

Landscape configuration drives fall armyworm dominance over native stemborers in smallholder maize systems in the Congo Basin

Onésime Kankonda

`onesime.kankonda@unikis.ac.cd`

Université de Kisangani

Rosette Akiki

Université de Kisangani

Maurice Pandashalo

Université de Kisangani

Trésor Selemani

Université de Kisangani

Joël Kabuanga

Université du Bas-Uélé

Marcellin Cokola

Université Evangélique en Afrique

Sylvain Ntambo Mbuya

Université de Kolwezi

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Abstract

Landscape configurational and compositional attributes play crucial roles in shaping pest dynamics within tropical agroecosystems, yet their influence on interactions between invasive and native maize pests remains poorly understood. We surveyed maize fields across six landscapes in the Congo Basin and used statistical models to assess how landscape complexity and habitat aggregation affect infestations by the invasive fall armyworm (*Spodoptera frugiperda*) and native stemborers. Here we show that fall armyworm infestations dominate, reaching up to 93%, and are positively associated with complex, aggregated landscapes characterized by high fractal dimension and contagion, while native stemborer presence declines under these conditions. Increased forest cover and edge density reduce fall armyworm infestations. These findings reveal that landscape configuration drives an ecological shift favoring invasive pest dominance, highlighting the need for landscape-informed and regionally adaptable integrated pest management strategies in tropical maize systems.

1. Introduction

The fall armyworm (*Spodoptera frugiperda* J.E. Smith, Lepidoptera: Noctuidae) (FAW) is one of the world's most destructive invasive pests of maize. Native to the Americas, it has rapidly expanded across Africa, Asia and, more recently, Europe, causing substantial yield losses and threatening food security across continents (Goergen et al., 2016; Sharanabasappa et al., 2018; Xiao-xu et al., 2021; Cean et al., 2024). Its exceptional dispersal capacity, broad host range, and remarkable ecological plasticity, defined as the ability to adapt to a wide range of environmental conditions, make it an important model organism for examining pest dynamics at a global scale (Johnson, 1987; Tay et al., 2023; Zhao et al., 2023).

In sub-Saharan Africa, maize hosts a community of native stemborers, primarily *Busseola fusca* and *Sesamia calamistis* (Lepidoptera: Noctuidae) (Ong'amo et al., 2014; Kankonda et al., 2017; Moeng et al., 2018). The arrival of FAW has substantially altered these pest assemblages, not only increasing overall infestation pressure but also shifting the relative dominance of native species (Ntiri et al., 2019; Hailu et al., 2021). Following oviposition on maize leaves, FAW larvae initially feed on foliage before burrowing into the whorl, where they often encounter stemborers such as *B. fusca* (Kenis et al., 2023; Sokame et al., 2021; Mutyambai et al., 2022). After completing larval development, FAW larvae pupate in the soil, and the emerging moths disperse to colonise neighbouring fields (Sparks, 1979; Hardke et al., 2015).

Globally, numerous studies have shown that landscape heterogeneity influences how insect pests disperse, establish, and persist within crop patches (Chaplin-Kramer et al., 2011; Macfadyen et al., 2011; Doehler et al., 2023). Yet, the strength and direction of these effects depend strongly on species traits, such as dispersal ability, feeding breadth, and foraging behaviour (Tscharntke & Brandl, 2004; Martin et al., 2019; Rother et al., 2025). Despite growing interest in landscape-mediated pest ecology, the mechanisms by which landscape structural and configurational heterogeneity shape FAW populations remain poorly understood, particularly in tropical smallholder farming systems, where the impacts of this invasive pest are most acute. Improving this understanding is essential for predicting pest outbreaks

and designing resilient management strategies in the context of agricultural intensification and climate change (Mazzi & Dorn, 2012 ; Rusch, 2022).

Here, we propose that landscape spatial heterogeneity acts as a selective ecological filter, favouring highly mobile and generalist invaders such as FAW while constraining less mobile, specialist native stemborers (Chaplin-Kramer et al., 2011; O'Reilly-Nugent et al., 2016). Accordingly, we hypothesise that FAW responds more positively to landscape complexity and habitat aggregation than native stemborers, resulting in contrasting infestation patterns across heterogeneous maize landscapes. Because insect responses to landscape structure are scale dependent, particularly in highly dispersive species, we further expect these effects to be detectable at the landscape scale relevant to FAW movement and colonisation dynamics.

Therefore, this study aims to assess how key landscape attributes, specifically patch shape complexity, forest proportion, habitat aggregation, and edge density, influence maize infestation by FAW and native stemborers across a tropical lowland forest landscape.

2. Materials and methods

2.1. Description of the surveyed region

The study was conducted in the hinterland of Kisangani (0°30'0" N, 25°12'0" E; 430 m a.s.l.) (Figure 1). The area is predominantly characterised by a mixed semi-evergreen Guineo – Congolian rainforest, which constitutes most of the native vegetation (White, 1983; Lebrun & Gilbert, 1954). The rainfall pattern is bimodal, with rains occurring mainly from March to June (the first rainy season) and from September to December (the second rainy season). Mean annual rainfall is approximately 1,837 mm, while mean monthly temperatures generally fluctuate around 25.1°C (Likoko et al., 2019; Yakusu et al., 2023).

2.2. Sampling design

Maize infestations by FAW and stemborers was surveyed across six sites: Bangoka 1 (N 00°28'105"; E 025°12'147"; 426 m a.s.l.), Masako (N 00°35'09.4"; E 025°14'59.1"; 429 m a.s.l.), Bawi (N 00°42'325"; E 025°12'147"; 426 m a.s.l.), Malimba (N 00°43'151"; E 025°15'819"), Bangoka 2 (N 0°29'19.74"; E 25°12'29.71"; 428 m a.s.l.), and Mobi (N 0°22'36.48"; E 025°22'42.82"; 422 m a.s.l.). Larvae of FAW and stemborers were collected from 31 maize fields managed by smallholder farmers, mainly at the maize pre- tasselling stage.

Each field was divided into four sections, with a 25 m² quadrat established in each section. The total number of maize plants, the number of plants infested exclusively by FAW or stemborers, and those showing symptoms of co-infestation were recorded. To determine the composition of lepidopteran pest community, ten infested maize plants were randomly selected from each quadrat and dissected to

collect larvae. Maize crop age, expressed in weeks, was recorded for each field following the developmental stages described by Ritchie et al. (1997).

2.3. Landscape index generation

A Sentinel-2 image with a spatial resolution of 20×20 m, projected in WGS 1984 UTM Zone 35N, acquired in September 2022, was used to derive the landscape indices. Around each central field within the sampled sites, a circular buffer with a radius of one kilometre was delineated, resulting in six landscapes buffers, each covering approximately 3.14 km² (Figure S1). The Random Forest machine-learning algorithm (Breiman, 2001; Liaw & Wiener, 2002) implemented in Google Earth Engine (Gorelick et al., 2017), was used to quantify the total proportion of forest (FP), including both primary and secondary forests. Three additional indices describing landscape complexity were calculated using FRAGSTATS (McGarigal & Marks, 1995): fractal dimension (FD), edge density (ED), and contagion (CONTAG). These four indices were selected as explanatory variables to assess the effects of landscape attributes on maize infestation by FAW and stemborers. Because recovery of larvae is difficult and may underestimate actual pest pressure, the proportion of infested plants was used as the response variable, as it provides a more robust indicator of the impact of FAW and stemborers (Koffi et al., 2022; Siaw et al., 2024).

2.4. Statistical data analysis

To evaluate the influence of landscape structure on pest pressure, the percentage of maize infestation was modelled using a generalised additive mixed model (GAMM) implemented in the `mgcv` package (Wood, 2017). Infestation was specified as a binomial response, with fractal dimension, forest proportion, edge density, and contagion included as smooth terms ($k = 3-5$).

To account for the hierarchical sampling design, in which multiple maize fields were nested within six landscape buffers, random effects were incorporated to address the non-independence of observations. In the GAMM, site (landscape buffer) and crop age were specified as random intercepts, thereby accounting for spatial dependence and temporal variation among fields. This structure ensured that the estimated effects of landscape variables represented genuine ecological relationships rather than artefacts of sampling design. Model fits were visualised using `ggplot2` (Wickham, 2016), and residual diagnostics indicated a good model fit, with residuals symmetrically distributed around zero and no evident systematic patterns (Figure S2).

To investigate the joint responses of FAW and stemborers to landscape structure, a distance-based redundancy analysis (dbRDA) was conducted in the `vegan` package (Oksanen et al., 2022). A Bray–Curtis dissimilarity matrix was generated from the infestation data, using the same four landscape predictors. The significance of the global model and individual marginal terms was assessed using 999 permutations.

Finally, a hierarchical modelling of species communities (Hmsc) (Ovaskainen & Abrego, 2020) was applied to jointly model FAW and stemborer infestations as a function of FD, FP, ED, and CONTAG. Four Markov Chain Monte Carlo (MCMC) chains of 10,000 iterations each were run, and convergence was evaluated using Gelman–Rubin diagnostics (Gelman et al., 2013). Posterior regression coefficients were used to quantify species–environment relationships, while residual species-to-species correlations (Ω) were examined to identify potential co-infestation patterns unexplained by environmental predictors (Tikhonov et al., 2020). Site was treated as a random factor to account for the shared environmental context within each landscape and to enable joint inference on FAW and stemborer responses. All analyses were conducted in R version 4.5.1 (R Core Team, 2025), with statistical significance set at $\alpha = 0.05$.

3. Results

3.1. Site-specific variation in infestation rates of FAW and stemborers

Infestation rates varied markedly among sites (Table 1). Mobi and Bawi recorded the highest total infestation rates (0.94 ± 0.01 and 0.65 ± 0.04 , respectively), whereas Malimba showed the lowest (0.19 ± 0.12). FAW was the predominant pest, with its incidence closely mirroring the overall infestation pattern and peaking at Mobi (0.93 ± 0.01). Stemborer infestation remained consistently low, reaching a maximum of 0.037 ± 0.008 ($\times 100$) at Bawi and being absent at Masako. Co-occurrence of FAW and stemborers was rare, with the highest values observed at PK17_2 ($0.028 \pm 0.019 \times 100$) and Masako ($0.024 \pm 0.024 \times 100$). These results indicate that infestation pressure was largely driven by FAW, while stemborers and co-infestations contributed minimally across sites.

3.2. Effect of landscape attributes on maize infestation by FAW

The generalised additive mixed model (GAMM) analysis indicated that landscape attributes significantly influenced the probability of maize infestation by FAW, explaining 73% of the observed variation (adjusted $R^2 = 0.729$) (Figure 2; Table S1). Fractal dimension was associated with a substantial increase in infestation probability, suggesting that more complex and irregular patch shapes promote FAW establishment ($p = 0.0325$). In contrast, forest proportion exerted a strong negative effect ($p < 0.001$), with greater forest cover significantly reducing infestation probability. Edge density also showed a significant negative relationship with infestation ($p < 0.001$), implying that highly fragmented landscapes with extensive edge environments were associated with lower infestation probabilities. Conversely, contagion exhibited a positive relationship with infestation ($p = 0.0019$), indicating that increased habitat aggregation may facilitate pest spread and persistence.

3.3. Contrasting responses of FAW and stemborers to landscape spatial heterogeneity

The dbRDA revealed that the global model was highly significant ($F = 11.43$, $p = 0.001$), indicating that the selected landscape attributes explained a substantial proportion of the variation in maize pest infestations by FAW and stemborers (Table S2). Among the predictors, fractal dimension was the dominant driver ($F = 34.91$, $p = 0.001$), followed by contagion ($F = 7.02$, $p = 0.017$). Forest proportion had a marginal effect ($F = 3.78$, $p = 0.060$), while edge density had a negligible effect ($F = 0.01$, $p = 0.970$). Species scores revealed contrasting responses along the dbRDA axes: FAW exhibited a positive association with the first dbRDA axis (0.672 on dbRDA1), whereas native stemborers showed a negative association (-0.538 on dbRDA1). This pattern indicates that landscape complexity and patch aggregation promote FAW abundance while limiting stemborer occurrence (Table S3). The Hmsc β -coefficients further confirmed these divergent species–landscape relationships (Figure 3). FAW infestation was positively associated with fractal dimension, consistent with the dbRDA results indicating higher infestation in landscapes with greater patch irregularity and complexity. In contrast, stemborer infestation was negatively associated with fractal dimension, suggesting that complex landscape structure hinders their colonisation. Baseline infestation levels were higher for stemborers than for FAW. However, other predictors, including forest proportion, edge density, and contagion, exerted minimal influence on either pest within the Hmsc framework (Table S4). Taken together, the dbRDA and Hmsc approaches consistently identified fractal dimension as a key landscape attribute shaping pest dynamics, with contrasting effects on the invasive FAW and native stemborer species.

4. Discussion

The strong dominance of fall armyworm (FAW) observed in this study likely results from the interaction between its invasive traits and the spatial structure of the landscape. FAW's high dispersal capacity, rapid reproductive rate, and broad host range confer a clear advantage over native, more oligophagous stemborers (Day et al., 2017; Montezano et al., 2018). Similar declines in resident stemborer populations following FAW invasion have been reported across sub-Saharan Africa and India (Ntiri et al., 2019; Divya et al., 2021; Hailu et al., 2021), mirroring earlier cases of competitive displacement in African maize systems, such as the replacement of *Busseola fusca* by *Chilo partellus* (Kfir, 1997; Mutamiswa et al., 2017). The limited co-occurrence observed in this study likely reflects differences in phenology, resource use, and environmental tolerance, resulting in asymmetric competitive outcomes (Sokame et al., 2021).

Beyond species traits, our results showed that pest infestations were strongly influenced by landscape configuration, quantified using fractal dimension, contagion, and edge density. FAW abundance increased with higher fractal dimension and contagion, indicating that irregular and spatially aggregated landscapes may enhance dispersal and colonisation by highly mobile generalists (Chaplin-Kramer et al., 2011; O'Reilly-Nugent et al., 2016). Recent studies have confirmed that landscape configuration attributes can shape insect responses independently of landscape composition by modifying connectivity, movement pathways, and encounter rates (Martin et al., 2019; Hederström et al., 2025). Comparable effects have been reported for other invasive insects, including *Bactrocera dorsalis*, whose spread varied according to landscape spatial configuration (Wen et al., 2023).

In contrast, FAW responded negatively to increasing edge density, suggesting that high fragmentation may disrupt effective dispersal and reduce colonisation efficiency. This pattern is consistent with evidence that excessive edge density can increase mortality risk, reduce host continuity, or generate dispersal thresholds for invasive insects (With & Crist, 1995; Wen et al., 2023; Fahrig et al., 2011). Stemborers showed the opposite response, with lower abundances in highly complex landscapes, consistent with their dependence on stable, grass-dominated habitats that provide alternative hosts outside the maize-growing season (Le Ru et al., 2006; Mailafiya et al., 2009). Unlike FAW, these less mobile specialists appear to be regulated primarily by landscape composition rather than spatial configuration (Tscharntke & Brandl, 2004). Overall, our findings highlight that landscape heterogeneity can have contrasting effects on invasive and resident pests, highlighting the need to explicitly distinguish between landscape composition and configuration in landscape-level pest management. These results suggest that landscape-level interventions aimed at pest suppression should explicitly account for spatial configuration to avoid inadvertently favouring invasive, highly mobile pests such as fall armyworm.

5. Conclusion

Overall, our results show that fall armyworm (FAW) infestation increases with landscape complexity and patch aggregation, whereas native stemborers decline under the same conditions. These findings highlight the need to move beyond field-level approaches and explicitly consider both landscape composition and spatial configuration in pest management. Strategies that promote habitat diversity or forest cover should therefore account for spatial arrangement to avoid unintentionally favouring highly mobile invasive pests such as FAW. Future research should assess the role of natural enemies across landscape gradients and integrate long-term monitoring with landscape-simulation models to identify spatial configurations that limit FAW outbreaks while supporting biodiversity and smallholder livelihoods.

Declarations

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Author contributions

O.M. **Kakonda** contributed to conceptualization, methodology, project administration, supervision, formal analysis, writing the original draft, and review and editing. R.B. **Akiki** contributed to methodology, data collection, and review and editing. M.Z. **Pandashalo** contributed to methodology, data collection, and review and editing. T.M. **Selemani** contributed to data analysis. J.M. **Kabuanga** contributed to review and

editing. M.C. **Cokola** contributed to writing, review and editing. S.N.**Mbuya** contributed to writing, review and editing. All authors reviewed and approved the final version of the manuscript

Data availability

No datasets were generated or analysed during the current study

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest

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Table

Table 1. Mean ($\pm$ SE) infestation rates of maize by FAW(*Inf_Sf*), stemborers (*Inf_Sb*), and their co-occurrence across sites. *Inf_total* represents overall infestation. Within a column, values with the same letter are not significantly different.

Site	N	Inf_total	Inf_Sf	Inf_Sb (x 100)	Co_occur (x 100)
Bawi	15	0.65 $\pm$ 0.04ab	0.61 $\pm$ 0.03a	0.04 $\pm$ 0.01a	0.006 $\pm$ 0.004a
Malimba	2	0.19 $\pm$ 0.12a	0.16 $\pm$ 0.13b	0.01 $\pm$ 0.01a	0.017 $\pm$ 0.017a
Masako	3	0.48 $\pm$ 0.10ab	0.36 $\pm$ 0.01b	0a	0.024 $\pm$ 0.024a
Mobi	2	0.94 $\pm$ 0.01b	0.93 $\pm$ 0.01a	0.01 $\pm$ 0.01a	0a
PK17_1	4	0.52 $\pm$ 0.02ab	0.51 $\pm$ 0.03ab	0.003 $\pm$ 0.003a	0.007 $\pm$ 0.007a
PK17_2	5	0.41 $\pm$ 0.08ab	0.38 $\pm$ 0.03b	0.001 $\pm$ 0.001a	0.028 $\pm$ 0.019a
χ^2		14,544794	20,091532	10,082529	6,316759
P		0,01249517	0,001201253	0,072930314	0,276605385

Figures

Image not available with this version

Figure 1

Map of maize sampling sites near Kisangani, DRC, showing major land-cover types used to assess how landscape structure influences *Spodoptera frugiperda* infestation patterns

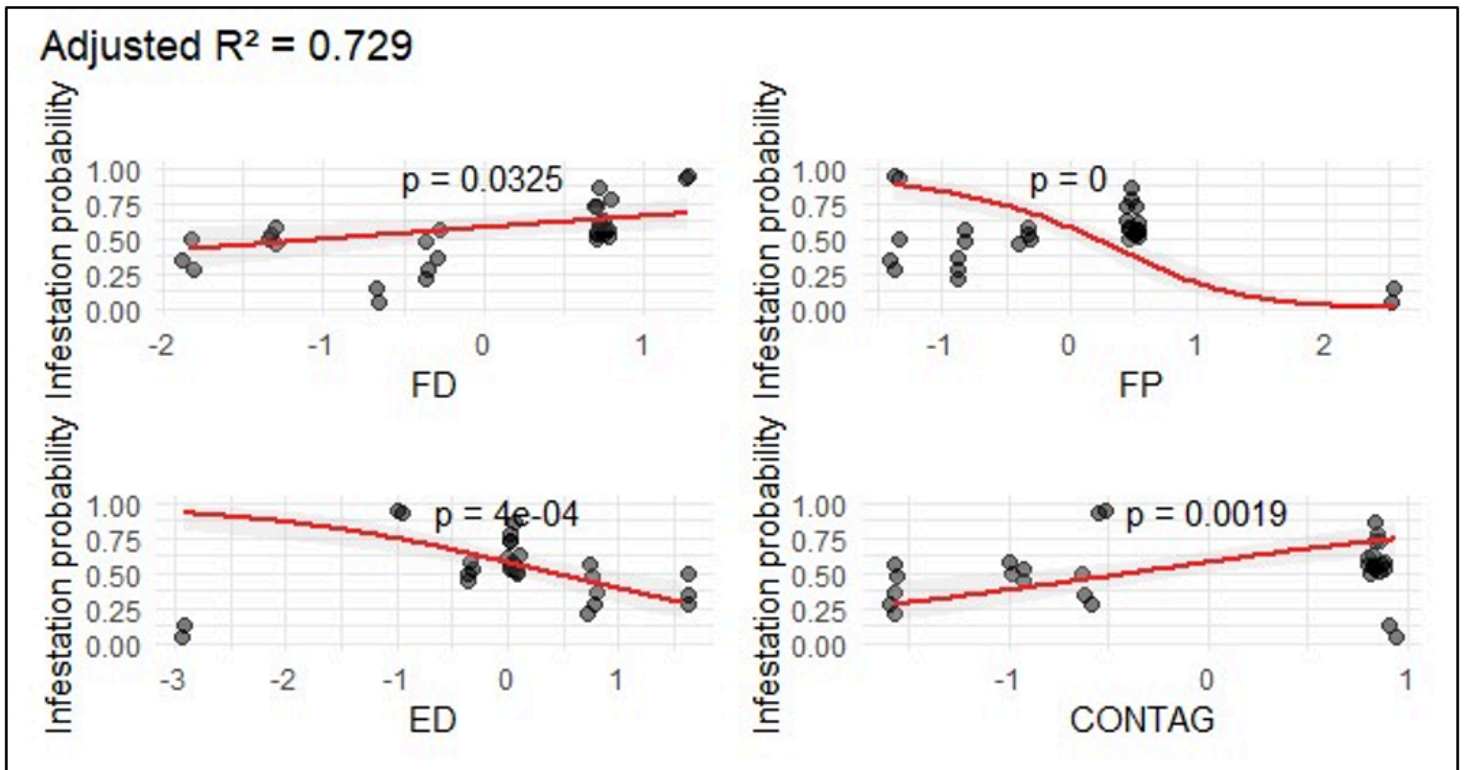


Figure 2

Generalized additive mixed model fits showing maize infestation probability in relation to landscape attributes. Fractal dimension (FD) and contagion (CONTAG) significantly favor infestation, while forest proportion (FP) and edge density (ED) showed a strong negative association.

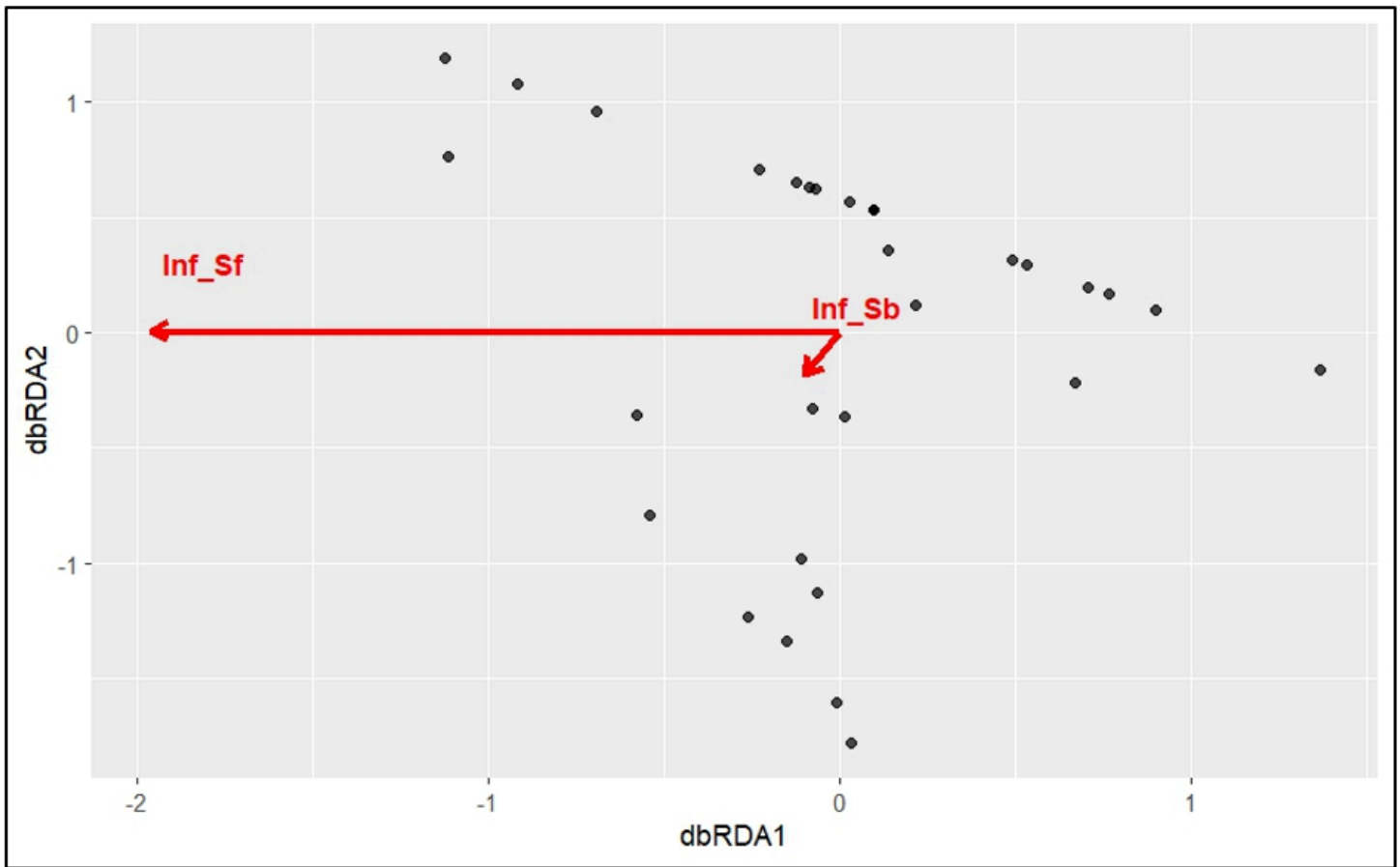


Figure 3

Distance-based redundancy analysis (dbRDA) ordination showing the relationships between maize pest infestations and landscape structure. Arrows represent species scores

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