1 **Chronic disturbance of moist tropical forests favours deciduous over evergreen tree**

2 **communities across a climate gradient in the Western Ghats**

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19 **ABSTRACT**

20 It is well established that climatic factors such as water stress and chronic anthropogenic

21 disturbances such as biomass extraction influence tropical forest tree community structure,

22 richness and composition. However, while the standalone effects of these two drivers on plant

23 communities are well-studied, their interactive effects are not. Moist tropical forests in India's

24    Western Ghats face a dual threat from increasingly erratic precipitation (and consequent water

25    stress), and an intensifying anthropogenic footprint. Here, we sampled 120 tree plots (0.05 ha

26    each) across forests with varying histories of biomass extraction and a gradient in climate water

27    deficit (CWD, a proxy for water stress) within a 15,000 $km^2$ landscape in the northern Western

28    Ghats and examined whether and how disturbance history modulates relationships of tree

29    community structure and composition with climate. As expected, tree species richness increased

30    with decreasing water stress in less- and historically-disturbed forests but remained low in

31    repeatedly-disturbed forests. The increase in evergreen species richness with decreasing water

32    stress was far slower in repeatedly-disturbed forests than other categories, and the relative

33    abundance of evergreens in the repeatedly-disturbed forests (25%) was half that in less-disturbed

34    forests (50%) of comparable water stress in the driest parts. Overall, we show that disturbance

35    can amplify threats from climate change to wet forest-associated evergreen tree species, many of

36    which are threatened, while benefiting more widely distributed dry forest-associated deciduous

37    species. In the northern Western Ghats, where much of the remaining forest cover is disturbed

38    and dominated by deciduous tree species, the persistence of evergreen tree flora hinges on

39    protecting existing evergreen forest patches from future disturbances and restoring locally

40    appropriate evergreen species in secondary forests.

41 **INTRODUCTION**

42 Plant community assembly is the culmination of abiotic and biotic factors acting over different

43 spatial and temporal scales (Ramos et al., 2023; Zheng et al., 2022). Although climate is the

44 major factor shaping plant diversity and composition (Harrison et al., 2020), in the

45 Anthropocene, human-mediated disturbances act in conjunction with such environmental factors

46 and contribute to altered tree richness, abundance and composition (Bentsi-Enchill et al., 2022),

47 with cascading impacts on ecosystem function (Hooper et al., 2012). However, the effects of

48 anthropogenic disturbances and environmental factors on plant community assembly are often

49 studied in isolation. Few studies have examined their combined effects on plant diversity and

50 structure, and those that have, are primarily focused on seasonally dry tropical forests (Ramos et

51 al., 2023; Rito et al., 2017; Zorger et al., 2019). Despite wet tropical forests (forests receiving >

52 2000 mm of annual rainfall) harbouring more than half of the global terrestrial biodiversity

53 (Malhi et al., 2014) and being increasingly threatened by habitat degradation and biodiversity

54 loss (Saatchi et al., 2021), studies on the interactive effects of anthropogenic and environmental

55 factors on plant communities have been overlooked in these sensitive ecosystems.

56 For plants, annual precipitation is an important factor influencing plant richness and

57 composition across large environmental gradients (Harrison et al., 2020; Krishnadas et al., 2016).

58 Besides annual precipitation, water stress during dry months is critical in determining species

59 distributions (Esquivel-Muelbert et al., 2017), thereby influencing vegetation types (Hirota et al.,

60 2011). On almost half of the Earth's terrestrial surface, climate change is expected to lead to less

61 water availability (McLaughlin et al., 2017), thereby greater water stress. Reduced water

62 availability may limit species distributions (Saiter et al., 2016) and induce deciduousness in the

63 vegetation, particularly in wetter, evergreen forests (Saiter et al., 2016; Seiler et al., 2014),

64    thereby driving tropical biome transitions, like those between wet and dry forests (Dexter et al.,

65    2018). These transition zones represent unstable states where the vegetation is most sensitive to

66    climatic disturbances (Hirota et al., 2011). Like climate, anthropogenic disturbances can mediate

67    shifts in vegetation types. Although deforestation is a major global threat to biodiversity, tropical

68    forests are increasingly imperilled by chronic anthropogenic disturbances like selective logging

69    and fuelwood extraction (Barlow et al., 2016). Despite research indicating that the interactive

70    effects of climatic and anthropogenic factors can have significant consequences on the resilience

71    of plant communities and affect vegetation types (Hirota et al., 2011; Shivaprakash et al., 2018),

72    studies explicitly testing for these effects are sparse. The need for assessing the interactions

73    between climate and anthropogenic factors has been highlighted (Krishnadas et al., 2021). While

74    some studies have investigated the interactive effects of climatic factors like precipitation and

75    chronic anthropogenic disturbances on plant diversity and structure (Rito et al. 2017; Ramos et

76    al. 2023), no studies have examined the effect of these interactive effects on vegetation

77    transitions. Although studies have suggested that fire mediates the transformation of forests to

78    drier vegetation types (savannization) (Sansevero et al., 2020; M. Wang et al., 2023), the

79    implications of chronic anthropogenic disturbances (hereafter, CAD) and environmental factors

80    on vegetation type transitions are less explored.

81        The Western Ghats-Sri Lanka biodiversity hotspot harbours a high diversity of vascular

82    plants, many of which are endemic to the region (Gunawardene et al., 2007). It has lost a

83    substantial extent of its original vegetation cover (<30% remaining) due to human activities

84    (Mittermeier et al., 2011; Myers et al., 2000). The region exhibits high levels of topographic and

85    climatic heterogeneity, creating suitable habitats to support diverse vegetation types along a

86    gradient of deciduous to evergreen forests, each of which harbours unique fauna (Gunawardene

87    et al., 2007). Woody plant diversity in the Western Ghats exhibits a clear latitudinal gradient

88    with decreasing plant richness in northern portions primarily driven by the past geo-climatic

89    history and niche conservatism (Gopal et al., 2023). Additionally, the topography of the

90    mountain ranges leads to a distinct gradient in rainfall from the low elevations to the mountain

91    crest, wherein precipitation increases towards the higher elevations (Venkatesh et al., 2021).

92    Distinct forest types are associated with different rainfall and elevation bands (Joseph et al.,

93    2012). These varying rainfall patterns give rise to water availability gradients, which are known

94    to be important drivers of tree diversity and structure (Terra et al., 2018) and are responsible for

95    a wide diversity of trees and vegetation types in the Western Ghats of India (Joseph et al., 2012;

96    Page & Shanker, 2018).

97         Despite the high biodiversity in this region, the forests in the Western Ghats are

98    threatened by a range of anthropogenic disturbances that have led to the loss of 35.3% of its

99    forest cover from the 1920s to 2013 (Reddy et al., 2016). The forests here are at an elevated risk

100   of degradation as they have the third highest human population density among all global hotspots

101   (Cunningham & Beazley, 2018). This is particularly true for the northern Western Ghats, where

102   the privately-owned forests are periodically clear-felled (every ten years) to harvest fuelwood,

103   resulting in CAD. Apart from the repeatedly disturbed privately-owned forests, the northern

104   Western Ghats also harbour government-owned Reserved Forests and Protected Areas, which

105   were historically disturbed. There are also sacred groves, many of which harbour among the least

106   disturbed forest habitats in the region. These disturbance and water availability gradients in the

107   northern Western Ghats make it a suitable system to study the interplay of climate and CAD on

108   plant vegetation types.

109        Given this background, we investigated the effects of CAD and climate on the diversity

110    and structure of plant communities. To do this, we sampled 120 vegetation plots across three

111    forest categories with varying degrees of protection and along a precipitation gradient. We

112    specifically asked the following questions: (1) How does tree composition differ across forest

113    categories? (2) How do climatic water deficit (CWD) and CAD impact the vegetation structure

114    and overall tree species richness? (3) How do CWD and CAD affect the proportion of evergreen

115    trees and richness of evergreen and deciduous trees? We expected that filtering mediated by

116    human disturbance and climate would result in differences in tree composition and diversity. We

117    expected a higher proportion and richness of evergreen trees to be found in the wetter (low

118    CWD) and cooler regions in the high-elevation forests, as compared to the drier (high CWD),

119    low-elevation forests. Moreover, we predicted that repeated chronic anthropogenic disturbance

120    would further lower evergreen tree richness and proportion, leading to a more deciduous

121    vegetation type.

122

123    **METHODS**

124    **Study Area**

125    We conducted the study in the south-western part of Maharashtra in India (15.72–17.74°N;

126    73.29–74.19°E) between October 2022 and March 2023. The study site forms the northern part

127    of the Western Ghats-Sri Lanka Biodiversity Hotspot, which is classified as one of the "hottest"

128    biodiversity hotspots globally, based on the high degree of endemism and levels of

129    anthropogenic threats (Myers et al. 2000). The climate here is tropical, with average annual

130    rainfall ranging from 2150–7450 mm, and the annual temperature varying between 16–35°C (Jog

131    2009).

132    We sampled sites experiencing varying levels of disturbance across an elevational

133    gradient, ranging from 8 to 1054 m a.s.l. (Fig. S1). The sites were classified as less-disturbed,

134    historically-disturbed and repeatedly-disturbed. For the less-disturbed sites, we sampled the

135    sacred groves. The landscape harbours several sacred groves, locally known as "*Devrais*", which

136    are protected by the local villages and home to relatively less disturbed patches of forests (Gadgil

137    & Vartak, 1976). They provide refuge to many endemic, evergreen and medicinal plants

138    (Blicharska et al., 2013; Kulkarni et al., 2018). Since some sacred groves experience

139    opportunistic fuelwood and timber collection, these sites were classified as less-disturbed. We

140    classified the government-managed forests (Protected Areas (PAs) and Reserved Forests (RFs))

141    as historically disturbed sites. The PA sites were spread across the Sahyadri Tiger Reserve and

142    Radhanagari Wildlife Sanctuary, and the RF sites were spread across Chiplun and Sawantwadi

143    Forest Divisions. The PAs were designated in the late 1950s (Radhanagari) and mid-1980s

144    (Sahyadri), and these sites have a long human-use history for shifting cultivation and have likely

145    been clear-felled in the past (Chandran, 1997; Ghate et al., 1998), unlike the sacred groves. The

146    existing stunted evergreen forests here result from forest recovery after clear felling (Ghate et al.

147    1998). Since there are no PAs in lower elevations, all the PA sites were located in relatively

148    higher elevations (584–1012 m a.s.l). The elevation range of RF sites ranged between 26–386 m

149    a.s.l. While no form of resource utilisation by humans is permitted in PAs, some forms of

150    resource use, like cattle grazing and deadwood collection, are still allowed in RFs. We classified

151    the private forests as repeatedly-disturbed forests. The private forests sampled in the region

152    experience the highest level of chronic anthropogenic disturbance among the three forest

153    categories as people clear fell these forests every five to ten years to sell fuelwood (Kulkarni and

154    Mehta, 2013). The prevailing forest type here has been reported to be tropical moist deciduous in

155 the lower elevations, and semi-evergreen to evergreen in the higher elevations, with stunted

156 evergreen trees being present after recovery from clear-felling (Champion & Seth, 1968; Ghate

157 et al. 1998). The dominant tree families in the high-elevation PAs are Melastomataceae and

158 Myrtaceae (Joglekar et al., 2015; Kanade et al., 2008). While there is a considerable amount of

159 information from the higher-elevation protected and non-protected forests (Joglekar et al. 2015;

160 Kulkarni et al. 2018), there is very little information on vegetation type and composition in the

161 low-elevation forests of the northern Western Ghats.

162 **Vegetation Sampling**

163 We conducted the field study in an approximately 15,000 km$^2$ landscape in the northern Western

164 Ghats (Fig. S1). To capture the gradients of CAD and climate, we laid 120 50×10m$^2$ plots that

165 were evenly distributed across less-disturbed sacred groves (n=40), historically-disturbed

166 government-owned forests (Reserved Forests and Protected Areas) (n=40), and repeatedly-

167 disturbed privately-owned forests (n=40), across low and high elevations. Henceforth, we will

168 refer to these three categories of forests as less-disturbed, historically-disturbed and repeatedly-

169 disturbed forests. In each plot, we recorded the identity, girth and height of all woody stems ≥10

170 cm Girth at Breast Height (GBH). We also recorded the number of cut stems in each plot as an

171 indicator of human disturbance. All trees were classified as evergreen or deciduous using

172 regional floras and expertise within the team (NP). We excluded climbers from further analyses.

173 **Analysis**

174 All the analysis was carried out in R ver. 4.3.1(R Core Team, 2023)

175 **Tree composition across land-use types**

176 To find out the difference in the composition of trees across the six forest categories in low- and

177 high-elevations, we used 3-D non-metric multidimensional scaling (NMDS) with Bray-Curtis

178     dissimilarity metric using the R package 'vegan' (Oksanen et al., 2022) and 'vegan3d' (Oksanen

179     et al., 2018). We used 3-D NMDS since 2-D NMDS had stress values greater than 0.2. The

180     difference in species composition among the categories was tested using the 'ANOSIM' or

181     analysis of similarities function in the R package 'vegan', along with a permutation test

182     (permutations = 999).

183     **Influence of CAD and CWD on species richness**

184     We examined the influence of climate and CAD on the species richness per plot. We used the

185     predictor, CWD, to account for the climatic gradient across our study site. We obtained the CWD

186     values for each vegetation plot from a global gridded layer available at http://chave.ups-

187     tlse.fr/pantropical_allometry.htm#CWD (Chave et al., 2014). CWD is a measure of the water

188     stress experienced by plants in the dry months. It is measured as the difference between

189     precipitation and evapotranspiration in dry months when evapotranspiration exceeds

190     precipitation (Krishnadas et al. 2021). The values are always negative, and a less negative CWD

191     indicates a higher water availability for plants. It has been known to play a key role in assessing

192     the sensitivity of vegetation to drought (Vicente-Serrano et al., 2013) and transitions of

193     evergreen forests to dry deciduous forests in Bolivia (Seiler et al., 2014). In the Western Ghats

194     too, studies have shown CWD to influence plant diversity (Krishnadas et al., 2021, Gopal et al.,

195     2023); however, the interactive effects between CWD and CAD are not known. In our area of

196     interest, elevation and CWD are strongly positively correlated (Spearman's $\rho = 0.79$; $p < 0.001$),

197     indicating that high-elevation sites had lower water deficit than low-elevation sites. We used

198     GLMs to evaluate the combined (interactive) effect of CWD and forest category on the observed

199     species richness per plot with a Poisson error structure (since the response variable was not over-

200     dispersed).

201 **Influence of CAD and CWD on vegetation structure**

202 We estimated the basal area of trees ($m^2\,ha^{-1}$). We square root transformed the basal area since it

203 was not normally distributed (Shapiro-Wilk's Test; $p < 0.05$). We used the General Linear Model

204 (Gaussian error structure) to test the relationship between basal area, disturbance categories, and

205 CWD.

206 **Influence of CAD and CWD on the proportion of evergreen trees and richness of evergreen**

207 **and deciduous trees**

208 We examined the influence of CWD and CAD on the proportion of evergreen trees and richness

209 of evergreen and deciduous trees per plot. We used GLMs to evaluate the combined (interactive)

210 effect of CWD and forest category on the proportion of evergreen trees with a binomial error

211 structure and the richness of evergreen and deciduous trees with a Poisson error structure.

212 **RESULTS**

213 We identified 97% of the 7001 ($\geq$ 10 cm GBH) individual trees across our 120 plots. Two

214 individuals were identified till the genus level. Six individuals that could not be identified were

215 excluded from further analyses. We recorded 192 plant species (166 trees) from 52 families

216 (Table S1). The most speciose families were Fabaceae and Moraceae, accounting for 14.6% of

217 all species. We recorded a total of 10,071 stems. The mean ($\pm$ SE) stem density was 1678.5

218 ($\pm$79.8) stems/ha, and the basal area was 32 ($\pm$ 1.7) $m^2$/ha. A summary of tree richness is

219 presented in Figure S3.

220 **Woody plant composition across land-use types**

221 The 'ANOSIM' analysis revealed significant differences in tree composition among the six

222 different forest categories ($R_{anosim} = 0.44$, $p = 0.001$, stress $= 0.17$) (Fig. S2). The NMDS plots

223 suggested that the tree composition in high-elevation forests tended to be different than low-

224     elevation ones (Fig. S2). Even at a particular elevation-level, tree composition differed across

225     disturbance categories.

226     **Influence of CAD and CWD on species richness**

227     The GLM result showed that the interaction between CWD and disturbance category had a

228     significant effect on the species richness of trees (Fig. 1; Table S2). The observed species

229     richness per plot increased with decreasing CWD for less-disturbed sites but was lower and

230     tended to decrease with decreasing CWD for repeatedly-disturbed sites (Fig. 1; Table S2).
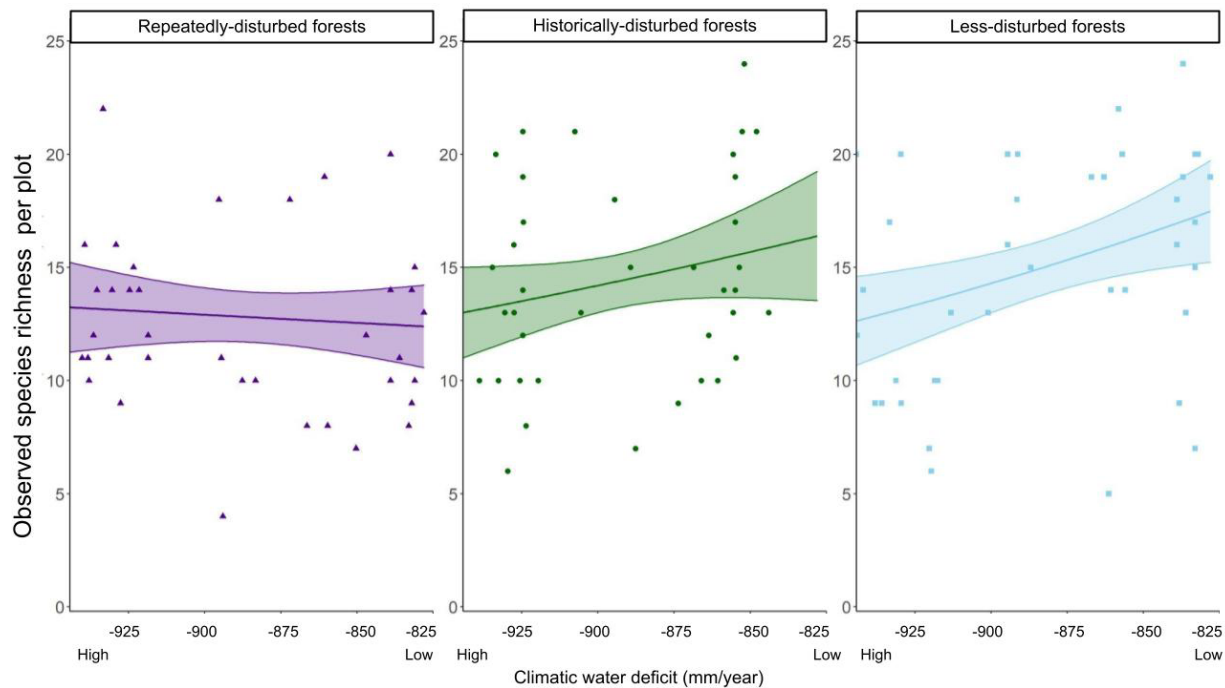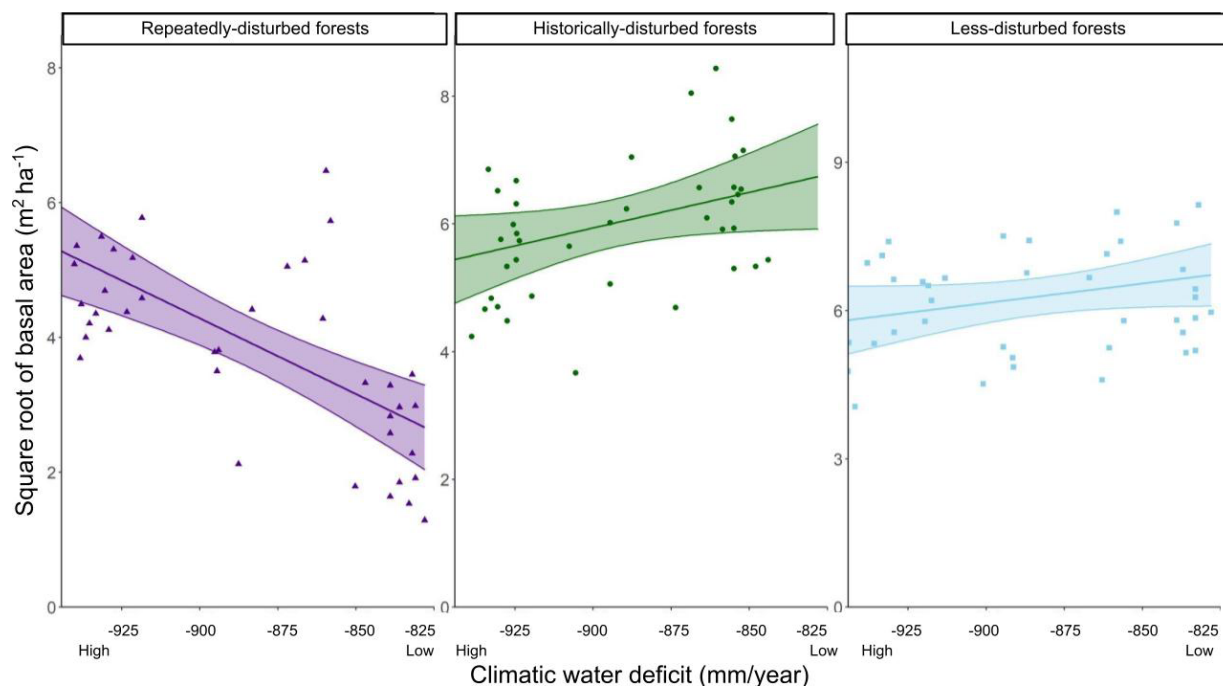


231

232     **Figure 1.** Plots showing the relationship between climatic water deficit and observed species

233     richness per plot across the three disturbance categories. The solid line with a band indicates the

234     best-fitted line for the Generalized Linear Model (Poisson error structure) with associated 95%

235     CI. Higher values of CWD (less negative) imply lower water stress experienced by plants.

236

237     **Role of disturbance in influencing forest structure**

238     The interaction between disturbance categories and CWD was significant for the basal area ($R^2 =$

239     0.51; Fig. 2; Table S3). Basal area increased with CWD for historically-disturbed and less-

240     disturbed sites but decreased with CWD for the repeatedly-disturbed site (Fig. 2). This indicates

241     that the trees are larger in wetter regions when chronic anthropogenic disturbance is lower.

242     However, in chronically-disturbed sites trees are smaller in wetter regions. A summary of basal

243     area, tree density, and canopy cover is provided in Table S4.



244

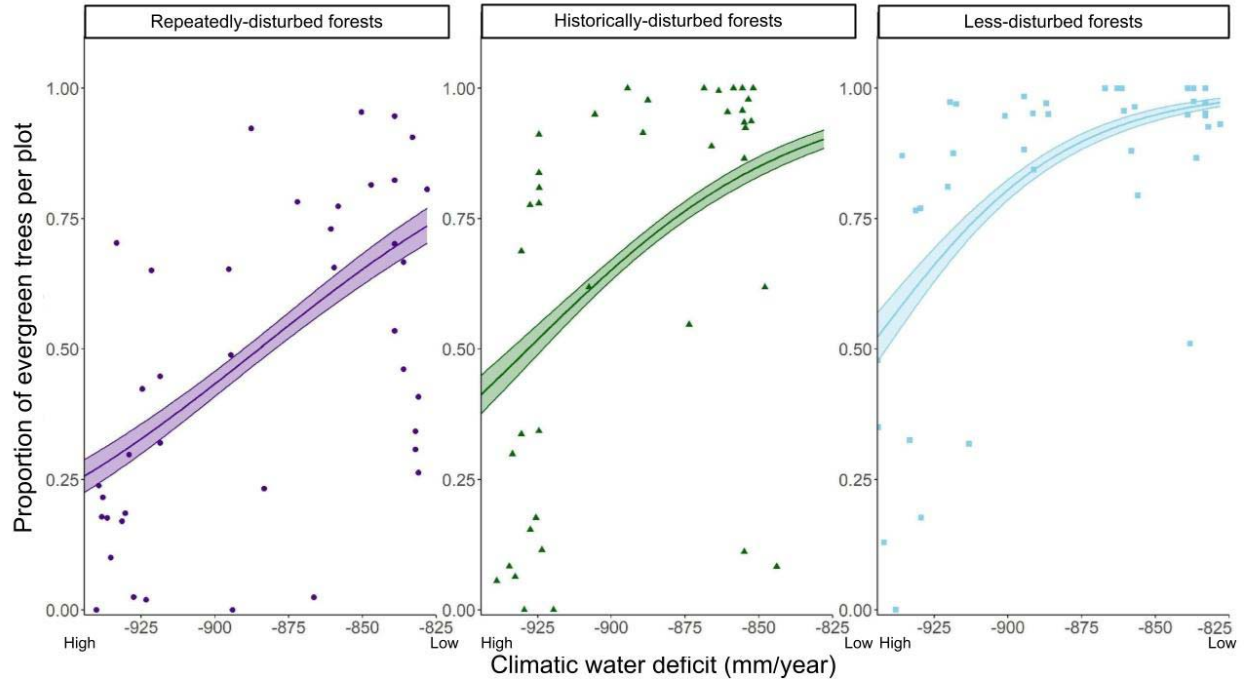245     **Figure 2.** Plots showing the relationship between climatic water deficit and square root of basal

246     area per hectare, across the three disturbance categories. The solid line with a band indicates the

247     best-fitted line for the Generalized Linear Model (Gaussian error structure) with associated 95%

248     CI. Higher values of CWD (less negative) imply lower water stress experienced by plants.

249

**Influence of CAD and CWD on the proportion of evergreen trees and richness of evergreen and deciduous trees**

The GLM results showed that the interaction terms between CWD and disturbance category significantly affected the proportion and richness of evergreen trees. The proportion of evergreen trees per plot increased with the increase in CWD values (which implies less water deficit) and this increase was the fastest in less-disturbed forests and slowest in repeatedly-disturbed forests (Pseudo $R^2$ = 0.38, Fig. 3; Table S5). In regions with low CWD values (indicating higher water deficit i.e., drier areas), the predicted proportion of evergreen trees is more than 0.5 for less-disturbed forests but only 0.25 for repeatedly disturbed forests, indicating dominance of deciduous trees in repeatedly-disturbed sites (Fig. 3). In regions with high CWD values (indicating lower water deficit i.e., wetter areas) the predicted proportion of evergreen trees for less-disturbed forests was close to 1 but for repeatedly-disturbed forests it was around 0.75. Similarly, the increase in the number of evergreen tree species per plot with decreasing CWD was very fast for less- and historically-disturbed sites but gradual for the repeatedly-disturbed sites, indicating that disturbance negatively impacted evergreen tree species richness (Pseudo $R^2$ = 0.33, Fig. 4A; Table S6). Consequently, the deciduous species richness per plot rapidly decreased with decreasing CWD for less-disturbed and historically-disturbed sites but this decrease was significantly more gradual in repeatedly disturbed sites (Pseudo $R^2$ = 0.36, Fig. 4B; Table S7).

269

**Figure 3.** Plots showing the relationship between climatic water deficit and proportion of

evergreen tree individuals per plot across the three disturbance categories. The solid line with a

band indicates the best fitted line for the Generalized Linear Model (binomial error structure)

with associated 95% CI. Higher values of CWD (less negative) imply lower water stress

experienced by plants.
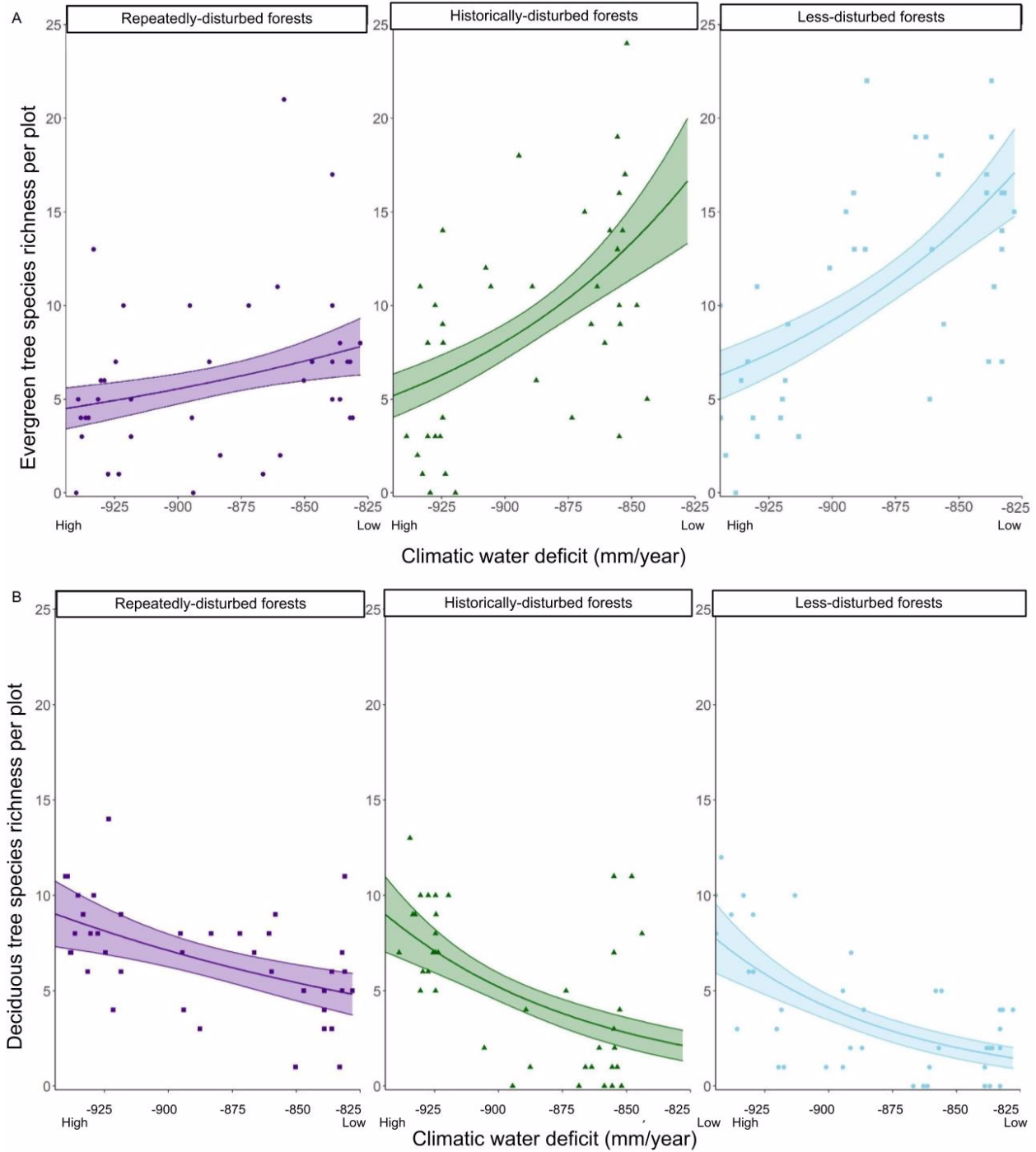
**Figure 4.** Plots showing the relationship between climatic water deficit and number of evergreen tree species per plot (A) and number of deciduous tree species per plot (B) across the three disturbance categories. The solid line with a band indicates the best-fitted line for the

279    Generalized Linear Model (Poisson error structure) with associated 95% CI. Higher values of

280    CWD (less negative) imply lower water stress experienced by plants.

281

282    **DISCUSSION**

283    While previous studies have mostly examined the effects of CAD and climate on vegetation in

284    isolation, we examined the interactive effects of the two drivers on diversity, structure and

285    composition of trees in a biodiversity hotspot. Our results demonstrate that CAD and CWD

286    significantly influence woody plant composition, overall tree species richness and structure. We

287    found that CAD disrupts the relationship between CWD and vegetation type, resulting in an

288    increased representation of deciduous trees in chronically disturbed forests, an aspect rarely

289    documented in previous studies. This study provides a scientific basis for planting evergreen

290    trees in ecological restoration efforts in low-elevation, chronically disturbed forests, which

291    predominantly harbour deciduous trees. Given the absence of Protected Areas in low elevations

292    and significant differences in vegetation composition in high- and low-elevation forests, the

293    existing Reserved (historically-disturbed forests) and Community-owned sacred groves (less-

294    disturbed forests) must be protected from further degradation and conversion in partnership with

295    local stakeholders.

296    **CAD-induced shift from evergreen to deciduous forests**

297    Most studies have looked at the impacts of CAD and climate in isolation. Given our poor

298    understanding of the interactive effects between CAD and climate, this study helps fill that

299    knowledge gap. Higher water deficit induces deciduousness in the vegetation and contributes to

300    the transition from evergreen to deciduous vegetation type (Saiter et al. 2015). While CAD is

301    thought to impact plant diversity and structure (Rito et al. 2017), very few studies have

302    documented CAD causing shifts in vegetation types (Bradshaw & Hannon, 1992) as documented

303    in this study. We demonstrate that CAD disrupts this relationship between CWD and

304    evergreenness. We find that for given levels of CWD, CAD results in a significantly lower

305    representation of evergreen trees and species in the community. The greater representation of

306    deciduous trees with CAD could be because of several reasons: source, dispersal and

307    establishment limitation, poor competitive ability of evergreen tree species in more open

308    conditions and greater propensity of deciduous trees to coppice (Chandran 1997). The species

309    composition of neighbouring forests shapes plant composition in a forest patch through seed

310    dispersal (Butaye et al., 2002). In the low-elevation areas of our study site, there are very few

311    remaining patches of intact, evergreen forests. Additionally, our previous study shows that CAD

312    negatively impacts the prevalence of avian frugivores (Biswas et al., 2023), which play an

313    important role in the seed dispersal of fleshy-fruited evergreen plants (Naniwadekar et al., 2019).

314    Thus, the absence of evergreen tree species and reduced habitat use by frugivores in repeatedly-

315    disturbed forests could result in source limitation. Even if the seeds are dispersed in these open

316    degraded patches, evergreen seedlings, which tend to have a higher shade tolerance (Baldocchi et

317    al., 2010; Kitajima et al., 2013), may not be able to establish in low canopy cover conditions

318    (Swinfield et al., 2016). Human disturbances such as clear felling of forests initiate secondary

319    succession, which often begins with a resource-rich condition associated with increased light

320    availability due to reduced canopy cover (Dalling, 2008). Often, the pioneer or early successional

321    species in degraded forests are shade-intolerant deciduous trees (Jin et al., 2017). Deciduous tree

322    species usually adopt a resource-acquisitive strategy and have higher growth rates, unlike

323    evergreen tree species that adopt a resource-conservative strategy (L. Wang et al., 2023). Thus,

324    deciduous tree species can be expected to be competitively superior in more open conditions,

325    resulting in the filtering of evergreen tree species recruits in degraded habitats. Furthermore,

326    deciduous trees are known to coppice well (Chandran 1997) and are associated with degraded

327    habitats, as seen in our study. Future studies need to determine the relative influence of different

328    processes in causing the shift from evergreeness to deciduousness. Our findings offer evidence

329    that there is a need for active restoration efforts with focus on evergreen plants in degraded

330    habitats of the northern Western Ghats since natural regeneration may not be able to restore

331    evergreen plants, which were likely present in the past.

332        The distribution of humid tropical forests (HTFs) is best characterised by high rainfall

333    regimes with low water stress environments (Zelazowski et al., 2011). Climate change

334    projections predict that rainfall will decrease in parts of the Western Ghats (Katzenberger et al.,

335    2021; Rajendran et al., 2012). Thus, chronic anthropogenic disturbance and lowered precipitation

336    can trigger shifts in vegetation type to drier vegetation in these humid tropical forests. Moreover,

337    a greater proportion of evergreen tree species are under the threatened category than deciduous

338    tree species (Fig. S4). Thus, the transition from evergreen to deciduous forests also has

339    consequences for threatened plant species in the region.

340

341    **Sacred groves as reservoirs of biodiversity**

342    We found that the community-owned, less-disturbed forests, i.e., sacred groves, had comparable

343    richness and structure as the state-owned, historically-disturbed forests. This contrasts with the

344    central Western Ghats, where state-owned forests performed better on diversity and structure

345    metrics than community-owned sacred groves (Osuri et al., 2014). The drivers of higher plant

346    diversity in sacred groves could be multifold, as they could be remnants of historically

347    contiguous forests or could have been actively restored in the historical past. The existing

348  evergreen tree cover in two sacred groves in central Western Ghats was attributed to cultural

349  practice-driven forest recovery from around 1000 years before the present (Bhagwat et al., 2013).

350  Therefore, there is a need to understand the socio-ecological history of these sacred groves that

351  can throw more light on the observed diversity of woody plants in these groves.

352      Sixty percent of sacred groves in the central Western Ghats originally present in official

353  records were lost and there was a decrease in above-ground biomass and proportion of evergreen

354  species in existing ones (Osuri et al., 2014; Bhagwat et al., 2005). Similarly, there is documented

355  evidence of sacred groves in the northern Western Ghats being cleared and lost for almost 50

356  years (Gadgil and Vartak, 1976). The drivers of loss are many, including logging,

357  encroachments, and habitat conversion. With monoculture plantations replacing private forests

358  and increased development, the pressures on the sacred groves as a source of timber and

359  fuelwood for local communities will increase. Partnerships between conservation practitioners,

360  government departments and local communities are critical to safeguard these groves in a

361  socially just manner.

362

363  **Value of low-elevation forests**

364  We recorded a higher taxonomic diversity of woody plants in our low-elevation sampling sites

365  than the high-elevation ones, especially for the repeatedly-disturbed and less-disturbed forests

366  (Figure S3). Previous studies documenting plant diversity across elevational gradients have also

367  reported similar patterns, with species richness decreasing with elevation (Musciano et al., 2021;

368  Malizia et al., 2020). In the Western Ghats, forests at or below 500 m have the least

369  representation in the protected area network (Bawa et al., 2007). Moreover, only around 1% of

370  land in the northern Western Ghats is legally protected (Blicharska et al., 2013). All the PAs in

371    our study region are in high elevations, leaving the highly diverse, lowland forests unprotected.

372    PAs, which are the high-elevation historically disturbed sites, had the least abundance of cut

373    stems, indicating their efficacy in reducing extractive pressures. The privately or community-

374    owned forests here are prone to habitat degradation (Kulkarni and Mehta, 2013) and conversion,

375    mostly to cash crop plantations (Kale et al., 2016). More than one-third of the geographic area of

376    two tehsils in Sindhudurg District is under cashew plantation (area: 533.5 $km^2$) (Rege et al.,

377    2022). This study did not estimate areas under rubber and mango plantations, which are also

378    prevalent in the region. Most of these plantations were erstwhile private or community-owned

379    forests. Therefore, these remnant patches of RFs and sacred groves in the low elevations are

380    important reservoirs of diverse assemblages of woody plants and other biodiversity. The RFs are

381    relatively less protected than PAs and are more vulnerable to getting denotified and converted to

382    other land uses (Patil 2023). Protection and active restoration, wherever needed, must be

383    prioritised in these forests so that they can continue to sustain high levels of biodiversity.

384          The higher number of cut stems and low basal area of trees in the repeatedly disturbed

385    private forests (Table S4) of high elevations suggests that these forests experience greater CAD

386    than those in the low elevations. As CWD is strongly correlated with elevation, forests with low

387    CWD are high-elevation forests. Generally, an opposite trend is observed globally, where low-

388    elevation forests are more vulnerable to logging, deforestation and habitat conversion, even in

389    the world's biodiversity hotspots (Hamunyela et al., 2020; Tapia-Armijos et al., 2015). This may

390    be attributed to the easy access to large trees by logging companies in the foothills compared to

391    the stunted but steep forests of the highlands (Danielsen et al., 2010). However, in our study

392    area, the high-elevation forests, which receive a high amount of rainfall (> 5000 mm), are

393    relatively easily accessible as they are on the Deccan plateau. These high-elevation, privately-

394 owned forests are also a source of fuelwood for the locals, who may rely on it to provide warmth

395 in their homes during the cooler and wetter seasons. A study across an altitudinal gradient in the

396 western Himalayas revealed a similar occurrence. Fuelwood consumption was found to be 2.6

397 times higher at high elevations (above 2000 m) than its use at low elevations (up to 500 m),

398 owing to people's need to heat spaces and water in harsh weather (Bhatt and Sachan, 2004). The

399 fuelwood is also utilised by the sugar factories in the region, most of which are in the high-

400 elevations. Fuelwood collection can lead to forest degradation (Sassen et al., 2015) and

401 negatively affect regeneration, thereby changing the vegetation type (as documented in this

402 study) and leading to biodiversity decline. Evergreen forests in the Western Ghats harbour a

403 higher diversity of endemic and threatened trees than the deciduous forests (Chandran 1997;

404 Ghate et al. 1998). Thus, the relative needs of industry and local communities for fuelwood must

405 be determined to find suitable alternatives to fuelwood and restore the degraded private forests in

406 these regions.

**Conservation implications**

408 Tropical wet forests are vulnerable to climate fluctuations and anthropogenic disturbance. We

409 can expect CAD to shift the wetter forests to drier vegetation types. This effect will be

410 exacerbated by reduced water availability due to climate change. Thus, there is a need to find

411 suitable alternatives to reduce CAD in tropical forests since conversion to deciduous forests will

412 be associated with a significant loss of threatened and endemic plant diversity, which is generally

413 higher in wet tropical forests. Due to the degraded nature of privately owned forests in the

414 northern Western Ghats, primarily driven by periodic clear felling of forests that cater to the

415 fuelwood needs of nearby factories, there is a need to find suitable alternatives to fuelwood in

416 these factories. Given the agroforestry-friendly government policies and the increased advent of

417  technology that allows easy conversion of forests to agroforestry plantations, many existing

418  privately-owned forests will likely be converted to agroforestry plantations. Given compositional

419  and diversity differences in low- and high-elevation forests, ecological restoration efforts of

420  degraded, low-elevation private forests must be prioritised in partnership with local landowners.

421  This is especially important for the lower elevations, which do not harbour any Protected Areas

422  but continue to harbour significant threatened and endemic biodiversity. The existence of

423  restored habitat patches in a predominantly human-modified landscape will enable the threatened

424  biodiversity to persist in the long term. Given that the existing degraded forest patches harbour

425  predominantly deciduous forests due to CAD, ecological restoration efforts should plant

426  evergreen tree species, particularly in the lower-elevation forests.

427

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712    **SUPPLEMENTARY MATERIAL**

713    **Table S1.** Checklist of woody plant species detected in 120 ($50 \times 10$ m$^2$) plots. The table also

714    provides information on the number of plots in which the species was detected and the total

715    number of individuals detected.

716

| Sr. No | Species | Family | Number of individuals | Number of plots where the species was found |
|---|---|---|---|---|
| 1 | *Acacia auriculiformis* | Fabaceae | 3 | 2 |
| 2 | *Actephila excelsa* | Phyllanthaceae | 1 | 1 |
| 3 | *Actinodaphne lanceolata* | Lauraceae | 21 | 10 |
| 4 | *Adina cordifolia* | Rubiaceae | 3 | 1 |
| 5 | *Aglaia elaeagnoidea* | Meliaceae | 46 | 12 |
| 6 | *Aglaia lawii* | Meliaceae | 51 | 13 |
| 7 | *Agrostistachys indica* | Euphorbiaceae | 4 | 1 |
| 8 | *Albizia lebbeck* | Fabaceae | 20 | 7 |

| 9 | *Albizia procera* | Fabaceae | 1 | 1 |
| 10 | *Alstonia scholaris* | Apocynaceae | 3 | 3 |
| 11 | *Anacardium occidentale* | Anacardiaceae | 8 | 3 |
| 12 | *Antiaris toxicaria* | Moraceae | 11 | 6 |
| 13 | *Aphanamixis polystachya* | Meliaceae | 1 | 1 |
| 14 | *Aporosa cardiosperma* | Phyllanthaceae | 113 | 19 |
| 15 | *Ardisia solanacea* | Primulaceae | 163 | 7 |
| 16 | *Artocarpus gomezianus* | Moraceae | 1 | 1 |
| 17 | *Artocarpus heterophyllus* | Moraceae | 12 | 6 |
| 18 | *Atalantia racemosa* | Rutaceae | 43 | 11 |
| 19 | *Bauhinia racemosa* | Fabaceae | 5 | 3 |
| 20 | *Beilschmiedia dalzellii* | Lauraceae | 42 | 13 |
| 21 | *Bergera koenigii* | Rutaceae | 12 | 8 |

| 22 | *Bischofia javanica* | Phyllanthaceae | 21 | 1 |
|----|----------------------|----------------|-----|----|
| 23 | *Blachia denudata* | Euphorbiaceae | 21 | 3 |
| 24 | *Bombax ceiba* | Malvaceae | 19 | 15 |
| 25 | *Bridelia retusa* | Phyllanthaceae | 74 | 32 |
| 26 | *Buchanania lanzan* | Anacardiaceae | 21 | 6 |
| 27 | *Butea monosperma* | Fabaceae | 2 | 2 |
| 28 | *Callicarpa tomentosa* | Lamiaceae | 22 | 12 |
| 29 | *Canarium strictum* | Burseraceae | 1 | 1 |
| 30 | *Capparis rotundifolia* | Capparaceae | 2 | 1 |
| 31 | *Carallia brachiata* | Rhizophoraceae | 12 | 5 |
| 32 | *Careya arborea* | Lecythidaceae | 114 | 41 |
| 33 | *Caryota urens* | Arecaceae | 48 | 23 |
| 34 | *Casearia graveolens* | Salicaceae | 52 | 25 |

| 35 | *Cassia fistula* | Fabaceae | 2 | 2 |
|----|------------------|----------|---|---|
| 36 | *Catunaregam spinosa* | Rubiaceae | 149 | 30 |
| 37 | *Celtis philippensis* | Cannabaceae | 7 | 5 |
| 38 | *Celtis timorensis* | Cannabaceae | 1 | 1 |
| 39 | *Chionanthus mala-elengi* | Oleaceae | 12 | 4 |
| 40 | *Chukrasia tabularis* | Meliaceae | 1 | 1 |
| 41 | *Cinnamomum verum* | Lauraceae | 14 | 7 |
| 42 | *Clausena anisata* | Rutaceae | 1 | 1 |
| 43 | *Cleidion spiciflorum* | Euphorbiaceae | 18 | 2 |
| 44 | *Clerodendrum infortunatum* | Lamiaceae | 2 | 2 |
| 45 | *Croton zeylanicus* | Euphorbiaceae | 1 | 1 |
| 46 | *Cryptocarya wightiana* | Lauraceae | 9 | 3 |
| 47 | *Dalbergia sissoo* | Fabaceae | 16 | 5 |

| 48 | *Delonix regia* | Fabaceae | 1 | 1 |
| 49 | *Dichapetalum gelonioides* | Dichapetalaceae | 35 | 9 |
| 50 | *Dillenia pentagyna* | Dilleniaceae | 13 | 9 |
| 51 | *Dimocarpus longan* | Sapindaceae | 193 | 23 |
| 52 | *Diospyros candolleana* | Ebenaceae | 147 | 27 |
| 53 | *Diospyros montana* | Ebenaceae | 13 | 10 |
| 54 | *Diospyros nigrescens* | Ebenaceae | 123 | 18 |
| 55 | *Diospyros oocarpa* | Ebenaceae | 70 | 10 |
| 56 | *Diospyros sylvatica* | Ebenaceae | 9 | 5 |
| 57 | *Donella lanceolata* | Sapotaceae | 3 | 1 |
| 58 | *Drypetes venusta* | Putranjivaceae | 23 | 6 |
| 59 | *Dysoxylum gotadhora* | Meliaceae | 46 | 9 |
| 60 | *Ehretia aspera* | Boraginaceae | 6 | 5 |

| 61 | *Elaeocarpus variabilis* | Elaeocarpaceae | 5 | 2 |
| 62 | *Elaeodendron paniculatum* | Celastraceae | 5 | 4 |
| 63 | *Erinocarpus nimmonii* | Malvaceae | 1 | 1 |
| 64 | *Erythrina stricta* | Fabaceae | 6 | 4 |
| 65 | *Eugenia kalamii* | Myrtaceae | 5 | 2 |
| 66 | *Euonymus indicus* | Celastraceae | 7 | 1 |
| 67 | *Falconeria insignis* | Euphorbiaceae | 12 | 6 |
| 68 | *Ficus amplissima* | Moraceae | 1 | 1 |
| 69 | *Ficus arnottiana* | Moraceae | 1 | 1 |
| 70 | *Ficus callosa* | Moraceae | 1 | 1 |
| 71 | *Ficus exasperata* | Moraceae | 5 | 3 |
| 72 | *Ficus hispida* | Moraceae | 41 | 12 |
| 73 | *Ficus microcarpa* | Moraceae | 1 | 1 |

| 74 | *Ficus nervosa* | Moraceae | 7 | 7 |
|----|-----------------|----------|---|---|
| 75 | *Ficus racemosa* | Moraceae | 32 | 16 |
| 76 | *Ficus talbotii* | Moraceae | 1 | 1 |
| 77 | *Ficus tsjakela* | Moraceae | 2 | 2 |
| 78 | *Ficus virens* | Moraceae | 1 | 1 |
| 79 | *Firmiana colorata* | Malvaceae | 1 | 1 |
| 80 | *Flacourtia montana* | Salicaceae | 26 | 13 |
| 81 | *Garcinia gummi-gutta* | Clusiaceae | 8 | 4 |
| 82 | *Garcinia indica* | Clusiaceae | 39 | 8 |
| 83 | *Garcinia talbotii* | Clusiaceae | 64 | 16 |
| 84 | *Glochidion heyneanum* | Phyllanthaceae | 16 | 6 |
| 85 | *Glochidion hohenackeri* | Phyllanthaceae | 9 | 5 |
| 86 | *Glochidion zeylanicum* | Phyllanthaceae | 3 | 3 |

| 87 | *Glycosmis pentaphylla* | Rutaceae | 15 | 9 |
| 88 | *Gmelina arborea* | Lamiaceae | 15 | 9 |
| 89 | *Gomphandra tetrandra* | Stemonuraceae | 4 | 3 |
| 90 | *Grewia serrulata* | Malvaceae | 14 | 5 |
| 91 | *Grewia tiliifolia* | Malvaceae | 66 | 22 |
| 92 | *Gymnosporia rothiana* | Celastraceae | 1 | 1 |
| 93 | *Helicteres isora* | Malvaceae | 13 | 8 |
| 94 | *Heterophragma quadriloculare* | Bignoniaceae | 4 | 4 |
| 95 | *Holigarna arnottiana* | Anacardiaceae | 130 | 20 |
| 96 | *Holigarna grahamii* | Anacardiaceae | 39 | 20 |
| 97 | *Homalium ceylanicum* | Salicaceae | 6 | 3 |
| 98 | *Hydnocarpus pentandrus* | Achariaceae | 17 | 7 |
| 99 | *Ixora brachiata* | Rubiaceae | 376 | 45 |

| 100 | *Ixora pavetta* | Rubiaceae | 7 | 3 |
| 101 | *Jatropha curcas* | Euphorbiaceae | 1 | 1 |
| 102 | *Justicia adhatoda* | Acanthaceae | 9 | 1 |
| 103 | *Knema attenuata* | Myristicaceae | 24 | 4 |
| 104 | *Kydia calycina* | Malvaceae | 1 | 1 |
| 105 | *Lagerstroemia microcarpa* | Lythraceae | 61 | 27 |
| 106 | *Lagerstroemia parviflora* | Lythraceae | 1 | 1 |
| 107 | *Lannea coromandelica* | Anacardiaceae | 12 | 7 |
| 108 | *Lasiosiphon glaucus* | Thymelaeaceae | 32 | 12 |
| 109 | *Leea indica* | Vitaceae | 111 | 34 |
| 110 | *Lepisanthes tetraphylla* | Sapindaceae | 23 | 11 |
| 111 | *Ligustrum robustum* | Oleaceae | 23 | 10 |
| 112 | *Litsea glutinosa* | Lauraceae | 2 | 1 |

| 113 | *Litsea nigrescens* | Lauraceae | 3 | 1 |
| 114 | *Litsea stocksii* | Lauraceae | 23 | 7 |
| 115 | *Lophopetalum wightianum* | Celastraceae | 18 | 2 |
| 116 | *Macaranga peltata* | Euphorbiaceae | 125 | 29 |
| 117 | *Machilus glaucescens* | Lauraceae | 11 | 5 |
| 118 | *Mallotus nudiflorus* | Euphorbiaceae | 1 | 1 |
| 119 | *Mallotus philippensis* | Euphorbiaceae | 86 | 27 |
| 120 | *Mallotus resinosus* | Euphorbiaceae | 9 | 2 |
| 121 | *Mammea suriga* | Calophyllaceae | 49 | 3 |
| 122 | *Mangifera indica* | Anacardiaceae | 49 | 20 |
| 123 | *Mappia nimmoniana* | Icacinaceae | 25 | 9 |
| 124 | *Margaritaria indica* | Phyllanthaceae | 2 | 2 |
| 125 | *Melastoma malabathricum* | Melastomataceae | 3 | 1 |

| 126 | *Melia dubia* | Meliaceae | 1 | 1 |
|-----|---------------|-----------|---|---|
| 127 | *Melicope lunu-ankenda* | Rutaceae | 1 | 1 |
| 128 | *Memecylon talbotianum* | Melastomataceae | 8 | 4 |
| 129 | *Memecylon umbellatum* | Melastomataceae | 778 | 56 |
| 130 | *Memecylon wightii* | Melastomataceae | 1 | 1 |
| 131 | *Meyna laxiflora* | Rubiaceae | 32 | 15 |
| 132 | *Microcos paniculata* | Malvaceae | 64 | 19 |
| 133 | *Miliusa tomentosa* | Annonaceae | 14 | 6 |
| 134 | *Mimusops elengi* | Sapotaceae | 25 | 14 |
| 135 | *Mitragyna parvifolia* | Rubiaceae | 3 | 2 |
| 136 | *Monoon fragrans* | Annonaceae | 2 | 2 |
| 137 | *Morinda coreia* | Rubiaceae | 3 | 3 |
| 138 | *Murraya paniculata* | Rutaceae | 3 | 3 |

| 139 | *Myristica beddomei* | Myristicaceae | 21 | 4 |
| 140 | *Myristica malabarica* | Myristicaceae | 12 | 2 |
| 141 | *Neolamarckia cadamba* | Rubiaceae | 3 | 2 |
| 142 | *Neolitsea zeylanica* | Lauraceae | 5 | 2 |
| 143 | *Nothopegia castaneifolia* | Anacardiaceae | 75 | 31 |
| 144 | *Ochna obtusata* | Ochnaceae | 4 | 2 |
| 145 | *Pavetta sp* | Rubiaceae | 1 | 1 |
| 146 | *Phyllanthus emblica* | Phyllanthaceae | 17 | 7 |
| 147 | *Pongamia pinnata* | Fabaceae | 3 | 1 |
| 148 | *Prunus ceylanica* | Rosaceae | 1 | 1 |
| 149 | *Psydrax dicoccos* | Rubiaceae | 16 | 11 |
| 150 | *Pterocarpus marsupium* | Fabaceae | 6 | 4 |
| 151 | *Pterospermum diversifolium* | Malvaceae | 5 | 3 |

| 152 | *Putranjiva roxburghii* | Putranjivaceae | 3 | 3 |
| 153 | *Sageraea laurina* | Annonaceae | 48 | 12 |
| 154 | *Sapindus trifoliatus* | Sapindaceae | 1 | 1 |
| 155 | *Saraca asoca* | Fabaceae | 86 | 6 |
| 156 | *Schleichera oleosa* | Sapindaceae | 39 | 9 |
| 157 | *Securinega sp* | Phyllanthaceae | 1 | 1 |
| 158 | *Semecarpus anacardium* | Anacardiaceae | 4 | 1 |
| 159 | *Senegalia catechu* | Fabaceae | 29 | 6 |
| 160 | *Solenocarpus indicus* | Anacardiaceae | 2 | 2 |
| 161 | *Spondias pinnata* | Anacardiaceae | 2 | 2 |
| 162 | *Sterculia foetida* | Malvaceae | 1 | 1 |
| 163 | *Sterculia guttata* | Malvaceae | 9 | 8 |
| 164 | *Sterculia urens* | Malvaceae | 1 | 1 |

| 165 | *Stereospermum colais* | Bignoniaceae | 38 | 22 |
| 166 | *Strombosia ceylanica* | Olacaceae | 12 | 3 |
| 167 | *Strychnos nux-vomica* | Loganiaceae | 8 | 7 |
| 168 | *Symplocos macrophylla* | Symplocaceae | 89 | 16 |
| 169 | *Syzygium caryophyllatum* | Myrtaceae | 18 | 9 |
| 170 | *Syzygium cumini* | Myrtaceae | 249 | 64 |
| 171 | *Syzygium gardneri* | Myrtaceae | 1 | 1 |
| 172 | *Syzygium hemisphericum* | Myrtaceae | 48 | 12 |
| 173 | *Syzygium rubicundum* | Myrtaceae | 9 | 4 |
| 174 | *Tabernaemontana alternifolia* | Apocynaceae | 116 | 40 |
| 175 | *Tamilnadia uliginosa* | Rubiaceae | 3 | 3 |
| 176 | *Tectona grandis* | Lamiaceae | 118 | 13 |
| 177 | *Terminalia bellirica* | Combretaceae | 60 | 28 |

| 178 | *Terminalia chebula* | Combretaceae | 25 | 11 |
| 179 | *Terminalia elliptica* | Combretaceae | 298 | 41 |
| 180 | *Terminalia paniculata* | Combretaceae | 437 | 49 |
| 181 | *Tetrameles nudiflora* | Tetramelaceae | 1 | 1 |
| 182 | *Tetrapilus dioicus* | Oleaceae | 125 | 31 |
| 183 | *Tritaxis glabella* | Euphorbiaceae | 45 | 5 |
| 184 | *Vitex altissima* | Lamiaceae | 7 | 2 |
| 185 | *Wendlandia thyrsoidea* | Rubiaceae | 2 | 2 |
| 186 | *Wrightia arborea* | Apocynaceae | 22 | 6 |
| 187 | *Wrightia tinctoria* | Apocynaceae | 23 | 9 |
| 188 | *Xantolis tomentosa* | Sapotaceae | 151 | 37 |
| 189 | *Xylia xylocarpa* | Fabaceae | 120 | 16 |
| 190 | *Zanthoxylum rhetsa* | Rutaceae | 45 | 15 |

| 191 | *Ziziphus rugosa* | Rhamnaceae | 1 | 1 |
| 192 | *Ziziphus xylopyrus* | Rhamnaceae | 1 | 1 |

717

718   **Table S2.** Treatment contrast table showing coefficient estimates and associated 95% CI for the

719   Generalized linear model with Poisson error structure that examined relationship between

720   observed species richness per plot (not including lianas) ($\geq$ 10 cm GBH) and climatic water

721   deficit and land-use categories. Pseudo $R^2$ = 0.09.

| Predictor variable | Estimate (95% CI) | $p$ |
|---|---|---|
| Intercept: Less-disturbed forests | 5.17 (3.41– 6.94 ) | < 0.001 |
| Historically-disturbed forests | -0.73 (-3.54 – 2.07) | 0.61 |
| Repeatedly-disturbed forests | -3.12 (-5.68 – -0.58) | 0.016 |
| Climatic water deficit (CWD) | 0.002 (0.001 – 0.004) | 0.006 |
| CWD $\times$ Historically-disturbed forests | -0.001 (-0.004 – 0.002) | 0.62 |
| CWD $\times$ Repeatedly-disturbed forests | -0.003 (-0.006 – -0.0005) | 0.02 |

722

723 **Table S3.** Treatment contrast table showing coefficient estimates and associated 95% CI for the

724 General linear model with Gaussian error structure that examined the relationship between the

725 square root of basal area ($m^2ha^{-1}$) and CWD and land-use categories. $R^2 = 0.51$.

| Predictor variable | Estimate (95% CI) | $p$ |
|---|---|---|
| Intercept: Less-disturbed forests | 13.23 (5.84 – 26.13) | < 0.001 |
| Historically-disturbed forests | 2.76 (-1.8×10$^{-4}$ – 0.02) | 0.68 |
| Repeatedly-disturbed forests | -29.17 (-44.9 – -19.00) | < 0.001 |
| Climatic water deficit (CWD) | 0.01 (-15.9 – 10.36) | 0.1 |
| CWD × Historically-disturbed forests | 0.003 (-0.048 – -0.019) | 0.66 |
| CWD × Repeatedly-disturbed forests | -0.03 (-0.018 – 0.01) | < 0.001 |

726

727 **Table S4.** Table summarises information (Mean ± SE) on tree density, basal area, canopy cover

728 and number of cut stems per plot across different land-use categories in low and high elevations.

| Structural variables | Repeatedly-disturbed forests (Low) | Repeatedly-disturbed forests (High) | Historically-disturbed forests (Low) | Historically-disturbed forests (High) | Less-disturbed forests (Low) | Less-disturbed forests (High) |
|---|---|---|---|---|---|---|
| | | | | | | |

| Tree density $(ha^{-1})$ | 1081 ($\pm$90.7) | 889 ($\pm$99.2) | 1137 ($\pm$81.9) | 1565 ($\pm$185.8) | 1041 ($\pm$106.9) | 1288 ($\pm$112.4) |
|---|---|---|---|---|---|---|
| Basal area ($m^2$ $ha^{-1}$) | 24.3 ($\pm$ 2.9) | 11.2 ($\pm$ 2.3) | 32.3 ($\pm$ 3.3) | 42.6 ($\pm$ 2.7) | 36.2 ($\pm$ 2.6) | 46.4 ($\pm$ 5.5) |
| Canopy cover (%) | 39.6 ($\pm$2.2) | 14.1 ($\pm$2.9) | 48.6 ($\pm$2.4) | 45.4 ($\pm$1.3) | 46.5 ($\pm$2.6) | 50 ($\pm$1.5) |
| Number of cut stems per plot | 15.8 ($\pm$ 3.3) | 24.7 ($\pm$ 3.3) | 6.2 ($\pm$ 1.3) | 2.2 ($\pm$ 1.3) | 5.0 ($\pm$ 1.1) | 10 ($\pm$ 2.4) |

729

730 **Table S5.** Treatment contrast table showing coefficient estimates and associated 95% CI for the

731 Generalized linear model with binomial error structure that examined relationship between

732 proportion of evergreen individuals ($\geq$ 10 cm GBH) and climatic water deficit and land-use

733 categories. Pseudo $R^2 = 0.38$.

| Predictor variable | Estimate (95% CI) | $p$ |
|---|---|---|
| Intercept: Less-disturbed forests | 28.44 (25.28 – 31.74) | < 0.001 |
| Historically-disturbed forests | -7.88 (-11.92 – 3.92) | < 0.001 |
| Repeatedly-disturbed forests | -12.52 (-16.44 – -8.69) | < 0.001 |
| Climatic water deficit (CWD) | 0.03 (0.026 – 0.034) | < 0.001 |

| | | |
|---|---|---|
| CWD × Historically-disturbed forests | -0.008 (-0.012 – -0.003) | < 0.001 |
| CWD × Repeatedly-disturbed forests | -0.012 (-0.016 – -0.008) | < 0.001 |

734

735 **Table S6.** Treatment contrast table showing coefficient estimates and associated 95% CI for the

736 Generalized linear model with Poisson error structure that examined the relationship between the

737 number of evergreen tree species (not including lianas) (≥ 10 cm GBH) and climatic water

738 deficit and land-use categories. Pseudo $R^2 = 0.33$.

| Predictor variable | Estimate (95% CI) | $p$ |
|---|---|---|
| Intercept: Less-disturbed forests | 9.96 (7.85 – 12.11) | < 0.001 |
| Historically-disturbed forests | 1.16 (-2.36 – 4.69) | 0.52 |
| Repeatedly-disturbed forests | -3.99 (-7.41 – -0.56) | 0.02 |
| Climatic water deficit (CWD) | 0.009 (0.006 – 0.01) | < 0.001 |
| CWD × Historically-disturbed forests | 0.0014 (-0.002 – 0.005) | 0.48 |
| CWD × Repeatedly-disturbed forests | -0.004 (-0.008 – 0.00005) | 0.052 |

739

740 **Table S7.** Treatment contrast table showing coefficient estimates and associated 95% CI for the

741 Generalized linear model with Poisson error structure that examined the relationship between the

742    number of deciduous tree species (not including lianas) ($\geq$ 10 cm GBH) and climatic water

743    deficit and land-use categories. Pseudo $R^2 = 0.36$.

| Predictor variable | Estimate (95% CI) | $p$ |
|---|---|---|
| Intercept: Less-disturbed forests | -11.4 (-15.4 – -7.5 ) | < 0.001 |
| Historically-disturbed forests | 1.89 (-3.8 – 7.5) | 0.51 |
| Repeatedly-disturbed forests | 8.5 (3.8 – 13.3) | < 0.001 |
| Climatic water deficit (CWD) | -0.014 (-0.02 – -0.01) | < 0.001 |
| CWD $\times$ Historically-disturbed forests | 0.002 (-0.004 – 0.008) | 0.56 |
| CWD $\times$ Repeatedly-disturbed forests | 0.009 (0.004 – 0.014) | < 0.001 |

744

745
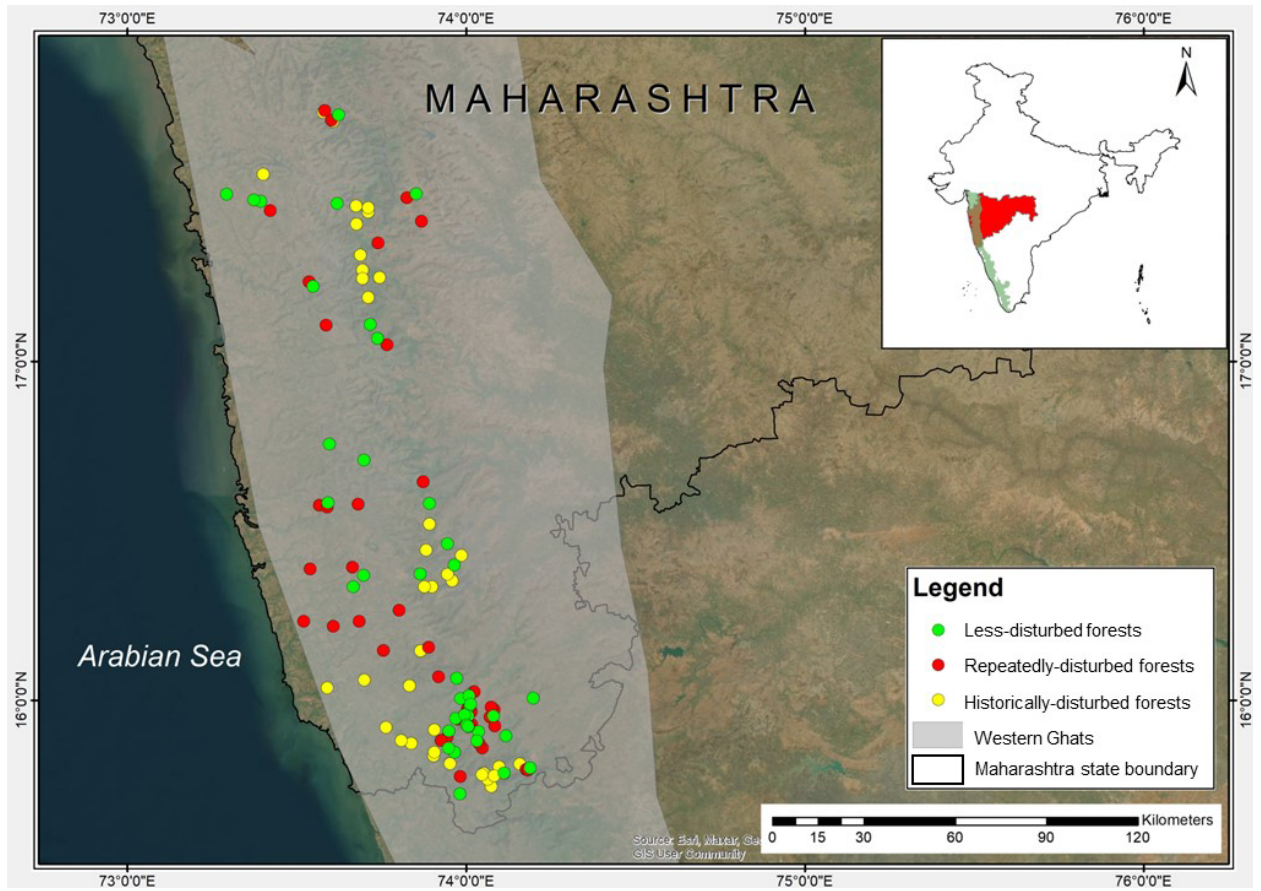
**Figure S1.** Map showing the vegetation plots distributed in our study region in Maharashtra state in India. The three forest categories are spread across low (8–514 m ASL) and high elevations (577–1054 m ASL).

750
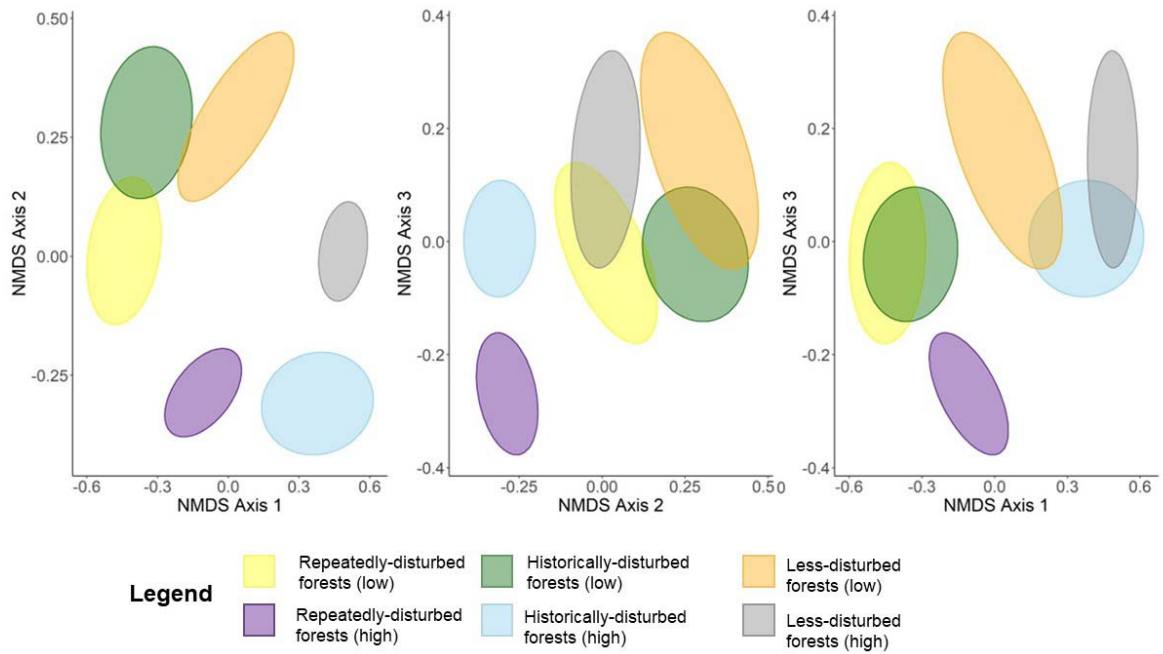
**Figure S2.** Plot of Non-metric Multidimensional Scaling showing differences in plant composition between low and high elevations and between the different land-use categories.
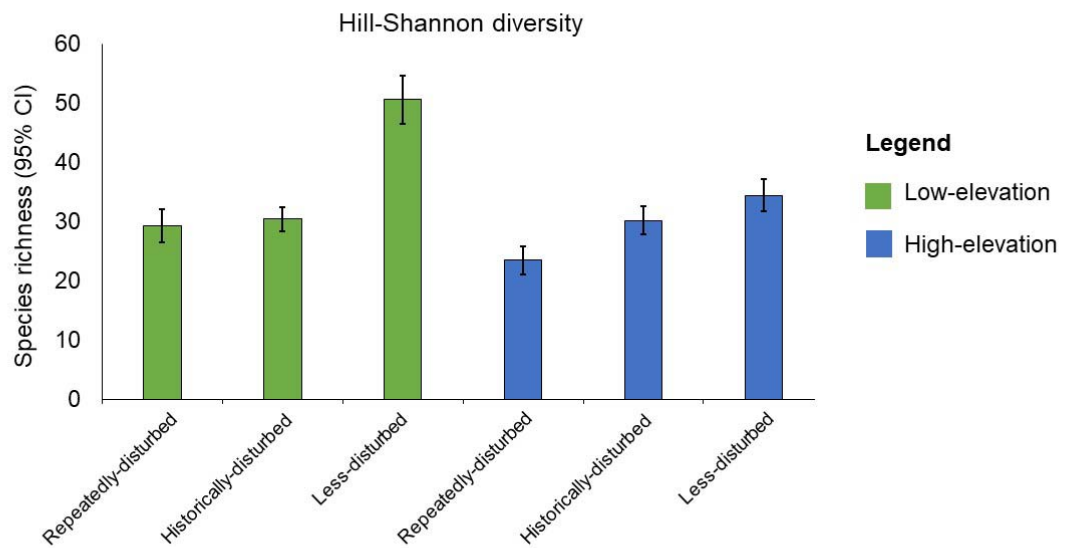


753

754     **Figure S3**. Hill-Shannon diversity (95% CI) of the three different land-use types, across low and

755     high elevations clearly showing significantly higher diversity of woody plants in less-disturbed

756     low elevation forests. We used the sample-coverage-based method to estimate the species

757     richness of plant communities in the different forest categories (low and high, less-, historically-

758     and repeatedly-disturbed forests) (Roswell et al. 2021). The least sample coverage was in the

759     low-elevation sacred groves (97%). Therefore, we rarefied the diversity measure of all other

760     categories to 97% sample coverage. We bootstrapped the data 50 times to estimate 95%

761     confidence intervals.

762
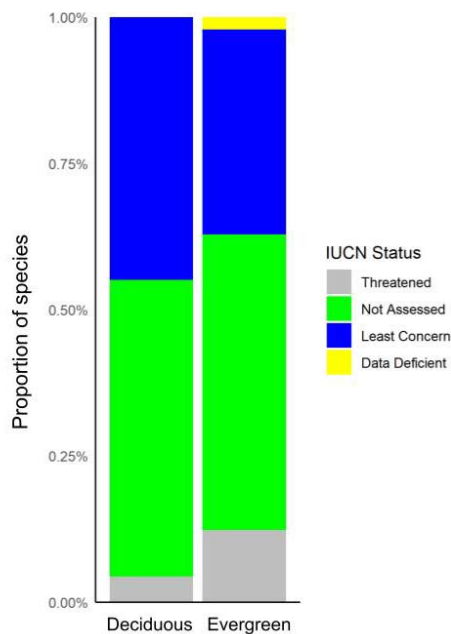


763

764     **Figure S4.** The stacked bar plot demonstrates that almost 50% of the plant species in this study

765     have not been assessed. It also demonstrates that the proportion of threatened evergreen species

766     is almost twice that of the deciduous species. This study will contribute to generating important

767     information about the not-assesed, Data Deficient and Threatened species for the region.