Patterns and consequences of invasion of tropical montane forests by *Cestrum aurantiacum* Lindl. in the Western Ghats

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In the montane forest-grassland mosaics of the Western Ghats, land cover conversion to silviculture and agriculture over the last five decades has resulted in both loss of natural habitats and widespread invasion of remnant habitat patches. While invasion of the grassland habitats of the mosaic has been relatively well studied, there have been few attempts to understand the extent to which forest habitats (locally known as *sholas*) have been affected by the spread of exotic species. Here we examine the patterns and impacts of invasion of *shola* forest understoreys by *Cestrum aurantiacum* Lindl., an exotic shrub species. At the landscape scale, we demonstrate that the presence and abundance of this invasive in *shola* understories is negatively related to distance from tea plantations. Further, the intensity of invasion is higher in areas with greater seasonality of temperature and lower mean annual precipitation. At the patch scale, invasion is greatest at *shola* edges and away from stream courses. We find that *C. aurantiacum* abundance has negatively affected the regeneration of native *shola* tree species as well as the abundance of native *shola* understorey shrubs. Fifty three percent of invaded plots had no native shrubs present. In plots where both *C. aurantiacum* and native shrubs were present in large enough numbers, we found evidence of negative spatial dependence between stem locations of *C. aurantiacum* and native shrubs. Our findings have important implications for the management and conservation of these mosaics.

KEYWORDS

tropical montane forest, Western Ghats, *shola*, land cover change, invasion, *Cestrum aurantiacum* Lindl., multitype point pattern analysis

1 Introduction

Tropical montane ecosystems occur on all continents across the globe, and are thought to be especially vulnerable to multiple drivers of global change (Loeffler et al., 2011; Salinas et al., 2021). These include climatic changes such as warming and altered precipitation regimes, but also pervasive land-use changes such as the intensification of agriculture,

expansion of silviculture and built-up areas for human habitation (He et al., 2023). With complex topographies that support a diversity of natural vegetation types and multiple interacting change drivers, the responses of these ecosystems to ongoing and future global change are complex and difficult to predict (Loeffler et al., 2011; Salinas et al., 2021). For example, rates of invasion of montane ecosystems have been increasing rapidly across the globe, but the reasons for this remain poorly understood (Iseli et al., 2023), and are likely to vary across regions.

The "sky-islands" of the mountain tops of the Western Ghats in southern India, a global biodiversity hotspot, are a tropical montane ecosystem that typifies the above scenario. These forest–grassland mosaics consist of distinctive stunted evergreen forests (locally known as *sholas*) set in a matrix of grasslands. They are rich in endemic biodiversity and hold great significance, not only from an evolutionary perspective, but also for their provision of critical ecosystem services including climate and hydrological regulation for the entire southern peninsular region (Sukumar et al., 1995; Bose et al., 2016; Joshi et al., 2018). Over the course of the past hundred and fifty years, but accelerating over the past five decades, large sections of these mosaic habitats have been converted to other land uses such as agricultural and silvicultural plantations, mainly at the expense of grasslands (Prabhakar, 1994; Joshi et al., 2018). This has resulted in extensive land-cover change across the region, with more than sixty percent of the grassland habitats converted to exotic tree plantations, and also the widespread invasion of remnant patches of natural habitats (Joshi et al., 2018; Arasumani et al., 2019; Sriramamurthy et al., 2022).

One visible and widely acknowledged effect of the conversion of grasslands to exotic tree plantations has been the increase in invasive alien species in the remnant grasslands (Thomas and Palmer, 2007, *pers. obs.*). While one of main species of exotic plantation trees, *Acacia mearnsii*, itself is a dominant and aggressive invader of the remnant natural grasslands (Thomas and Palmer, 2007; Arasumani et al., 2019), other woody invasive shrubs, including scotch broom *Cytisus scoparius* and common gorse *Ulex europaeus* have also invaded the grasslands extensively in recent years (Sriramamurthy et al., 2022). While these woody invasions of the grasslands have received lot of research attention (Joshi et al., 2018; Arasumani et al., 2019; Sriramamurthy et al., 2020), far less research attention has been paid to the less visible invasions, often in the understoreys, of *shola* forest patches. This is an important knowledge gap, as the patterns and consequences of invasions within *shola* forests are likely to differ from those in grasslands, such that the management of invasives in the *sholas* versus the grasslands, will require different strategies.

Over the past few decades, *shola* forests have witnessed the spread of an exotic woody invader, *Cestrum aurantiacum* Lindl. The genus *Cestrum* is native to Central and South America where it thrives in montane forests (Monro, 2012). The abundant, attractive and fragrant flowers of this genus are the reason it has been introduced as an ornamental plant in many regions, where it has subsequently become naturalized, and in several cases, turned invasive, including in parts of Africa, Asia, Australia and multiple oceanic islands (Henderson, 2007; Harvey et al., 2012; Junaedi, 2012; Gardener et al., 2013; Padmanaba et al., 2017; Makokha, 2018). In the Indian

subcontinent, *C. aurantiacum* has been reported across many montane regions including the Himalaya, the Western Ghats and in Sri Lanka (Kunwar, 2003; Sajeev et al., 2012; Wijesundara, 2012; Moktan and Das, 2013; Mandal and Joshi, 2015; Nayak et al., 2020). In general, *Cestrum* spp. are fast-growing and capable of vegetative reproduction (Symon, 1981). *C. aurantiacum* tends to form dense mats which can suppress the regeneration of other plant species (USDA, 2013; Witt and Luke, 2017). However, few studies have investigated the impacts of invasion by *C. aurantiacum* on native forest communities, and there is little primary data on the ecology and impacts of this particular species.

Here, we investigated the correlates and consequences of the invasion of *shola* forest communities by *C. aurantiacum*. Because *C. aurantiacum* was introduced as an ornamental plant in tea plantations, we hypothesized that *sholas* near tea plantations would be more heavily invaded by *C. aurantiacum* than *sholas* further away. We also expected that *C. aurantiacum* abundance within *sholas* would be related to other climatic and habitat factors such as rainfall and local topography, which influence stand structure and soil moisture, and thereby the optimal conditions for this species. Finally, we expected that *C. aurantiacum* invasion has led to reduced native *shola* tree regeneration, as well as reduced abundances of native *shola* understorey shrubs, possibly through negative competitive interactions.

2 Methods

2.1 Study area

The study was conducted across 60 km^2 in the western and southern parts of the Upper Nilgiris Plateau (11.17°N,76.77°E and 11.50°N, 76.43°E), that still hold large areas of natural *shola*–grassland mosaics, dating to at least 40,000 years ago (Caner et al., 2007). Please see Supplementary Figure S1 for a map of the study area. Other dominant land cover types in the region, such as non-native tree plantations and commercial tea plantations, were established relatively recently (Prabhakar, 1994), predominantly through the conversion of natural grasslands (Joshi et al., 2018). The region is rich in endemic plants (Blasco, 1971) and has extraordinary vertical and horizontal physiographic differentiation. Mean annual rainfall ranges from above 2500 mm on the Western side to 1200 mm towards the east (Von Lengerke, 1977; Caner et al., 2007). The dry season lasts for 3–4 months mainly between December and March. Temperature ranges from a mean maximum of 24 °C in April to a mean minimum of 5 °C in December. Frost occurs between November and March and mainly in the valleys rather than the higher hill slopes (Von Lengerke, 1977; Caner et al., 2007). The elevation range covered in this study extends from 1750–2400 m ASL.

2.2 *Cestrum*: a montane forest invasive in the Upper Nilgiris

The genus *Cestrum* in the family Solanaceae has 175 known species of shrubs, vines and small trees (de Rojas and D'Arcy, 1998;

Monro, 2012). The native range for this genus is Central and South America (Monro, 2012). Here most *Cestrum* species occur in montane areas, above 800 m elevation, in cloud forests and conifer and oak forests (de Rojas and D'Arcy, 1998; Monro, 2012). Introduced as ornamentals in various parts of the world, many species of this genus have now become invasive. Most *Cestrum* spp. bear berries with small seeds that remain viable in the seed bank and are bird-dispersed (Marambe et al., 2001; Geldenhuys, 2004; Gardener et al., 2013). They are also shade-tolerant (Geldenhuys, 2004), drought-tolerant, capable of growing on poor soils and have invaded a range of habitats from coastal dunes to savannahs, grasslands, plantations and closed forest (Henderson, 2007). Most are quite toxic to livestock, native mammals and humans (de Rojas and D'Arcy, 1998; Makokha, 2018). For these reasons, they are labelled as noxious weeds with moderate to high invasive potential (Nel et al., 2004; Henderson, 2007). In South Africa and Australia, extensive programs have been undertaken to clear areas of *Cestrum* species (Macdonald and Jarman, 1985; Stockard, 1996; Marais and Wannenburgh, 2008).

C. aurantiacum is an evergreen climbing shrub 1–6 m tall, with thin, unpleasant smelling leaves that are toxic to livestock. It is native to central America (Costa Rica, Guatemala, Honduras, Mexico and Nicaragua; CABI, 2023). In many parts of its invaded range, *C. aurantiacum* occurs in montane forests, between 1500 to above 2000m (Junaedi, 2012; Sajeev et al., 2012; Wijesundara, 2012; Moktan and Das, 2013; Makokha, 2018; Witt et al., 2018). In the Nilgiris, it has successfully invaded native forest fragments and the understorey of tree plantations above 2000 m (Saravanan et al., 2014, Figure 1). It appears to have spread from settled areas and tea plantations, where its abundance is highest (AAD *pers. obs*) and was likely imported as an ornamental plant for the estate managers' bungalows. In its native range, it appears to be well adapted to the cloud forest environment (de Rojas and D'Arcy, 1998; Monro, 2012), which would allow it to thrive in the dense shade of *sholas*.

2.3 Data collection

Shola woody communities were sampled using 0.04 ha plots (*n* = 87), that were located using a stratified random sampling design based on topography and surrounding land cover. Field data were collected between 2010–2012 (Das et al., 2017). We sampled a total of 52 *shola* forest patches in varying landscape contexts (i.e., natural grassland, tea plantation and non-native tree plantations). Within forest patches, plots were spaced at least 50 m apart. Species identity, height and diameter at breast height (dbh) were recorded for individuals >1 cm dbh. We also recorded the position of individual trees and shrubs within the plot by dividing it into 5m blocks and mapping the location of each stem within each block. Two transects of four 1 × 1 m seedling plots each were laid across each vegetation plot. Seedlings (individuals <50 cm height) of all woody species within these plots were censused. Distance to the nearest forest edge, GPS location of the plot corner, elevation, slope and aspect were also recorded in the field. We confirmed species identities using published flora (Gamble, 1923; Ramesh et al., 2008) and the help of an experienced taxonomist.

2.4 Data analysis

We modelled *C. aurantiacum* presence as a function of distance to the closest tea plantation edge using a GLM with binomial error and a logit link function (McCullach and Nelder, 1989). The results were used to find a threshold distance from tea plantations beyond which the probability of *C. aurantiacum* occurrence approached zero. We used this threshold to identify a subset of study plots within which *C. aurantiacum* presence was likely based on their distance from a tea plantation edge (n = 54). This was done to ensure that subsequent analysis of the correlates of *C. aurantiacum* abundance was free from the issue of zero-inflation (Martin et al., 2005). We used data from these plots to model *C. aurantiacum* abundance as a function of bio-climatic and habitat variables listed as follows: temperature seasonality (standard deviation of monthly temperature averages), mean annual precipitation, CV of precipitation (i.e., variation in monthly precipitation within a year), distance to tea plantation, distance to nearest *shola* edge, distance to stream. Bioclimatic predictors were sourced from Hijmans et al. (2005). This data is derived from interpolations of existing weather station data at a 1 km^2 spatial resolution. The values represent long term averages between 1950 and 2000. Distance from tea plantation was measured using high resolution imagery in Google Earth (Google Earth, 2013). Distance from nearest forest edge was recorded in the field and distance to
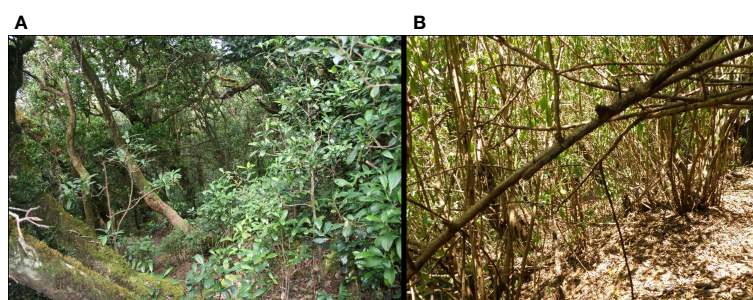

FIGURE 1
(A) *Shola* understorey with native shrubs (*Psychotria* spp.) present. (B) *Shola* understorey invaded by *Cestrum aurantiacum* with no native shrubs visible.

stream was calculated in QGIS after deriving a stream network from a DEM with 30m resolution (METI and NASA, 2011). All predictors were checked for collinearity and standardized prior to running the models. A set of competing models using these predictors were compared using Akaike Information Criteria to identify the model that best predicted *C. aurantiacum* abundance.

To assess impacts of *C. aurantiacum* invasion on native woody plants, we tested whether the number of *shola* tree seedlings and native shrubs in the plot were related to *C. aurantiacum* abundance using GLMs with a Poisson error term and a log link function. Analysis of spatial point patterns has been used to assess the presence of competitive interactions between plants (Gray and He, 2009; Pescador et al., 2020). Here, we assessed evidence for competitive interactions between *C. aurantiacum* and native shrub species by testing whether native shrubs (individuals belonging to three genera: *Psychotria*, *Lasianthus* and *Tarenna*) were located farther from *C. aurantiacum* individuals than what would be expected if their distributions were independent at the plot level. As most of the plots invaded by *C. aurantiacum* had no native shrubs present in the understorey, this test was run on only three plots which had sufficient sample size for both *C. aurantiacum* as well as native shrubs. We first tested whether the point pattern of *C. aurantiacum* and native shrubs within the plot conformed to a homogenous Poisson point process by dividing each of the three plots into nine sub plots and conducting a x^2 test to assess whether the point pattern departed from complete spatial randomness. After confirming homogeneity of the observed point pattern, we used the cross-type L-function (Lcross), a linearized version of Ripley's K function for multitype point patterns (Baddeley et al., 2016), to assess whether the point locations of native shrubs showed evidence of competitive inhibition relative to a null hypothesis in which their locations were independent of those of *C. aurantiacum* within each plot. The Ripley's K function for multitype points quantifies spatial aggregation between points of different types within a circle of radius r around a given focal point (Baddeley et al., 2016). The null hypothesis was modelled by splitting the data into the sub-patterns of points of each type and randomly shifting each of these sub-patterns, independently of the other using a toroidal shift and then calculating Lcross for the plot (Baddeley et al., 2016). As we had a square plot (20 × 20 m), we also used a toroidal shift to correct for edge effects while estimating Lcross (Baddeley et al., 2016). We used Monte Carlo simulations to test the significance of Lcross at the α = 0.05 level (Baddeley et al., 2016). All analyses were conducted in QGIS v.3.22 (QGIS Development Team, 2022) and statistical software R v.4.2.1 (R Core Team, 2022) using the packages: 'spatstat' (Baddeley et al., 2016), 'maptools' (Bivand and Lewin-Koh 2022).

3 Results

3.1 Correlates of *C. aurantiacum* abundance

C. aurantiacum was present in 17 of the 87 (19.5%) study plots. In these plots, the number of mature individual *C. aurantiacum*

stems ranged from 1–54 (mean of 17.6). The probability of *C. aurantiacum* presence was greatest between 0–2 km from a tea plantation edge and fell to near zero beyond 4 km from a tea plantation edge (Figure 2). Within plots ≤ 4 km from a tea plantation edge (n = 54), *C. aurantiacum* abundance was influenced by both bio-climatic (temperature seasonality and annual precipitation) and habitat factors (i.e., distance to tea edge, distance to *shola* fragment edge, distance to stream; Table 1). The β for seasonality of temperature (0.015 [0.0009]) indicates that *C. aurantiacum* abundance is higher in areas with greater seasonality of temperature. *Cestrum* abundance decreases with mean annual precipitation (−0.004 [0.0005]). Abundance decreases with distance from the *shola* edge (−0.014 [0.002]) and tea plantations (−0.0001 [0.0001]) and increases with distance from stream (0.0003 [0.0007]) (Figure 3).

3.2 Relationship between *C. aurantiacum* abundance and native shrubs and regeneration of native trees

Most of the plots (53%) where *C. aurantiacum* was present did not have any individuals belonging to native shrub genera. The number of individuals of native shrub species in the plot was significantly negatively related to *Cestrum* abundance (β = −0.07 [0.005], P < 0.001). *Cestrum* abundance had a significant but weak negative relationship with the number of native *shola* tree seedlings in a plot (−0.009 [0.002], P < 0.001; Figure S2). However, the number of *shola* tree saplings in a plot did not show a significant relationship to *C. aurantiacum* abundance (0.00006 [0.0007], P > 0.1).

The results of the point pattern analysis indicate support for competitive inhibition of native shrubs by *C. aurantiacum*. The Lcross metric indicates greater separation between native shrub

FIGURE 2
Probability of *Cestrum aurantiacum* presence in *shola* forest patches in the Upper Nilgiris modelled as a function of distance from tea plantation edge in meters. Modelled as a GLM with binomial error.
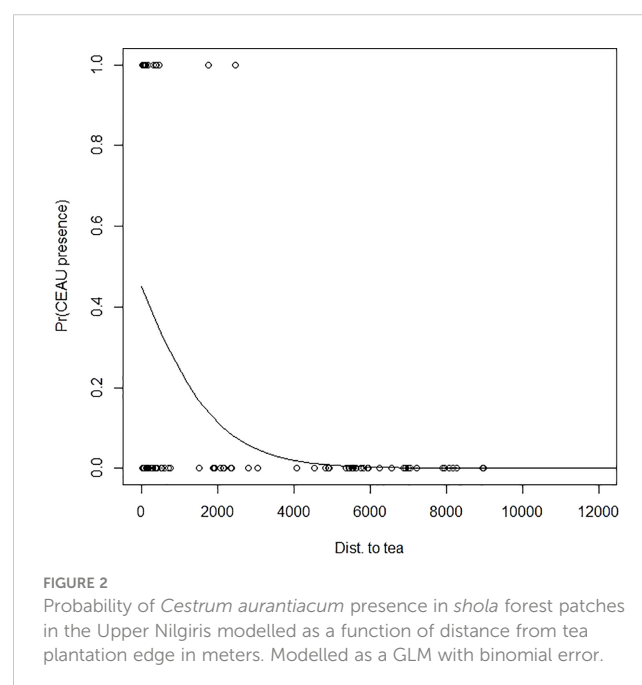
TABLE 1 Results of model selection using GLMs with Poisson error to model *Cestrum aurantiacum* abundance in sholas as a function of bio-climatic and distance variables.

S.no	Model*	AIC	ΔAIC	Mod lik	AIC_Weight
1	tmp.seas+ann.prec+d.tea+d.edge+d.stream	668.69	0	~1	~1
2	tmp.seas+prec.cv+d.tea+d.edge+d.stream	707.52	38.83	~0	~0
3	tmp.seas+d.tea+d.edge+ d.stream	729.67	60.98	~0	~0
4	tmp.seas+ann.prec	918.93	250.24	~0	~0
5	tmp.seas	936.54	267.85	~0	~0
6	prec.cv+d.tea+d.edge+d.stream	952.71	284.02	~0	~0
7	ann.prec+d.tea+d.edge+ d.stream	1105.4	436.71	~0	~0
8	d.tea+d.edge+ d.stream	1107.7	439.01	~0	~0
9	prec.cv	1140	471.31	~0	~0
10	d.stream	1178.2	509.51	~0	~0
11	d.tea+ d.edge	1332.1	663.41	~0	~0
12	d.tea	1345	676.31	~0	~0
13	d.edge	1444	775.31	~0	~0
14	ann.prec	1509.2	840.51	~0	~0

Predictor codes: tmp.seas = temperature seasonality, ann.prec = mean annual precipitation, prec.cv = cv of precipitation, d.tea = distance to tea edge, d.stream = distance to nearest stream, d.edge = distance to nearest shola edge.

locations and *C. aurantiacum* locations than expected under spatial independence, at scales of approximately 1–5 meters in two of the three plots, and some evidence in support of spatial dependence at the 0.5–1.5 m scale in the third plot (Figure 4).

4 Discussion

More than half (53%) of the woody species encountered in this study are endemic to the Western Ghats (Ramesh and Pascal, 1997). Woody invasive shrubs such as *Lantana camara* (< 2000 m; Najar et al., 2019) and *C. aurantiacum* (> 2000m) threaten this unique biodiversity. Here we show that the invasive spread of *C. aurantiacum* in the Upper Nilgiris is associated with the presence of tea plantations, as native *shola* forests embedded within a matrix of tea estates or within 4 km from a tea plantation edge, were more likely to have this species in the understorey, with its abundance increasing in *sholas* closer to tea plantations. Further, we found that increasing *C. aurantiacum* abundance appeared to negatively impact the presence and abundance of dominant native shrub genera *Psychotria*, *Lasianthus* and *Tarenna* as well as *shola* seedling regeneration. A number of studies including Bartuszevige et al. (2006); González-Moreno et al. (2013); Chen et al. (2017); Shiferaw et al. (2019), and the synthetic review by Vilà and Ibáñez
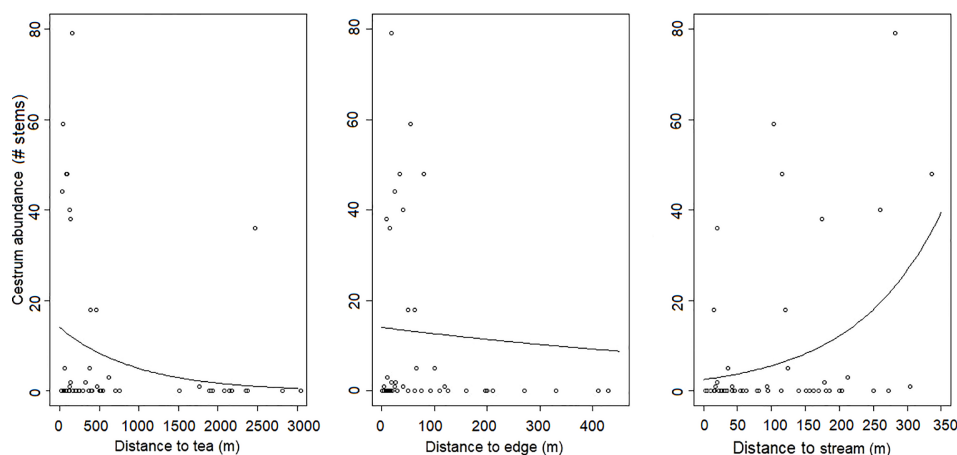

FIGURE 3

Cestrum aurantiacum abundance in *sholas* modelled as a function of distance to tea plantation edge, distance to nearest *shola* fragment edge and distance to stream, modelled using GLMs with Poisson errors.
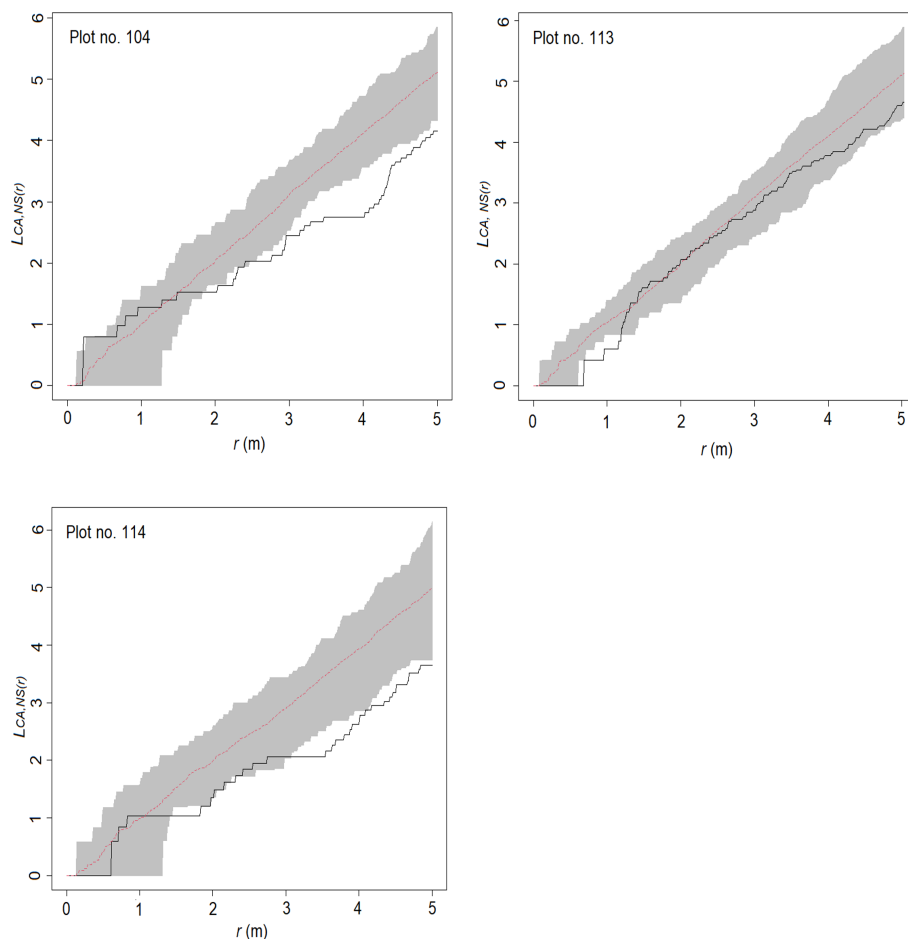
FIGURE 4
Lcross function for point locations of *Cestrum aurantiacum* (CA) and native shrub species (NS) in three plots in the Upper Nilgiris *shola* forests. In each case, the black solid line shows observed value while the red dashed line represents the expectation under complete spatial independence between the locations of CA and NS. Values of L (CA, NS) r > r indicate spatial aggregation, while L (CA, NS) r < r indicates spatial regularity. The grey shaded area represents the 95% confidence envelope of the Lcross function under the null expectation of spatial independence, calculated using Monte Carlo simulations.

(2011) have similarly found that landscape attributes play an important role (or a more important role than local site factors) in driving the presence of invasive species or the variation in invasion risk across space, while Milbau et al. (2009) outline a hierarchical framework where "…factors operating at a smaller scale are subordinate to factors operating at a larger scale, but if conditions at higher levels are satisfied, the small-scale factors may become indispensable for making accurate predictions".

4.1 Bioclimatic and site-level factors influencing the spread of *C. arurantiacum* and their links to land cover change

C. aurantiacum abundance was positively related to annual temperature seasonality – which in turn is highly negatively correlated to the elevation gradient in this study, indicating lower bio-climatic suitability at the highest part of the elevation gradient in this study (2200–2400 m). This species is susceptible to frost damage (AAD *pers. obs.*), which could explain why it does not occur in open grasslands (where frost occurs; Joshi et al., 2020) but rather

along roads (Nayak et al., 2020) and other edges where some shrub or tree cover is present (Jobin et al., 2023). The conversion of large expanses of native grasslands to timber plantations, tea and other landuses (Prabhakar, 1994; Joshi et al., 2018) may thus have facilitated the spread of this species, by creating connected edge habitats with suitable microclimatic conditions (reduced extent and intensity of frost; Von Lengerke, 1977) across the landscape.

Land cover changes and associated changes in anthropogenic disturbances may also favour the spread of this invasive species through the opening of canopies that increase light availability in the understory (Lozano and MacIsaac, 1997; Iseli et al., 2023). Junaedi (2012) found that *C. aurantiacum* presence was positively related to light intensity. Wijesundara (2012) reports it spreading in montane forest die-back gaps in Sri Lanka. Here we found the species to be more abundant in plots close to *shola*–tea plantation edges, which are more likely to have greater light penetration due to human disturbance. Finally, land cover changes are often associated with changes in the composition of pollinator and disperser communities (Raman, 2006), which in turn can facilitate invasive spread. In the Nilgiris, *C. aurantiacum* seeds are dispersed by common bird species that thrive in anthropogenic habitats, like

the red-whiskered bulbul (AAD *pers. obs.*). In Sri Lanka, its seeds are dispersed by the yellow-eared bulbul (Wijesundara, 2012), while flowers are reported to be pollinated by the Sri Lankan white-eye (*Zosterops ceylonensis;* Wijesundara, 2012).

4.2 Impacts of *C. aurantiacum* on native *shola* woody plant communities

Shola seedling regeneration was found to be lower in *C. aurantiacum* invaded sites. A similar finding has been reported for *Lantana* invaded sites in the Upper Nilgiris (Najar et al., 2019). The negative relationship between *C. aurantiacum* and native seedling regeneration could be due to either direct competitive effects or allelopathic interactions (Callaway and Ridenour, 2004). *Cestrum* spp. are reported to have anti-microbial properties (Prasad et al., 2013), which may lead to altered soil microbial communities in invaded sites (Elgersma and Ehrenfeld, 2011), thereby affecting native seedling regeneration. Alternatively, this association could also arise due to greater human disturbance in *sholas* near tea plantations, leading to lower levels of native species regeneration, while also allowing *C. aurantiacum* to spread faster (Lozano and MacIsaac, 1997). Further research is needed to elucidate the mechanisms behind this observation.

We found a strong negative relationship between *C. aurantiacum* abundance and the dominant native shrubs of the *shola* understorey, with some evidence in support of negative spatial interactions within the plot. There are several factors that could contribute to the impact of *C. aurantiacum* on native shrub populations. For instance, *C. aurantiacum* is native to cloud forest understoreys of central America and may therefore be well adapted to the microclimatic conditions of *shola* forest understoreys. This could enhance its impact within the context of this habitat (Kestrup and Ricciardi, 2009). It also grows in denser stands than native species, which has been associated with stronger impacts (Hejda et al., 2009). The combination of such environmental matching and greater fecundity (discussed below), could lead to large increases in abundance of *C. aurantiacum* in *shola* understories, sufficient to exclude native shrubs in parts of their range (MacDougall et al., 2009; Ricciardi et al., 2013).

While *C. aurantiacum* and native shrubs share common abiotic habitat requirements, they differ phylogenetically and also in key traits linked to growth and resource acquisition (trait divergence or phylogenetic distinctiveness; Ricciardi and Atkinson, 2004). Native *shola* understorey dominants all belong to the family Rubiaceae, while *C. aurantiacum* is a member of Solanaceae. Further, it displays traits associated with fast growth and rapid resource capture in comparison to native shrubs (high specific leaf area (SLA) – thinner, larger, more easily bruised leaves, low stem specific density; AAD *pers. obsv.*). Therefore, *C. aurantiacum* may avoid the effects of competitive interactions with native shrub species (Levine et al., 2003) by being sufficiently different from them in terms of phylogeny and key traits (Sofaer et al., 2018; Pearse et al., 2019).

Finally, *C. aurantiacum* exhibits characteristics associated with greater fecundity compared to native shrubs, i.e., more frequent and profuse flowering and fruiting (AAD *pers. obs.*). A South African study found it had comparable levels of fruit set to *Lantana* (Rambuda, 2001). Further research is required to assess the presence and relative contribution of each of the factors discussed above to the magnitude of *C. aurantiacum* impact on native shrubs.

4.3 Implications for conservation and management of *shola* habitats

Upper montane forests in the tropics and subtropics, like the *sholas*, often occur as relatively small patches (<10 ha), that are separated by native grasslands, tea plantations or non-native timber stands (Wijesundara, 2012; Das et al., 2017). Hence, these habitats may be more vulnerable to impacts of invasion in the same way that islands are, due to their restricted area and isolation (Pyšek et al., 2012). In particular, they may exhibit a different form of the relationship between invader abundance and per capita impact compared to continuous forest ecosystems, with associated implications for the timing and nature of management interventions (Sofaer et al., 2018; Strayer, 2020).

Tea estates constitute approximately 26% of the Upper Nilgiris Plateau above 1400 m ASL (Arasumani et al., 2019) and therefore potentially pose a serious threat to native forests through propagule rain from invasive plants. We observed wide variation in the quality of tea estate (holdings >100 ha) management across the landscape, ranging from abandonment of large areas planted with tea to intensely managed tea plantations. *Shola* patches in Korakundah tea estate, which has numerous certifications for ecological sustainability and fair trade, did not have *C. aurantiacum* in the understorey, indicating that estate management based on best practices could be effective in controlling the spread of this species. The COVID pandemic and related restrictions have probably hampered estate upkeep and management through shortages of tea estate labour and management personnel in areas important for conservation (Bates et al., 2021).

More recent work (Jobin et al., 2023) indicates that *C. aurantiacum* is also growing in the understorey of non-native timber plantations. It is also common in settlements and along road margins (AAD *pers obs*),. Together these landcover types probably contribute massive amounts of seed rain from *C. aurantiacum* across the Upper Nilgiris. Therefore, urgent attention to control of this species (particularly along road margins) in production and forestry landscapes surrounding natural *shola* forests – specifically targeting the interface between *sholas* and the surrounding land cover – is critical to mitigate the impacts of invasion. Experimental studies comparing the relative effectiveness of control methods for this species at different levels of invasion should be prioritized along with the restoration of native *shola* species (Mohandass et al., 2016; Najar et al., 2019).

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AAD conceptualized the research, collected the primary field data, ran the analysis and wrote and edited the manuscript. JR helped with conceptualization of the manuscript, and wrote and edited the manuscript. DJ helped with collection and analysis of field data, visualized the results, and edited the manuscript. All authors contributed to the article and approved the submitted version.

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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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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1198085/full#supplementary-material

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