

Modelling the distribution of the invasive *Ziziphus mauritiana* along road corridors in Zimbabwe

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Abstract

We investigate how human fruit consumption affects the spread of the alien invasive *Ziziphus mauritiana* along road corridors in northern Zimbabwe. A field survey was conducted to identify and map *Z. Mauritiana* stems at 25 randomly located 6-ha plots placed along two main roads connecting the Zambezi Valley to the Highveld region. The *L*-function was used to test for evidence of significant spatial clustering of the stems. The inhomogeneous point model fitted by maximum likelihood was also applied to check whether distance from the road explains variation in the number of stems per unit area. Finally, a *t* test was executed on log-transformed abundance data to test for significant differences in the mean number of saplings and adults between the Zambezi Valley and the Highveld. Results of the *L*-function indicated that *Z. mauritiana* had a clustered and linear distribution along roads both in the Zambezi Valley and Highveld regions. Results of the *t* test showed that the mean number of saplings per plot in the Zambezi Valley ($\mu_1 = 275$) was three times higher than in the Highveld ($\mu_2 = 78$), with $p < 0.01$. The mean number of adult trees was also significantly higher in the Zambezi Valley than in the Highveld.

Résumé

Nous cherchons à comprendre comment la consommation humaine de fruits affecte la dispersion de la plante exotique envahissante *Ziziphus mauritiana* le long des corridors routiers du nord du Zimbabwe. Une étude de terrain a été réalisée afin d'identifier et de cartographier les plants de cet arbre dans 25 parcelles de six hectares prises au hasard le long de deux routes principales reliant la vallée du Zambèze à la région des prairies de haute altitude. Une fonction-*L* a été utilisée pour tester les preuves de regroupement spatial des plants. Le modèle de point non homogène en adéquation avec la probabilité maximale s'appliquait aussi pour vérifier si la distance jusqu'à la route explique les variations du nombre de plants par unité de surface. Enfin, un test de *T* a été réalisé sur les données d'abondance log-transformées pour tester des différences significatives dans le nombre moyen de plants jeunes et adultes entre la vallée du Zambèze et les prairies d'altitude. Les résultats de la fonction-*L* indiquaient que *Z. mauritiana* avait une distribution regroupée et linéaire le long des routes dans les deux régions. Les résultats du test de *T* montraient que le nombre moyen de jeunes plants par parcelle dans la vallée du Zambèze ($\mu_1 = 275$) était trois fois plus élevé qu'en altitude ($\mu_2 = 78$), avec $p < 0.01$. Le nombre moyen d'arbres adultes était aussi significativement plus élevé dans la vallée du Zambèze qu'en altitude.

KEYWORDS

invasive species, point pattern analysis, recruitment success, species distribution

1 | INTRODUCTION

Human-mediated species invasions are now a significant component of current global environmental change (Hobbs et al., 2006; Masocha, 2009). There is a growing body of evidence indicating that the rate at which ecosystems are accumulating alien (non-native) species is accelerating as free trade and globalisation advance (Lockwood, Cassey, & Blackburn, 2005). Understanding the mechanisms of spread of alien species, as well as their impact on ecosystems, is a priority for research given that invasive species are a major contributor to biodiversity loss, impairment of ecosystem services and ecosystem degradation (Lee, 2002). Previous work has shown that worldwide alien invasive species are the second largest contributor to loss of native biodiversity after habitat destruction (Keane & Crawley, 2002; Pyšek & Richardson, 2010). The economic losses caused by invasive species exceed billions of United States of America dollars globally (Van Wilgen, Richardson, Maitre, Marais, & Magadlela, 2001; Wilcove, Rothstein, Dubow, Phillips, & Losos, 1998). In Zimbabwe, invasive plant species have been implicated as a major driver of rangeland degradation with communally managed rangelands being more negatively affected than commercially managed rangelands (Gusha, Mugabe, Masocha, & Halimani, 2016).

While the ecological and economic consequences of invasions are well documented, the factors and mechanisms underlying the spread of invasive alien species across landscapes remain poorly understood. Nevertheless, previous research indicates that invasion success is often associated with multiple anthropogenic disturbances including road disturbance (D'Antonio, Dudley, & Mack, 1999; Gelbard & Belnap, 2003; Hobbs, 1989; Hobbs & Huenneke, 1992). A variety of abiotic and biotic variables related to environmental suitability and propagule pressure may interact in a complex way with anthropogenic disturbance to determine the spread and distribution pattern of invasive plants in a landscape (Albright, Anderson, Keuler, Pearson, & Turner, 2009; Lockwood et al., 2005). Relatedly, changes in the abiotic environment associated with road infrastructure have direct implications for plant growth. In addition, some studies have documented that propagule pressure of alien species tends to be higher along road corridors compared to areas farther away (Pauchard & Alaback, 2006). Here, the term propagule pressure is used to refer to the number, frequency and spatial extent at which seeds or propagules of alien species are introduced in a new environment. Thus, consistent with pathway models of invasion, one would expect that the more frequent propagules of an alien species are introduced to a location, the more likely is the invasion success (Hulme, 2009; Lippe & Kowark, 2007).

Using the invasive *Ziziphus mauritiana* (Chinese apple tree) as an example, this study investigates whether roads act as conduits for its invasion in savannah landscapes. *Ziziphus mauritiana* is one

of the most common invasive alien trees species in southern Africa (Coates-Palgrave, 2002). It is native to Southeast Asia but was probably first introduced in the eastern coastal regions of Africa from where it has spread inland along roads. The species produces edible fleshy fruits that are well sought after and consumed in large quantities by locals and visitors when travelling along roads. It is therefore hypothesised that high propagule pressure along road verges and favourable linear micro-habitats associated with road infrastructure (Spellerberg, 1998) are the key factors explaining the distribution of *Z. mauritiana* in a savannah landscape.

Currently in Zimbabwe, *Z. mauritiana* is found mainly in the Lowveld areas, such as the Zambezi Valley located at altitudes ± 600 m above mean sea level (m.s.l.), in the northern districts of Guruve, Mount Darwin and Centenary. It is thought that early Asian traders introduced the tree to this area about 300 years ago (Coates-Palgrave, 2002). The seeds are mainly dispersed by humans, elephants, cattle and birds (Grice, 1998). *Ziziphus mauritiana* is well-adapted to arid to semi-arid regions (Williams, Morgan, McDonnell, & McCarthy, 2005). Observations in Zimbabwe suggest that although the tree has successfully established in Highveld areas located at altitudes greater or equal to 1,000 m above mean sea level, such as Harare, the species fails to flower and reproduce under the humid conditions prevailing there. This is mainly caused by the fact that its fruits are most commonly utilised as wild fruits, particularly in Zimbabwe (Nyanga, Nout, Gadaga, Boekhout, & Zwietering, 2008). Moreover in Zimbabwe, the fruit undergoes spontaneous fermentation; hence, it is distilled into a potent spirit (Gadaga, Mutukumira, Narvhus, & Feresu, 1999; Tredgold, 1986).

Although *Z. mauritiana* is one of the most widespread invaders in tropical ecosystems, most previous studies have concentrated on its economic value (Grice, 1998). Hence, not much is known about the ecological factors explaining its spread and distribution pattern in invaded landscapes. The following two hypotheses were tested in this study: (a) high propagule pressure explains the widely observed linear and clustered distribution of *Z. mauritiana* along major roads; and (b) in Zimbabwe, the recruitment and establishment success rates of *Z. mauritiana* are influenced by altitude, which is greater in the Zambezi Valley than the Highveld region. The aim of this study was to model and explain the spatial distribution pattern of *Z. mauritiana* along road corridors in Zimbabwe in relation to altitude. Understanding the pattern of invasion and ecological factors determining that pattern is important for controlling the further spread of this invasive species.

2 | MATERIALS AND METHODS

2.1 | Study site

Data on the occurrence and abundance of *Z. mauritiana* were collected during the peak of the growing season in February of 2011, along two main roads that connect the Zambezi Valley with

Harare (Zimbabwe's capital). The Zambezi Valley is located at altitudes around ± 380 m above m.s.l, and Harare is situated at around 1,749 m above m.s.l. The Zambezi Valley has a dry tropical climate, characterised by low and variable annual rainfall averaging between 450 and 650 mm per year and a mean annual temperature of 25°C. The area has two clearly defined seasons: a wet season (December–March) and a long dry season (April–November). The natural vegetation is mainly deciduous dry savannah that includes *Colophospermum mopane*, *Combretum* woodlands and riparian vegetation. Two main roads that originate in the Zambezi Valley and connect it with the Highveld region were selected for field survey (see Figure 1). Based on the high spatial resolution imagery available from Google Earth, the Guruve to Angwa and the Centenary to Muzarabani roads were digitised using heads-up digitising. For simplicity, the Guruve–Angwa road is hereafter referred to as the Guruve road while the Centenary–Muzarabani road is hereafter referred to as the Centenary Road. The road layers were exported in keyhole mark language (kml) format to a GIS software (Arcview version 3.2), which was used to randomly select 25 sample points along each selected road (Figure 2). The coordinates of each point were fed into a handheld global positioning system (GPS) receiver (Garmin etrex), which was used to locate them in the field. Each

plot extended 30 m on either side of the road and was 1,000 m in length. Thus, each plot was 3 ha in size.

2.2 | Data collection

Data on the number of *Z. mauritiana* saplings and adults were collected from each of the 25 sample plots. Saplings were defined as stems with a diameter at breast height (dbh) of <5 cm while adults were stems with a dbh (measured at 1.3 m) >5 cm following as described in Baroti, Gignox, and Mencil (1999). Apart from counting the number of stems belonging to these two life-stages, the location of each *Z. mauritiana* stem identified was mapped using a GPS. The GPS receiver was also used to measure the altitude of each plot. To obtain a fine scale map of the distribution of stems, first, a reference stem (usually the tallest and/or centrally located individual) was chosen and its location was measured with a GPS. The bearing, that is the angle each individual stem was from the reference stem,

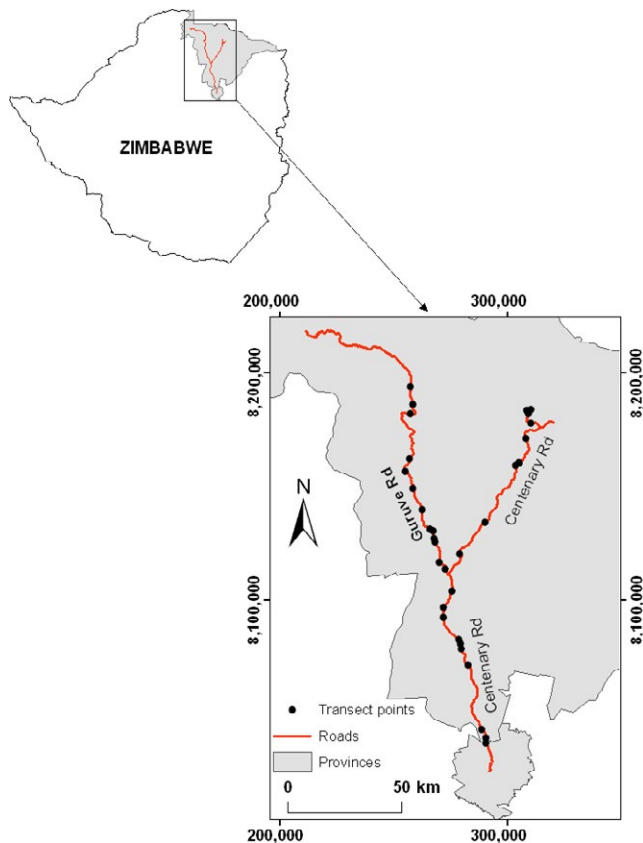


FIGURE 1 Location of the study site in Mashonaland Central Province (shaded area) of Zimbabwe. Black circles represent sampled plots distributed randomly along the Guruve and Centenary roads leading into the Zambezi Valley [Colour figure can be viewed at wileyonlinelibrary.com]

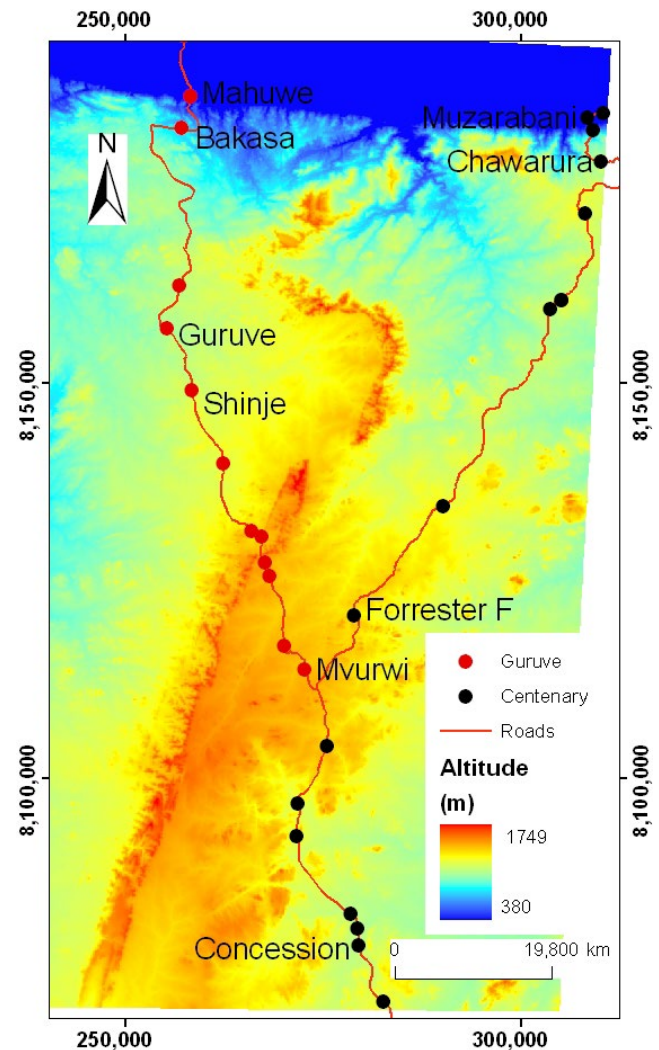


FIGURE 2 Spatial variation in altitude along the selected road transects in northern Zimbabwe. The coordinates are in Universal Transverse Mercator [Colour figure can be viewed at wileyonlinelibrary.com]

was measured clockwise using a compass. The distances other stems were from the reference stem was measured using a tape measure. The x - y coordinates of each stem with respect to the reference stem were computed using the radiation method as:

$$x_n = x_1 + r * \sin \theta * \pi / 180 \quad (1)$$

$$y_n = y_1 + r * \cos \theta * \pi / 180 \quad (2)$$

where x_1 and y_1 are the x and y coordinates of the reference tree, respectively; x_n and y_n denote the x and y coordinates of the target

stem, respectively; r = distance from base of the reference tree stem to the base of the target stem; $\sin(\theta)$ and $\cos(\theta)$ are the sine and cosine of the bearing measured at the target stem.

2.3 | Statistical analysis

For each plot, the L -function was applied on geo-referenced point data to test for evidence of significant spatial clustering of *Z. mauritiana* stems. The observed point patterns were compared against the null hypothesis of complete spatial randomness. Rather than assume

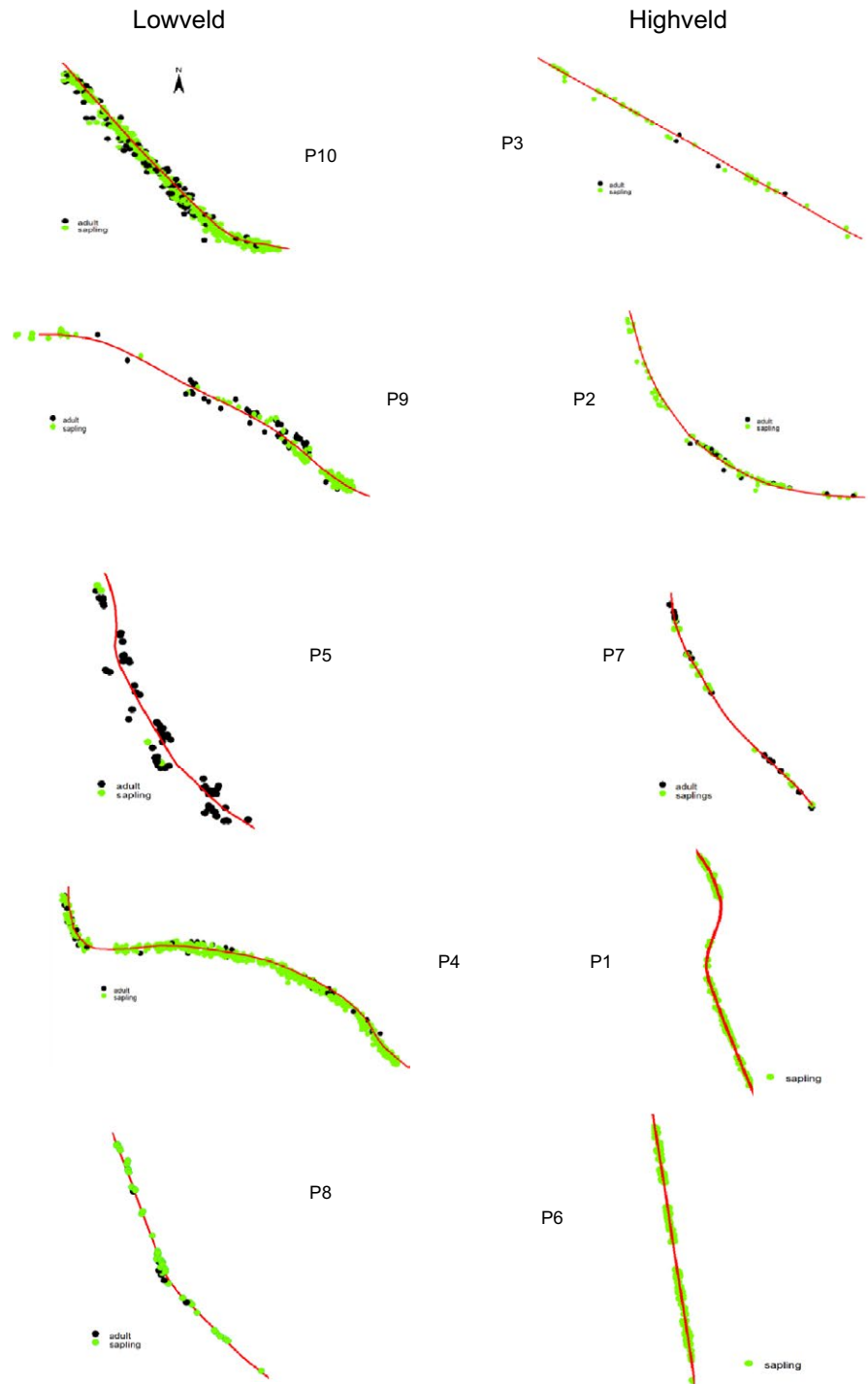


FIGURE 3 Point maps indicating distribution of *Ziziphus mauritiana* along sampled road stretches in the Lowveld and the Highveld areas of Zimbabwe. The maps shown are only for plots in which more than 40 stems were identified and geolocated [Colour figure can be viewed at wileyonlinelibrary.com]

the point process is stationary, the L -function was modelled as a heterogeneous Poisson process. Since the underlying distribution of spatial point processes is not known, Monte Carlo computer simulations were performed to generate 95% confidence envelopes (Stoyan & Penttinen, 2000). Significant spatial clustering was inferred if the observed curve for the L -function was above the theoretical curve for a heterogeneous Poisson point process and outside the 95% confidence envelope. Where the observed curve for the L -function was

below the theoretical and outside the 95% confidence envelope, the pattern was interpreted as regular. If the observed L -function overlaid the theoretical curve, the point pattern was interpreted as random. In the graphical display of the results of a random sample of 10 plots presented, the L -function is plotted against distance in metres. All spatial point pattern analyses were undertaken using spatstat (Baddeley & Turner, 2005), which runs under the open source R statistical software version 2.9.1 (R Development Core Team, 2009).

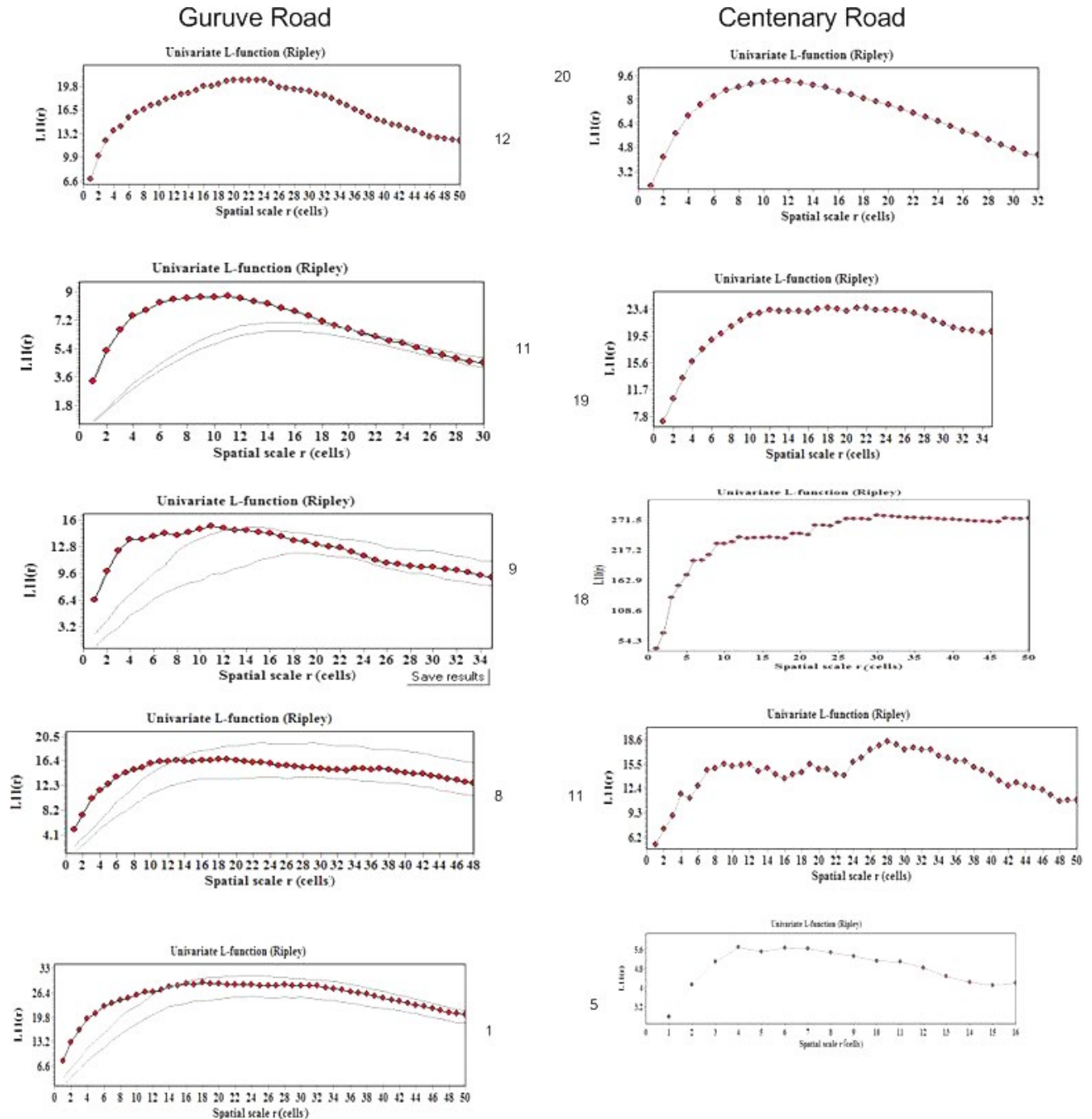


FIGURE 4 Univariate L -function plots indicating how the pattern of *Ziziphus mauritiana* changes with distance from roads along two major roads leading to the Zambezi valley in northern Zimbabwe. Significant spatial clustering of stems is indicated by the observed curve for the L -function which is above and outside the 95% simulation envelopes [Colour figure can be viewed at wileyonlinelibrary.com]

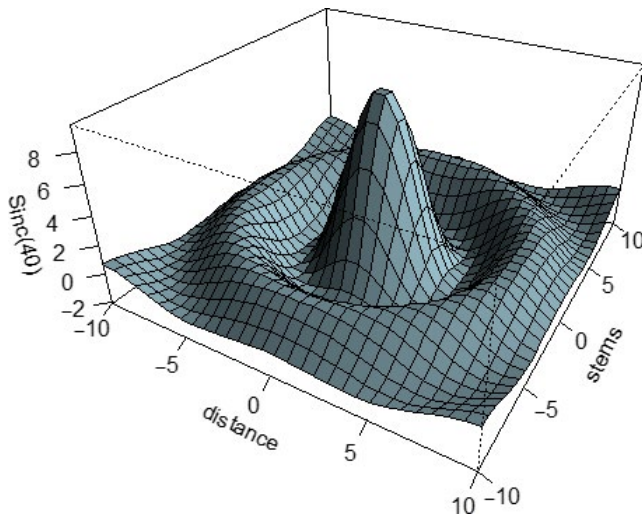


FIGURE 5 A perspective plot indicating the relationship between distance from the road and the conditional intensity (number of *Ziziphus mucronata* stems per unit area) based on a point model fitted to data from northern Zimbabwe. The conditional intensity is displayed on the vertical axis [Colour figure can be viewed at wileyonlinelibrary.com]

To test whether the number of stems (intensity) changes significantly with distance from the road, first, the vector layer of the digitised road was imported into spatsat. Then, the inbuilt distance function was used to calculate the distance in metres from the road to the plot edge. This operation generated a distance map, which was a surface. Finally, the inhomogeneous point process model with distance extracted from the distance map as the explanatory variable was fit by maximum likelihood to explain the variation in intensity of events. The intensity of events corresponds with the number of stems per unit area. This was the response variable. This analysis was done using spatstat in R software.

In the third analysis, a *t* test was performed on log-transformed count data to test for significant differences in the mean number of saplings and adults between the Zambezi Valley and the Highveld areas. To execute the *t* test, data on all plots that were located at an altitude higher than or equal to 1,200 m a.s.l. belonged to the Highveld sample group, whereas those data obtained from plots

located at an altitude ≤ 900 m a.s.l. constituted the Zambezi Valley sample group. Data on differences in the form of error plots indicate means at $\pm 95\%$ confidence level. The *t* test was run using Statistica version 7.0 (StatSoft, Inc.).

3 | RESULTS

The distribution of *Z. mauritiana* indicated a linear clustered pattern. Figure 3 presents the results of ten plots in which with 45 or more *Z. mauritiana* stems were recorded and mapped in the field. Regardless of whether the plots were from the Lowveld or Highveld, the data in Figure 3 indicate aggregation of stems along roads. The results for the *L*-function confirmed significant spatial clustering of the stems up to a distance of 20 m from the road edge (see Figure 4).

The results of the fitted point model indicated that the distribution of stems display a spatial trend related to distance from the road (Figure 4). The spatial trend was characterised by a sharp decrease in intensity of *Z. mauritiana* species within the vicinity of roads. Further, the spatial trend conditioned by distance indicates a second peak at a distance of 10 m from the road followed by a gradual decrease in the intensity of *Z. mauritiana* as distance from the road increased (Figure 5).

The results of the *t* test indicate significant differences between the Highveld and Lowveld both in the mean number of saplings and adult *Z. mauritiana* plants (see Figure 6). Specifically, the mean number of saplings in the Lowveld was 275, which was significantly ($p < 0.01$) higher than that for the Highveld with a mean of 78 saplings per 3-ha plot. The result for adult stems followed the same pattern. The mean number of adult stems in the Lowveld was 60. This was six times higher than the mean of nine adults for the Highveld sample. This difference was also statistically significant ($p < 0.01$).

4 | DISCUSSION

This study investigated the potential role of human fruit consumption in aiding invasion by a fleshy fruited introduced invasive

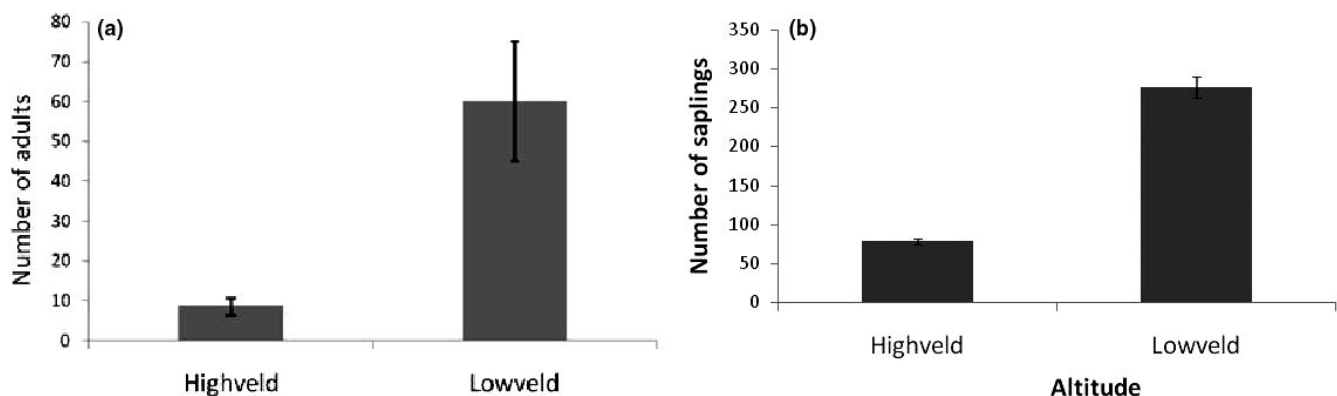


FIGURE 6 Error plots showing differences between the Highveld and the Lowveld areas of Zimbabwe in the number of adult (a) and sapling (b) *Ziziphus mucronata* plants. Bars indicate means and whiskers represent 95% confidence intervals

species *Z. mauritiana* along road corridors in northern Zimbabwe. The findings of this study demonstrate significant spatial clustering of *Z. mauritiana* stems. Specifically, the distribution of stems was linear and aggregated. This result is in line with previous results that reported roads act as conduits of alien plant species invasions in terrestrial ecosystems (Lockwood et al., 2005; Pauchard & Alaback, 2006). High propagule pressure along the road edges likely explains the linear pattern of invasion reported in this study. Sites farther away from the introduction locus, in this case roads, tended to be less invaded by *Z. mauritiana* compared to those further away and this is in agreement with previous work (Albright et al., 2009). The decline in the number of established stems with distance from the road was also noted previously (Gelbard & Belnarp, 2003) but the contribution of the current study lies in highlighting the important role human consumption of fruits play in facilitating invasion along roads. In this study, a linear distribution pattern of stems controlled by road geometry was observed regardless of whether the sampled plots were drawn from the Lowveld or Highveld regions. This finding implies by consuming the fruits and throwing them out of vehicles, people act as main vectors of seed dispersal and the enhanced propagule pressure along roads correlate with establishment success.

Another inference that can be drawn from the findings in this study is that road disturbance, in particular the removal of native biomass, reduces plant competition while at the same time creates gaps. Thus, *Z. mauritiana* may be exploiting these vacant niches as suggested in previous work (Alston & Richardson, 2006). The findings of the present study also suggest clear differences exist in the environmental conditions influencing establishment success or failure. The difference in recruitment success and establishment success between the Zambezi Valley and the Highveld is explained by the source-sink dynamics (Farina, 2008). The Zambezi Valley has higher recruitment and establishment success since it is the main source of propagules that are dispersed to the Highveld regions and within the source area, regeneration seems to exceed death. In the Highveld, recruitment and establishment are lower because the ability of trees to reproduce decreases with increasing altitude. The results imply that in the Highveld, land managers need to devote effort to trimming the species and chemically treating the stump to avoid sprouts. *Ziziphus mauritiana* tolerates or benefits from mutilation. Its roots are also deep (Grice, 1998) so mechanical treatment would not be effective.

5 | CONCLUSION

The study aimed at establishing the occurrence of *Z. mauritiana* with distance from the road as a factor. The study concluded that there is an inverse relationship between the occurrence of *Z. mauritiana* and distance from the road. High propagule pressure associated with human consumption of the fruits is likely the main ecological factor explaining the aggregated and linear distribution patterns of established stems. The study also concluded that recruitment and establishment success is higher in the Zambezi Valley, which is the

source region compared to the Highveld region, which act as the sink habitat.

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