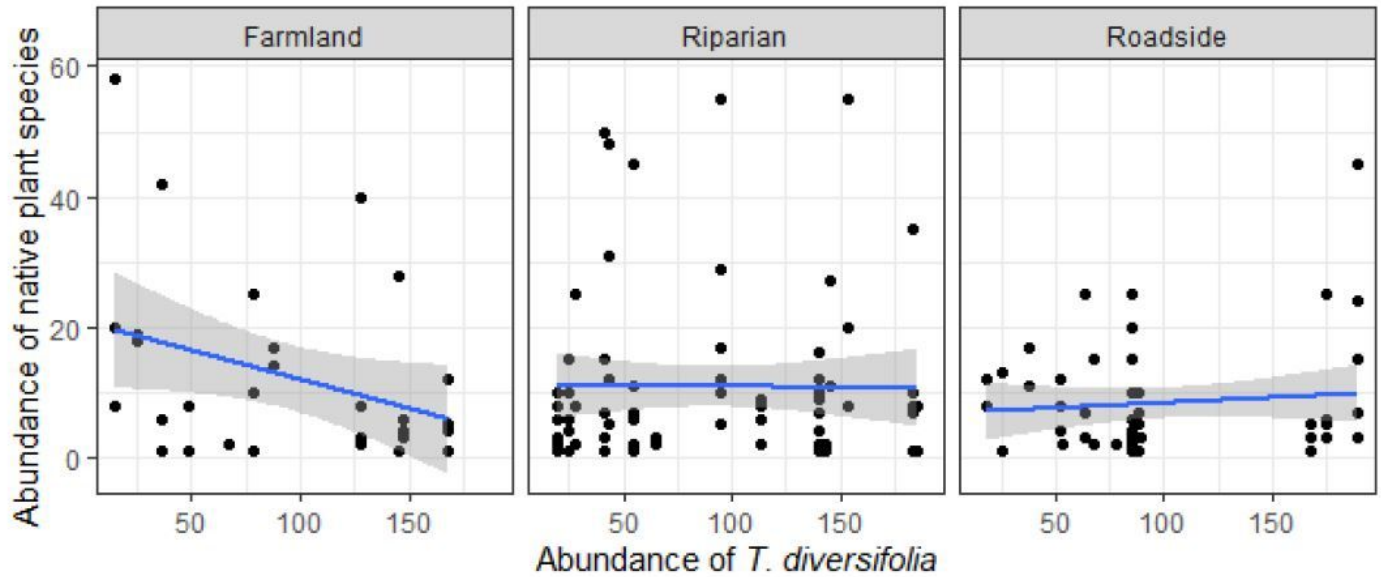


Figure 2

Relationships between the abundance of native species and *T. diversifolia* abundance across land-use types. The figure shows linear relationships of the response variable (abundance of native plant species) depending on the predictor variable (abundance of *T. diversifolia*) on farmland, riparian, and roadside. Blue lines represent linear regressions, and grey shading shows the 95% confidence interval of the fit

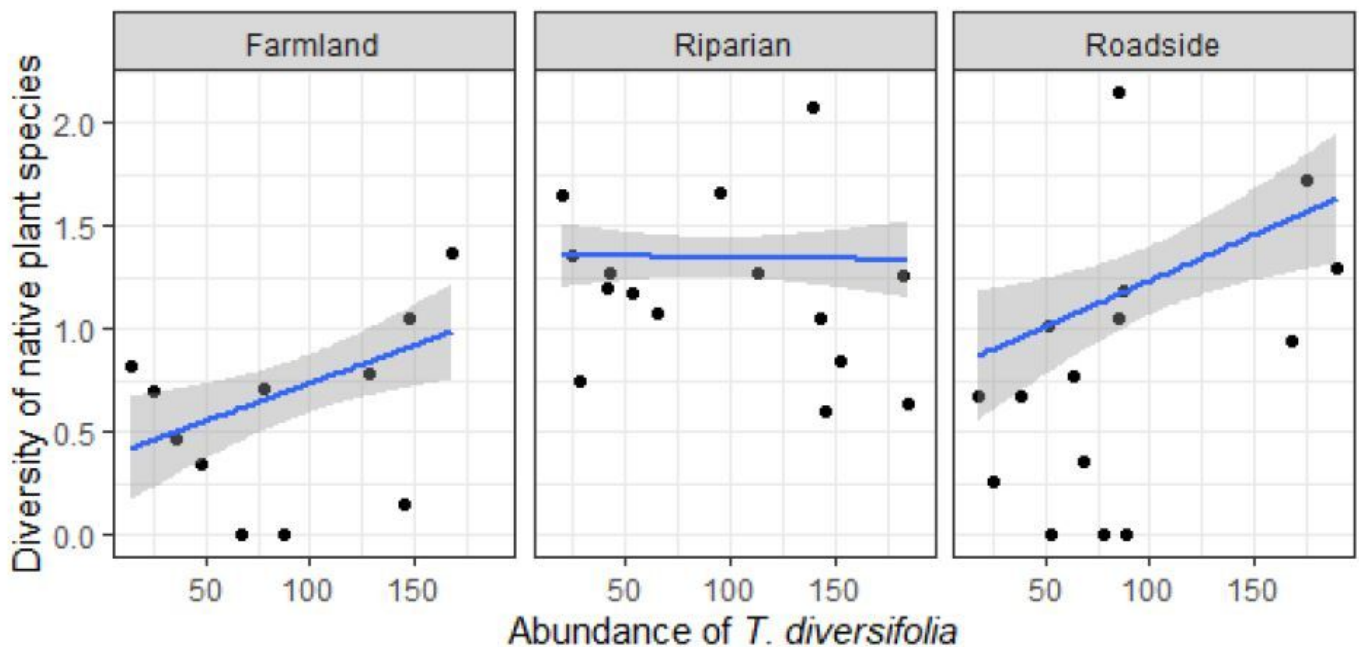


Figure 3

Relationships between the diversity of native species and *T. diversifolia* abundance across land-use types. The figure shows linear relationships of the response variable (diversity of native plant species) depending on the predictor variable (abundance of *T. diversifolia*) on farmland, riparian, and roadside. Blue lines represent linear regression lines and grey shading shows the 95% confidence interval of the fit

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [AnibabaetalSupportingMaterialBiologicalInvasions.pdf](#)