

1 Forest canopy resists plant invasions: a case study of

2 *Chromolaena odorata* in Sal (*Shorea robusta*) forests of Nepal

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15 Running Title: **Tree crown suppresses understory invasive species**

16 **Abstract**

17 Invasive Alien Species are a major threat to global biodiversity due to the tremendous ecological
18 and economic damage they cause in forestry, agriculture, wetlands, and pastoral resources.

19 Understanding the spatial pattern of invasive species and disentangling the biophysical drivers of
20 invasion at forest stand level is essential for managing forest ecosystems and the wider
21 landscape. However, forest-level and species-specific information on Invasive Alien Plant
22 Species (IAPS) abundance and their spatial extent is largely lacking. In this context we analysed

23 the cover of one of the world's worst invasive plants, *Chromolaena odorata*, in Sal (*Shorea*
24 *robusta*) forest in central Nepal. Vegetation was sampled in four community-managed forests
25 using 0.01 ha square quadrats, covering forest edge to the interior. *C. odorata* cover, floral
26 richness, tree density, forest canopy cover, shrub cover, tree basal area and disturbances were
27 measured in each plot. We also explored forest and IAPS management practices in Community
28 Forests. *C. odorata* cover was negatively correlated with forest canopy cover, distance to the
29 road, angle of slope, and shrub cover. Tree canopy cover had the largest effect on *C. odorata*
30 cover. No pattern of *C. odorata* cover was seen along native species richness gradients. In
31 conclusion, forest canopy cover is the overriding biotic covariate suppressing *C. odorata* cover
32 in Sal forests.

33 **Key words:** Biotic resistance, canopy cover, disturbance, forest management, invasive alien
34 species

35

36 **Introduction**

37 Invasive alien species of plants and animals are an important driver of global environmental
38 change and a major threat to biodiversity loss (Vitousek et al. 1997, Bellard et al. 2016, IPBES
39 2019). They have already caused tremendous economic losses in agriculture, forestry, pasture
40 and fisheries across different geographical scales (Diagne et al. 2021). These threats are ever-
41 growing due to development of transportation networks, and increased mobility of people and
42 commodities (Simberloff et al. 2013, Sardain et al. 2019). Invasive alien species compete with
43 native biota, alter and homogenize forest composition, change ecosystem functions, compromise
44 ecosystem services, and reduce native species diversity (Bellingham et al. 2018). They also
45 degrade habitat quality for wildlife (Murphy et al. 2013), and potentially impact across all types
46 of ecosystems as well as individual species. Nevertheless, impacts are contingent on the traits of
47 the invading species and the types of ecosystem exposed to the invasion (Martin et al. 2009,
48 Pyšek et al. 2012, Liebhold et al. 2017).

49 Distribution and abundance of Invasive Alien Plant Species (IAPS) varies across spatial scales
50 (Foxcroft et al. 2009). At larger geographical scales, the impact of IAPS is the result of an
51 interplay between of social, ecological and economic variables, including national gross
52 domestic production (GDP) and population density (Liu et al. 2005, Hulme 2009, Niemiec et al.
53 2018, Sardain et al. 2019). Road networks and mobility of people not only transport IAPS
54 propagules from one place to another, but also create locally disturbed areas which are suitable
55 for propagule establishment (González-Moreno et al. 2014, Fuentes-Lillo et al. 2021). These
56 factors are fundamental to the early stage of invasion. However, further augmentation of IAPS at

57 the local scale is determined by local environmental factors including habitat disturbance,
58 species invasiveness, habitat invasibility and propagule pressure (Stohlgren et al. 2006). Newly
59 arrived propagules have to pass climatic, edaphic and biological filters for successful invasion
60 (Davis 2009).

61 Resident ecological communities naturally tend to resist the establishment and spread of
62 incoming species, a phenomenon explained as 'biotic resistance hypothesis' (Levine et al. 2004,
63 Nunez-Mir et al. 2017). This hypothesis predicts that species-rich communities have a lower
64 vulnerability to invasion at the local scale (Levine et al. 2004). Analysis of native and invasive
65 plant species richness has found a negative relationship across communities and ecoregions in
66 continental United States (Beaury et al. 2020). However, the diversity resistance hypothesis is not
67 always supported by empirical studies (Byun & Lee 2018, Smith & Côté 2019). Rather there are
68 instances of congruence of higher native diversity and higher invasion, particularly at larger
69 spatial scales (Stohlgren et al. 2006). Similarly, it is also found that the native-invasive plant
70 species richness relationship is contingent to human disturbance, which mediates the relationship
71 (Fuentes-Lillo et al. 2021).

72 The main mechanism behind biotic resistance is competition (Nunez-Mir et al. 2017).
73 Competition for key resources - for example, light, water and nutrients, and space between
74 incoming species and the recipient community - may be the main mode of the interactions. The
75 attributes of resident communities that curtail the availability of key resources required for
76 incoming species may vary across resident communities and incoming species. Nevertheless,
77 higher species richness of a native community does not necessarily make the community more
78 competitive and invasion resistant (Levine 2000, Fridley et al. 2007). Besides species richness,
79 other attributes of communities, for example, density, crowding and biomass, potentially make

80 communities more competitive and resistant to invasion (Kennedy et al. 2002, Luo et al. 2018,
81 MacLaren et al. 2019). In forest stands, native species richness, tree density, canopy cover and
82 the shrub/sapling layer are important community attributes for invasion resistance (Gómez et al.
83 2019). Indeed, these attributes determine the availability of empty niches for successful
84 invasions. Forest stand attributes, therefore, may be relatively more important than other local
85 factors for invasion success on the forest floor by limiting the amount of light reaching the
86 surface of the ground (Charbonneau & Fahrig 2004, Fajardo & Gundale 2018, Bustamante et al.
87 2019). Shrub/saplings and ground vegetation layers potentially reinforce the impacts of canopy
88 cover by preventing intercepted light falling on the ground. Nevertheless, the impact of canopy
89 may also be dependent on the nature of invading species, as many shade tolerant invasive species
90 are favored in dense and undisturbed forest (Martin et al. 2009).

91 Distribution patterns generated from coarse scale spatial data, and models based on climatic
92 suitability, may not depict the local scale distribution and abundance of IAPS. Some areas of
93 forests, for example canopy gaps and forest margins, provide more conducive environments than
94 forest interiors for invasion success (Driscoll et al. 2016, Arellano-Cataldo & Smith-Ramírez
95 2016, Khaniya & Shrestha 2020). Therefore, understanding the drivers of local scale patterns of
96 IAPS abundance is crucial for their management at the site (forest stand) level (Foxcroft et al.
97 2009). However, how abundance of invasive alien plant species are correlated with stand
98 attributes, and how native species richness is related to IAPS richness for specific forest types, is
99 not well understood.

100 In this context we assessed the abundance of the invasive plant species *Chromolaena*
101 *odorata* (L.) R.M.King & H.Rob. in Sal (*Shorea robusta* Gaertn.) forest. Sal forest is a major
102 forest type in the tropical and subtropical parts of the Indian subcontinent and has been widely

103 invaded by *C. odorata*. The few studies that have analysed invasive species in forests have
104 shown a positive correlation between forest disturbances and light intensity (Joshi et al. 2006)
105 and lower species richness in invaded plots compared to non-invaded plots (Thapa et al. 2016,
106 Bhatta et al. 2020). Nevertheless, this inference was either drawn from studies conducted on
107 large-sized plot (Joshi et al. 2006) or from a small sample size (Thapa et al. 2016), and these
108 studies did not analyse the relationship between stand attributes and invasive species abundance.
109 Therefore, this study sets out to analyse how forest stand attributes, including local disturbance,
110 influence *C. odorata* coverage in Sal forest using small-sized plots across a canopy cover
111 gradient. We also test the hypothesis that native species rich plots are more resistant to invasion.

112

113 **Methodology**

114 **Study area**

115 This study was conducted in four community-managed forests (Community Forests) of central
116 Nepal; two in each of Makawanpur and Nawalparasi districts. All the sampled forests were
117 similar in terms of geography, climate, vegetation and management regime; however, the forests
118 in Nawalparasi were more fragmented than in Makawanpur (Figure 1). Community Forests are
119 the forest categories that are managed by local users formed into legally recognised
120 organizations. Nepal has exemplary success in the sustainable management of forest commons
121 through its Community Forestry program, with over 22,000 Community Forest User Groups
122 (CFUGs) formed and registered (Niraula et al. 2013, Pandey & Pokhrel 2021).

123 All four forests in this study are located in the foot-hills of the *Siwalik (Churiya)* range. The
124 Siwalik range is geologically young, forming an east-west band of unconsolidated hills that runs

125 parallel to the south of the main Himalayan ranges. Two forests (Sunachuri and Manakamana)
126 faced southwest, while other two (Janakalyan and Ghumauri) faced south. Sampled forests
127 contained some slopes and some flat land, with maximum slope of 40 degrees.

128 The sampled forests are located between 200-550 m elevation. The climate is subtropical and
129 monsoonal, with hot and humid summers, and cool dry winters. Average annual rainfall is 2,200
130 mm (recorded between 1971–2010) of which 80% falls during the monsoon (June to August),
131 with an average annual temperature of 24.6°C recorded between 2000-2010 (CBS 2011). The
132 forests in all four sites are dominated by Sal (*Shorea robusta*). Sal is a member of
133 Dipterocarpaceae, a tropical family mainly distributed in the Indo-Malayan region. It forms
134 extensive mono-dominant or mixed forests in the southern part of the Himalayas and in the
135 tropical to subtropical areas of the Indian subcontinent (Gautam & Devoe 2006). Sal is a robust,
136 gregarious, semi-deciduous tree species, and an important high-value timber species extensively
137 used in construction and furnishing. *Dillenia pentagyna* Roxb., *Buchanania latifolia* Roxb. and
138 *Mallotus philippensis* (Lam.) Müll. Arg. are the main sub-canopy species in Sal forests.
139 *Clerodendrum viscosum* Vent. is the most common native species of the shrub layer (Wesche &
140 Karsten 1997).

141 **Focal invasive species**

142 *Chromolaena odorata* (Common called *Siam weed*, Nepali name *Seto Banmara* ‘white forest
143 killer’, family Asteraceae), is among the 100 worst invasive alien species in the world (Lowe et
144 al. 2000). It now occurs in more than 100 countries in Asia, Oceania, Africa and America, and
145 has been reported as a problematic invasive weed in more than 35 countries
146 (<https://www.cabi.org/isc/datasheet/23248#todistribution>). It is a light-demanding species,

147 flourishing in disturbed forests, roadsides, fallow and abandoned lands. Its biological and
148 morphological attributes (such as long tap root, production of large quantities of wind dispersed
149 seeds, and relatively high specific leaf area) are shared by other IAPS, giving it a competitive
150 advantage over native species (Joshi et al. 2006, Pyšek & Richardson 2008, Malahlela et al.
151 2015, Rindyastuti et al. 2021). *C. odorata* can grow to three meters in height and forms a dense
152 layer above the ground (Figure 2). This plant has already severely invaded the lowland districts
153 of central and eastern Nepal at elevations below 1000 m and is now spreading into the western
154 lowlands (Tiwari et al. 2005).

155 **Vegetation sampling**

156 Vegetation sampling was conducted in November and December 2018. All the forests sampled
157 were linked to a disturbance source, i.e. roads or human settlement. We sampled the vegetation
158 along a belt transect from the disturbance source into the forest interior. In each forest two
159 transects were made. Before laying out the plot, the length of transect and number of plots were
160 identified. The distance between plots was between 100-200 m, depending on forest size, and in
161 each forest 28 to 30 plots were sampled.

162 Vegetation data were collected for plots of 10×10 m. Each plot was divided into four subplots
163 of 5×5 m. Diameter at Breast Height (DBH) of all tree individuals greater than 5 cm DBH were
164 measured within the plots. DBH was used to calculate the Basal Area ($\text{Area} = \pi r^2$) of trees in the
165 plot; Basal area of individual trees was summed up to get plot level Basal Area. Canopy cover
166 above the plot was measured using a spherical densitometer, with four readings taken at each
167 plot following the standard protocol (Lemmon 1956).

168 *Chromolaena odorata* cover was estimated from the center of each subplot. The cover of
169 subplots was combined to estimate cover for the 100 m² plot. The same method was used to
170 estimate shrub and herb cover.

171 In each plot, two quadrats of 1 m² were sampled randomly to record species richness. All
172 herbaceous plants, shrubs and tree seedlings were recorded in each quadrat.

173 In each plot, ground disturbance (grazing, tree/saplings lopping and trampling) was recorded on
174 a scale of 0 to 3, where 0 represents absence of disturbance and 3 being severely disturbed. Plots
175 lying between these two extremes were scored 1 and 2. Distance of the plot from the nearest road
176 was measured using Google Earth Pro.

177 To evaluate how community forest user groups are managing *Chromolaena odorata* in the study
178 sites, we interviewed community forest user group leaders (n=8, Chairman and Secretary in each
179 Community Forest) and one local knowledgeable person as indicated by the Community Forest
180 chairman (n=4, one in each Community Forest). Similarly, we also interviewed community
181 forest user group leaders (Chairman or Secretary) in 15 other community forest user groups in
182 other parts of the country (Tanahu, Chitwan, Gorkha, Sindhuli and Jhapa district) which had Sal
183 forest with *C. odorata* invasion. Some informal discussions with local people were also
184 conducted for each community forest visited in public areas where people gather, to explore the
185 general understanding of invasive species and their management.

186

187 **Data analysis**

188 For data analysis, rather than comparing individual forest we pooled plot data together and
189 analysed plot level data. Ground disturbance was calculated combining three variables i.e.
190 grazing, lopping and trampling, using Principal Component Analysis (PCA). PCA first axis score
191 was used to represent ground disturbance complex. The predictor variables were checked for
192 collinearity and only one of the collinear variables was selected for further analysis.
193 *Chromolaena odorata* cover was the response variable. We used Zero Inflated Beta regression to
194 evaluate impact of forest attributes on *C. odorata* cover as the response variable is a proportion
195 and contains many zeros (Bürkner 2017). Zero Inflated Beta regression is suitable when response
196 variable is vegetation cover and consists of proportion data between zero and one (Keim et al.
197 2017). *C. odorata* cover was modelled against each covariate individually and significant
198 covariates were chosen. A full model was run with *C. odorata* cover as response and with all the
199 non-collinear independent variables (canopy cover, shrub cover, native richness, herb cover,
200 disturbance complex and distance) as predictors. Predictor variables that did not explain any
201 variation in the model were subsequently dropped in the final model. Forest types (four
202 community forests) were included as the random variable in the model. The final model included
203 canopy cover, shrub cover, distance and slope as predictor variables. The R package BRMS
204 (Bayesian Regression Model using ‘Stan’) (Bürkner 2017) was used for the regression analysis.
205 The R^2 for each model was calculated using *add_criterion* function of BRMS (Bürkner 2017).
206 Each predictor variable was centered and scaled by subtracting its mean and dividing by its
207 standard deviation prior to regression analysis so as to facilitate model convergence as well as to
208 make relative effect size of predictor variables directly comparable (Muscarella et al. 2020).

209 We compared the differences in i) *C. odorata* cover among canopy cover classes, and ii) native
210 species richness between invaded and non-invaded plots. Canopy cover was categorized as low,

211 medium and high. Values below the 1st quartile were considered low and those above 3rd
212 quartile were considered high. Values lying around the median were considered as medium. *C.*
213 *odorata* cover among canopy cover class was visualized in box plots and compared using
214 Kruskal Wallis test.

215 All analyses were performed in R version 3.5.3 (R Core Team 2019).

216 **Results**

217 *Shorea robusta* was the most dominant canopy forming tree species in all the community forests
218 studied. A total of 120 native plant species were recorded from those four forests. Native species
219 richness ranged from one to 20 species per plot with a mean of 11.41 ± 3.48 . In addition to
220 *Chromolaena odorata*, six other invasive species, namely *Spermacoce alata* Aubl.,
221 *Mesosphaerum suaveolens* (L.) Kuntze, *Ageratum conyzoides* L., *Mimosa pudica* L., *Senna*
222 *tora* (L.) Roxb. and *Mikania micrantha* Kunth) were also recorded. *C. odorata* was present in
223 60% of the plots with cover ranging from 0 to 95%.

224 **Relationship between stand attributes and *C. odorata* cover**

225 *Chromolaena odorata* cover was negatively correlated with canopy cover, shrub cover, basal
226 area and tree density. The strongest correlation was with forest canopy cover ($r=-0.59$) followed
227 by basal area and tree density (Supplementary Table 1). Forest canopy cover was positively
228 correlated with basal areas and tree density. Native species richness had a weak negative
229 correlation with *C. odorata* cover. Native species richness had weak correlations with the
230 measured stand attributes (Supplementary Table 1). Similarly, native species richness was not
231 different between invaded and non-invaded plots (mean richness in invaded=11.58 and non-
232 invaded=11.18), nevertheless the spread was higher in invaded plots (Supplementary Figure 1).

233 **Environmental covariates affecting *C. odorata* cover**

234 Regression models containing canopy cover, distance from a road, shrub cover and slope had the
235 highest mean r^2 value. *C. odorata* cover declined linearly along the canopy cover gradient
236 (Figure 3). Similarly, *C. odorata* cover declined linearly away from a road, with increasing shrub
237 cover and slope (Supplementary Figures 2, 3 and 4). Canopy cover had the largest effect size on
238 *C. odorata* cover, -0.53 (CI: -0.79, -0.28) while it has relatively lower error for the regression
239 estimates (Table 2). Distance from a road had the second largest effect on *C. odorata* cover i.e. -
240 0.29 (-0.56, -0.02). Slope and shrub cover had relatively smaller effects (Table 2). Canopy cover,
241 the most important stand attribute affecting *C. odorata* cover, in turn increased with increasing
242 distance from the nearest road (Figure 4).

243 *Chromolaena odorata* cover did not show any trends with native species richness, herb cover
244 and ground disturbance complex.

245 *Chromolaena odorata* cover was different among the canopy cover classes (Figure 5). Its cover
246 was highest (mean \pm SE, 34.03 \pm 5.22) in forests with low canopy cover, and lowest (4.08 \pm 1.74)
247 when canopy cover was higher. Its mean cover was 12.98 \pm 3.13 when canopy cover was
248 moderate. The Kruskal Wallis test showed that *C. odorata* cover was different between the
249 canopy cover classes ($H_{2,2}=18.806$, $p<0.001$)

250 **Invasive species in forest management**

251 We recorded that community forest user groups are organizing regular bush clearing (*jhadi safai*)
252 of understory plants in their forests. However, these activities generally occur in forested areas
253 and rarely occur in open parts invaded by *Chromolaena odorata*. Community forest user groups

254 did not have any specific programs targeting *C. odorata* or other invasive plants, and their forest
255 management plans did not recognize invasive species as a problem.

256 **Discussion**

257 The results demonstrate that forest stand attributes and other environmental variables affect the
258 cover of *Chromolaena odorata* in the Sal forests of Nepal. We discuss how attributes of Sal
259 forests determine the cover of invasive species and highlight practical relevance of these findings
260 to the management of community and other fragmented or otherwise disturbed forests.

261 **Canopy cover is the overriding covariate affecting *C. odorata* cover**

262 We have demonstrated that canopy cover, shrub cover, slope, and distance from a road all have
263 some effect on *Chromolaena odorata* cover in Sal forest. *C. odorata* cover declines gradually
264 away from the roadside which is probably due to high propagule pressure along roads. Roadsides
265 in turn have lower canopy cover and more open areas, and are important driver of invasion from
266 local to the regional level (Flory & Clay 2006, Follak et al. 2018). Roads bring propagules as
267 well as create disturbances and open spaces (vacant niches), which consequently favour invasion.
268 Roads provide corridors for invasive species, connecting them with suitable habitats, therefore,
269 roadsides and forest edges often have high density of invasive species (Benedetti & Morelli
270 2017, Follak et al. 2018).

271 Accessible parts of Sal forests are subjected to anthropogenic disturbances involving lopping
272 trees, cutting saplings, and trampling of the ground during firewood and fodder collection
273 (Sharma et al. 2016). Anthropogenic disturbance has been shown to be an important variable
274 affecting invasive species in ecosystems including forests (Fuentes-Lillo et al. 2021, Mungi et al.
275 2021). Counterintuitively, we found that ground disturbance had a very weak correlation with

276 *Chromolaena odorata* cover, and it did not improve the regression model, which indicates that
277 ground disturbance is not a major factor governing the cover of *C. odorata* in forests in this
278 study.

279 Canopy cover showed a negative relationship with *C. odorata* cover in Sal forest. In the
280 composite model containing disturbance, and distance to disturbance sources, forest stand level
281 canopy cover was the overriding factor in determining *C. odorata* cover. *C. odorata* cover
282 declined linearly with increasing canopy cover. In general, this negative relationship supports
283 previous studies reporting *C. odorata* a light demanding preferring to grow in well-illuminated
284 areas (Joshi et al. 2006). In addition, as *C. odorata* is an understory shrub it cannot compete with
285 trees for light, consequently the canopy trees limit this crucial resource for *C. odorata*. Joshi et
286 al. (2006) also found that seed production of *C. odorata* is suppressed with low light intensity.
287 Similarly, lower light intensity also retards the germination of *C. odorata* seeds (Chauhan &
288 Johnson 2008). Higher canopy cover implies lower level of light availability below the forest
289 canopy. Many Invasive Alien Plant species prefer to grow in open areas in forests and forest
290 ecotones (Mavimbela et al. 2018). Open areas in forests provide sites for regeneration and
291 growth of IAPS and have higher proportion of IAPS density and coverage compared to closed-
292 canopy areas (Charbonneau & Fahrig 2004, Driscoll et al. 2016). Nevertheless, the impact of
293 canopy density may also be dependent on the nature of invading species, as shade tolerant
294 invasive species may be favoured where there is a dense canopy (Martin et al. 2009).

295 **Native species richness and *C. odorata* cover**

296 Conventional diversity resistance hypothesis asserts that sites with higher species richness have
297 lower susceptibility to exotic invasions, mainly at local scale (Fridley et al. 2007). However, this

298 hypothesis is not always supported by empirical studies (Peng et al. 2019); some studies
299 corroborate the hypothesis (Kennedy et al. 2002, Beaury et al. 2020) while others refute it (Wiser
300 et al. 1998). Alternatively, it is also argued that native species may even facilitate invasion
301 (Fischer et al. 2009). Our study in the Sal forests showed that *Chromolaena odorata* cover is not
302 correlated with the higher levels of native biodiversity (species richness. Our results are contrary
303 to those of a prior study (Thapa et al 2016) from similar forest from the region who reported non
304 invaded plots to be richer than invaded plots, however, we differ in our sampling approach and
305 richness of study system. Most of the published analysis of the effect of native richness on
306 invasion comes from studies on grasslands (Kennedy et al. 2002, Peng et al. 2019) and diversity
307 resistance experiments in forest systems are scarce. The main mechanism for invasion resistance
308 is thought to be competition. It has been suggested that richness alone may not resist invasion
309 rather there may be role of other factors co-varying with diversity which may contribute to the
310 invasion resistance of communities. In our case, forest canopy cover appears to be a more
311 important factor than species richness with respect to community competitiveness to invasion
312 resistance.

313 **Management implication**

314 *Chromolaena odorata* is one of the world's worst invasive alien plant species (Lowe et al. 2000).
315 National policy documents categorize its impacts as 'massive' in Nepal and its distribution in the
316 Himalayas is expected to expand with climate change (Shrestha & Shrestha 2019). This species,
317 along with other invasive species, demand immediate action so that their expansion to new
318 location can be curtailed. The existing biomass needs to be controlled so that ecological and
319 biodiversity loss can be prevented.

320 The Community Forestry program in Nepal is exemplary in restoring degraded forests and has
321 played a key role in increasing forest cover and averting deforestation in Nepal (Niraula et al.
322 2013). Local people have also observed that *C. odorata* abundance is suppressed with forest
323 protection and canopy closure (Personal communication). Although Community Forests do not
324 have specific plans and activities to control *C. odorata*, it appears that they have unwittingly
325 played an important role in controlling *C. odorata* in forests by protecting forest and increasing
326 forest canopy. Control of invasive species through increased forest cover could be an
327 ‘undocumented contribution’ of community forest user groups of Nepal. However, additional
328 data are needed from different physiographic regions and socio-economic settings to evaluate
329 this hypothesis.

330 Our findings have immediate practical relevance in forest management. Community Forests are
331 mostly small patches of forest interspersed with settlement and agriculture. These forest patches
332 are subjected to disturbance associated with biomass extraction, grazing and forest silviculture,
333 and many Community Forests are potentially vulnerable to invasion by *Chromolaena odorata*.
334 Community Forests should consider enhancing forest canopy cover to suppress the growth of *C.*
335 *odorata* (Khaniya & Shrestha 2020). Currently, Nepal has adopted intensive silvicultural
336 practices in Sal forests. Tree felled and canopy opened areas are highly susceptible to invasion
337 by *C. odorata* therefore such patches within forests should be monitored regularly to control this
338 invasion.

339 The results of this study showed that forest areas along roadsides have a higher cover of *C.*
340 *odorata*. Intact forest margins along roads potentially buffer propagule dispersal towards forest
341 interiors (Cadenasso & Pickett 2001). Therefore, increasing tree density and forest crown along
342 roadsides could be a strategy to control the cover and control the spread of *C. odorata* in

343 fragmented forests. Forest managers should consider restoring degraded forests and increasing
344 tree crown along roadsides and open areas so that invasive species can be suppressed while also
345 gaining other forest ecosystem services.

346 **Conclusion**

347 Our study clearly indicated that forest canopy cover can resist the invasion of *C. odorata* in Sal
348 forests. The resistance mechanism could be related to resource limitation, primarily light, to the
349 invading species. Disturbance of the ground or undergrowth is probably not a primary driver
350 facilitating invasion in forest when the invading species is light-demanding, as is *C. odorata*. Our
351 results provide practical insights for the management of Sal forests and degraded areas to avert
352 invasion by invasive species, and they may apply to other forest types and other light-demanding
353 IAPS.

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List of Tables and Figures

Table 1: Information on the four sampled community forest

Name of CF	Area (ha)	Elevation	Geographic location	Forest type and dominant species	Invasive species
Pashupati	195	250-450	Siwalik/Chure foot hills	Sal forest (<i>Shorea robusta</i>), with <i>Terminalia alata</i> , <i>Adina cordifolia</i> .	<i>Chromolaena odorata</i> dominant, with <i>Mikania micrantha</i> , <i>Parthenium hysterophorus</i> , <i>Spermacoce alata</i> , <i>Mesosphaerum suaveolens</i>
Sunachuri	266	250-350			
Janakalyan	182	200-300			
Ghumauri	207	250-540		Dominant shrubs: <i>Clerodendrum viscosum</i> , <i>Pogostemon benghalensis</i> .	

Table 2: Model summary of Bayesian regression analysis where *C. odorata* cover is response and other forest attributes are predictors.

Variables	Estimate	Estimated error	95% confidence interval	
			Lower	Upper
Intercept	-1.14	0.24	-1.63	-0.69
Canopy cover	-0.53	0.13	-0.79	-0.28
Shrub cover	-0.21	0.14	-0.48	0.06
Slope	-0.27	0.14	-0.54	-0.01
Distance	-0.29	0.14	-0.56	-0.02
sd (Random effect of sites)	0.27	0.31	0.01	1.10

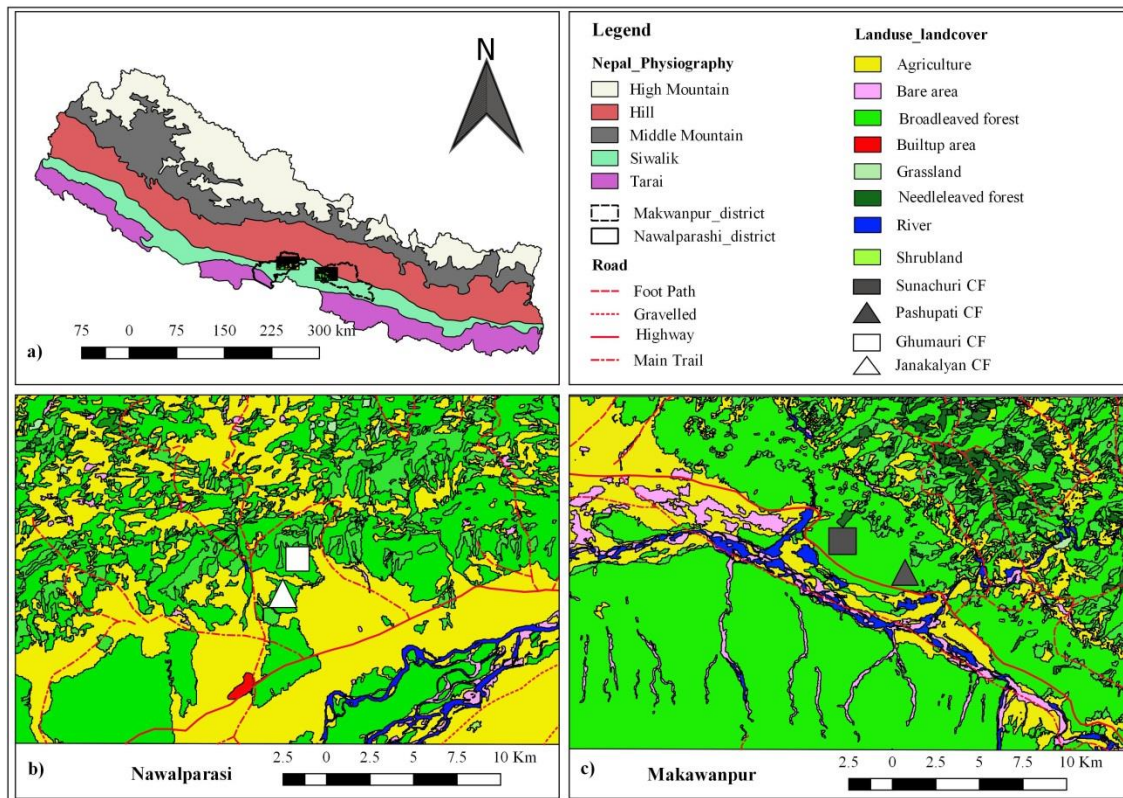


Figure 1: Maps showing the study areas; a) Location of Nawalparasi and Makawanpur district in the physiographic regions of Nepal, b) land cover of Nawalparasi site, c) land cover of Makawanpur site



Figure 2 *Chromoleana* morphology: a) an open area invaded by the species; b) flowerhead on stem; c) inflorescence detail; d) single flower head detail; e & f) leaf dorsal and ventral surface showing margin and venation. Pictures taken in Janakalyan community forest Nawalparasi.

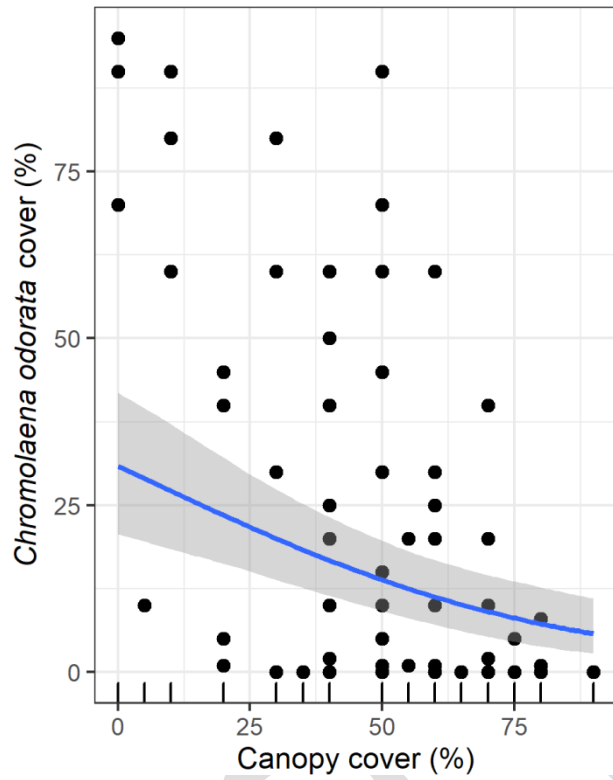


Figure 3: The relationship between *C. odorata* cover and canopy cover (%) showing the fitted line based on Bayesian regression analysis and its 95% confidence intervals around the fitted line.

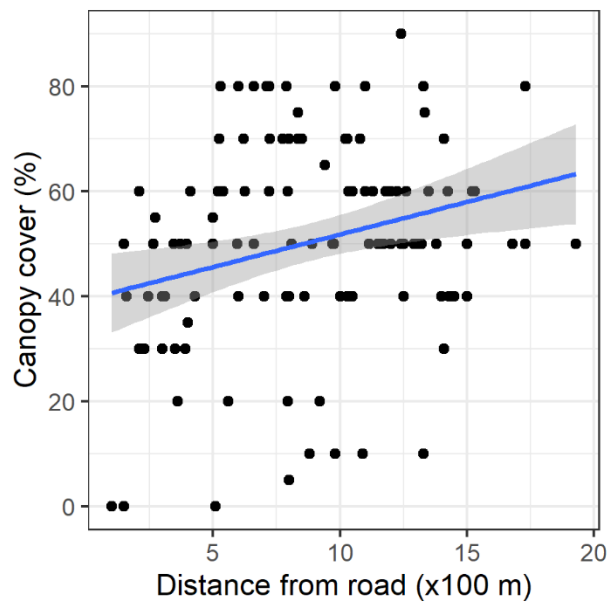


Figure 4: Relationship between canopy cover and distance to the nearest road along with the fitted linear regression line and its 95% confidence intervals around the fitted line

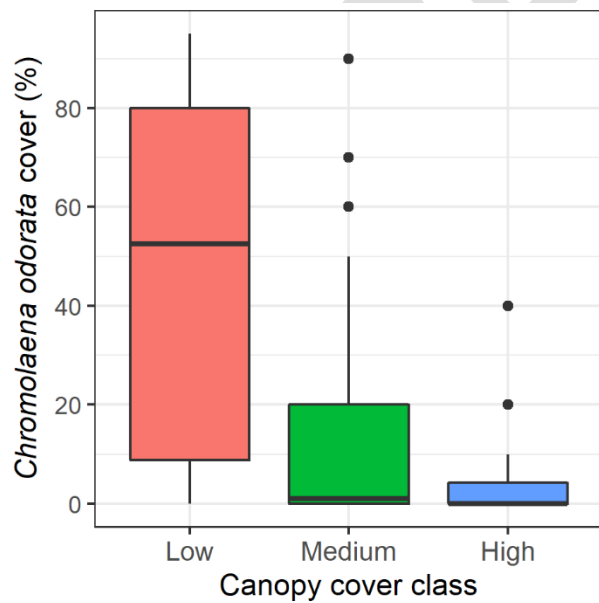


Figure 5: Box and Whisker plot showing *C. odorata* cover in different canopy classes. The medians (horizontal line), whiskers (vertical line), and outliers (points) above the maximum value and interquartile range are indicated in the plot.