

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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18

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<sup>2</sup> 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<sup>2</sup> landscape in the northern Western  
164 Ghats (Fig. S1). To capture the gradients of CAD and climate, we laid 120 50×10m<sup>2</sup> 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  $\geq 10$   
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-](http://chave.ups-tlse.fr/pantropical_allometry.htm#CWD)  
187 [tlse.fr/pantropical\\_allometry.htm#CWD](http://chave.ups-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 ( $\text{m}^2 \text{ha}^{-1}$ ). 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 ( $\pm 1.7$ )  $\text{m}^2/\text{ha}$ . A summary of tree richness is  
219 presented in Figure S3.

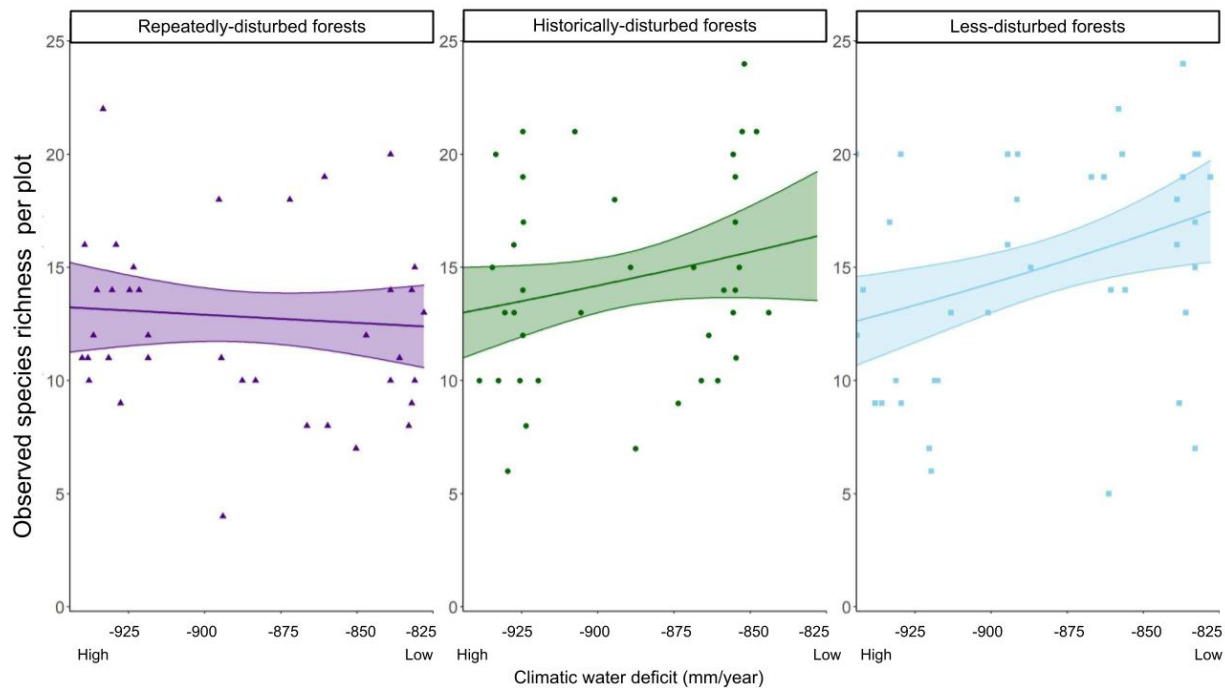
## 220 **Woody plant composition across land-use types**

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).

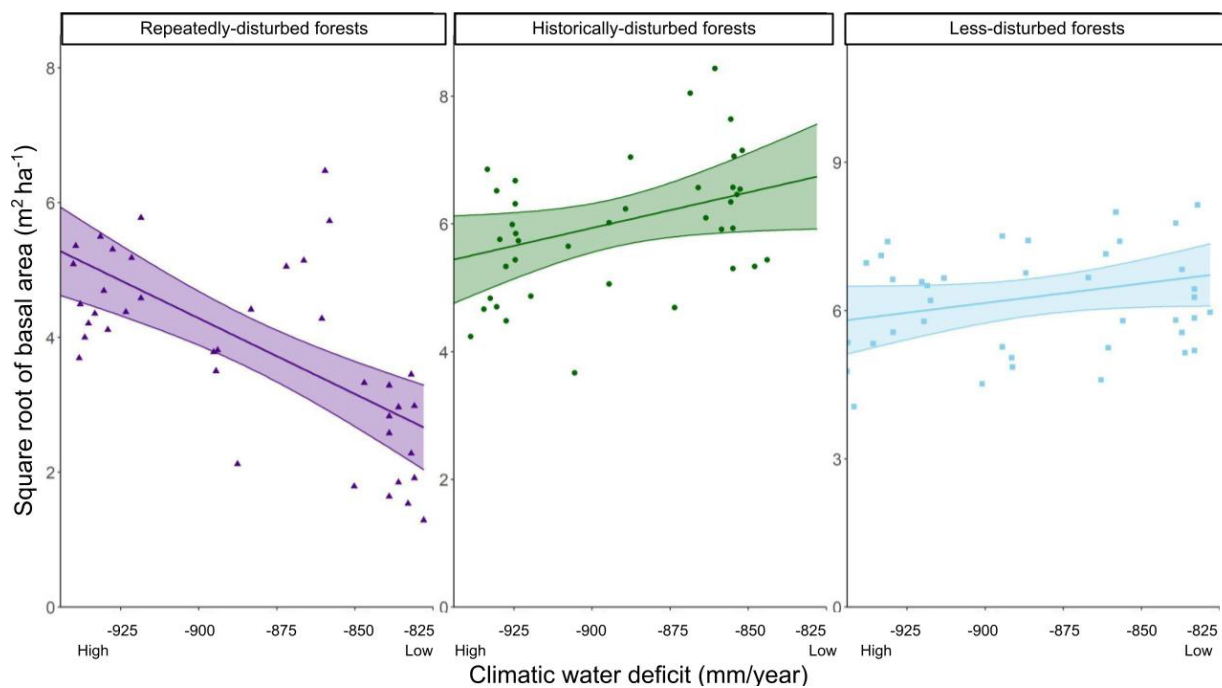


231 **Figure 1.** Plots showing the relationship between climatic water deficit and observed species  
232 richness per plot across the three disturbance categories. The solid line with a band indicates the  
233 best-fitted line for the Generalized Linear Model (Poisson error structure) with associated 95%  
234 CI. Higher values of CWD (less negative) imply lower water stress experienced by plants.

235

### 236 **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.



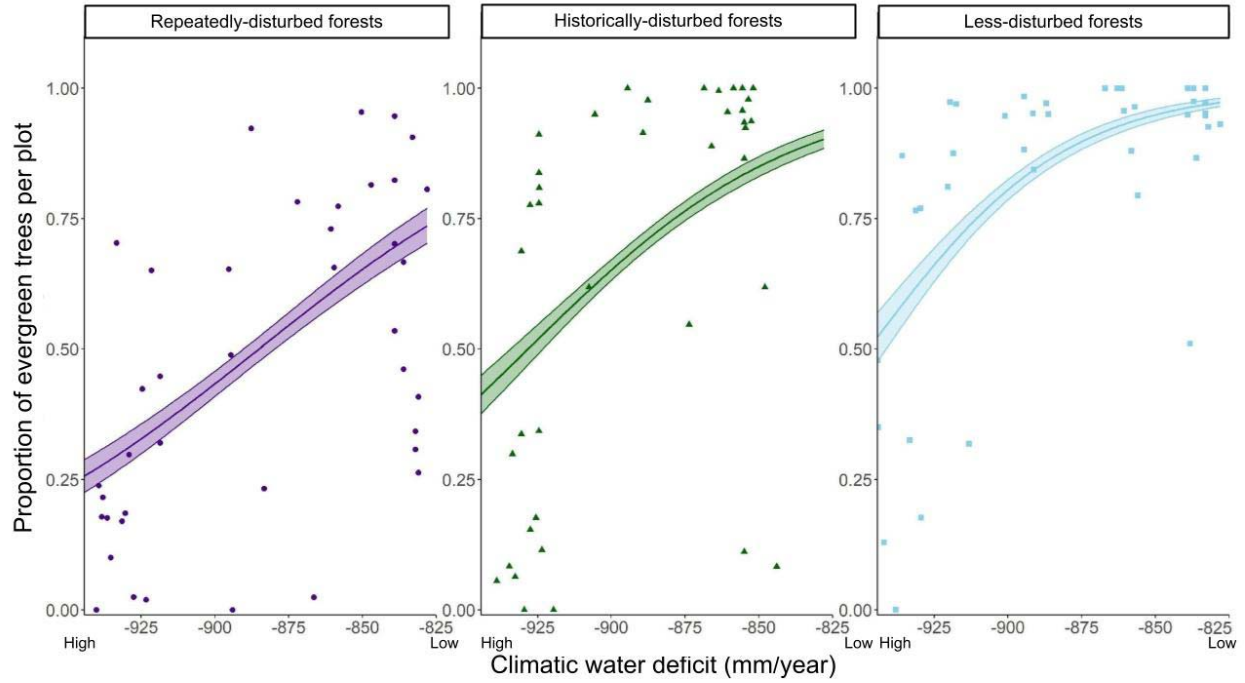
244

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

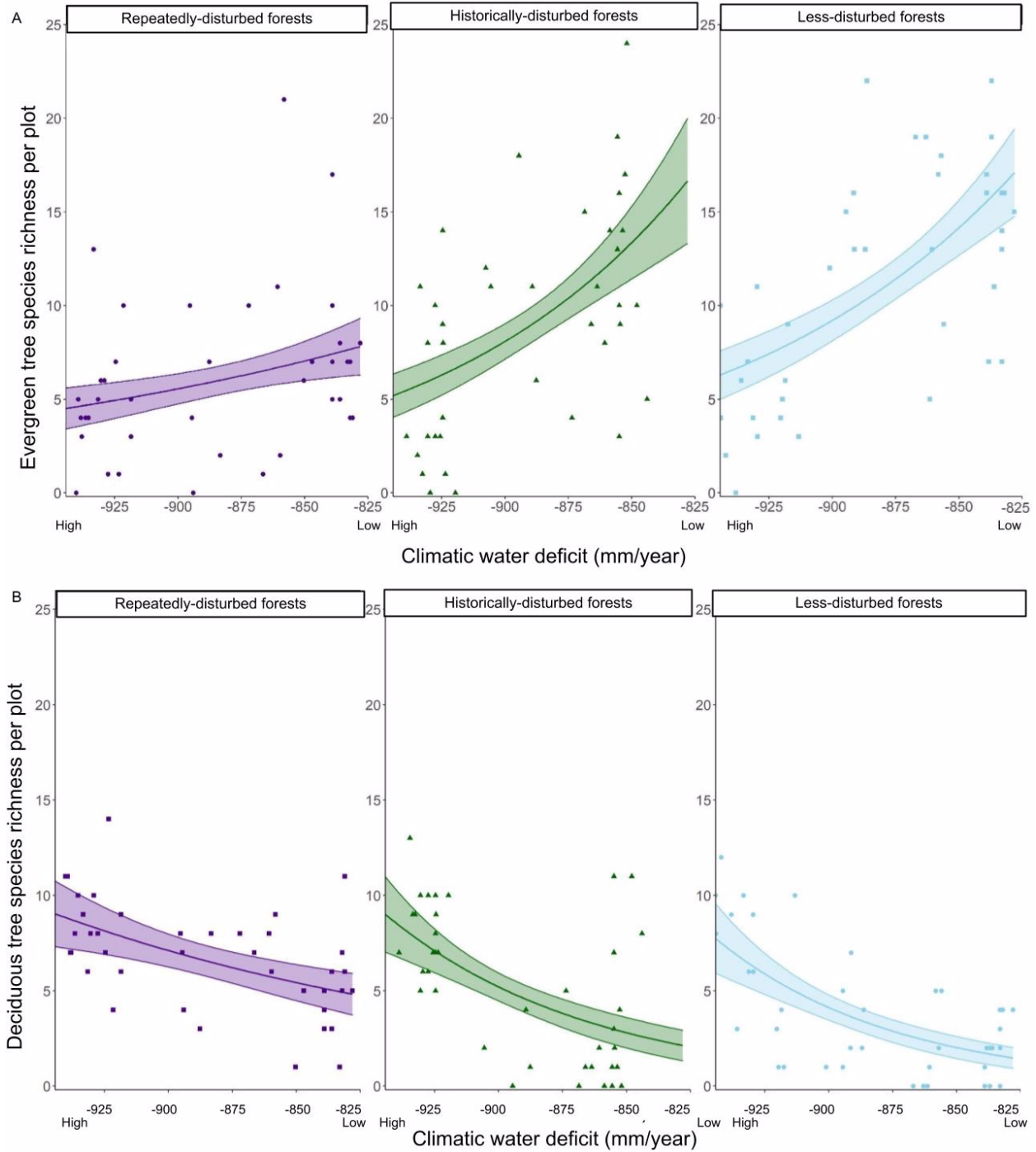
250 **Influence of CAD and CWD on the proportion of evergreen trees and richness of evergreen**  
251 **and deciduous trees**

252 The GLM results showed that the interaction terms between CWD and disturbance category  
253 significantly affected the proportion and richness of evergreen trees. The proportion of evergreen  
254 trees per plot increased with the increase in CWD values (which implies less water deficit) and  
255 this increase was the fastest in less-disturbed forests and slowest in repeatedly-disturbed forests  
256 (Pseudo  $R^2 = 0.38$ , Fig. 3; Table S5). In regions with low CWD values (indicating higher water  
257 deficit i.e., drier areas), the predicted proportion of evergreen trees is more than 0.5 for less-  
258 disturbed forests but only 0.25 for repeatedly disturbed forests, indicating dominance of  
259 deciduous trees in repeatedly-disturbed sites (Fig. 3). In regions with high CWD values  
260 (indicating lower water deficit i.e., wetter areas) the predicted proportion of evergreen trees for  
261 less-disturbed forests was close to 1 but for repeatedly-disturbed forests it was around 0.75.  
262 Similarly, the increase in the number of evergreen tree species per plot with decreasing CWD  
263 was very fast for less- and historically-disturbed sites but gradual for the repeatedly-disturbed  
264 sites, indicating that disturbance negatively impacted evergreen tree species richness (Pseudo  $R^2$   
265 = 0.33, Fig. 4A; Table S6). Consequently, the deciduous species richness per plot rapidly  
266 decreased with decreasing CWD for less-disturbed and historically-disturbed sites but this  
267 decrease was significantly more gradual in repeatedly disturbed sites (Pseudo  $R^2 = 0.36$ , Fig. 4B;  
268 Table S7).



269

270 **Figure 3.** Plots showing the relationship between climatic water deficit and proportion of  
271 evergreen tree individuals per plot across the three disturbance categories. The solid line with a  
272 band indicates the best fitted line for the Generalized Linear Model (binomial error structure)  
273 with associated 95% CI. Higher values of CWD (less negative) imply lower water stress  
274 experienced by plants.



275

276 **Figure 4.** Plots showing the relationship between climatic water deficit and number of evergreen  
277 tree species per plot (A) and number of deciduous tree species per plot (B) across the three  
278 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 (Baldochi 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 evergreenness 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<sup>2</sup>) (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.

#### 407 **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 × 10 m<sup>2</sup>) 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	<i>Acacia auriculiformis</i>	Fabaceae	3	2
2	<i>Actephila excelsa</i>	Phyllanthaceae	1	1
3	<i>Actinodaphne lanceolata</i>	Lauraceae	21	10
4	<i>Adina cordifolia</i>	Rubiaceae	3	1
5	<i>Aglaia elaeagnoidea</i>	Meliaceae	46	12
6	<i>Aglaia lawii</i>	Meliaceae	51	13
7	<i>Agrostistachys indica</i>	Euphorbiaceae	4	1
8	<i>Albizia lebbek</i>	Fabaceae	20	7

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

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

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

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

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



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

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

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

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

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

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

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

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



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

191	<i>Ziziphus rugosa</i>	Rhamnaceae	1	1
192	<i>Ziziphus xylopyrus</i>	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)	<i>p</i>
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 ( $\text{m}^2\text{ha}^{-1}$ ) and CWD and land-use categories.  $R^2 = 0.51$ .

Predictor variable	Estimate (95% CI)	<i>p</i>
Intercept: Less-disturbed forests	13.23 (5.84 – 26.13)	< 0.001
Historically-disturbed forests	2.76 ( $-1.8 \times 10^{-4}$ – 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 <sup>-1</sup> )	1081 (±90.7)	889 (±99.2)	1137 (±81.9)	1565 (±185.8)	1041 (±106.9)	1288 (±112.4)
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	24.3 (± 2.9)	11.2 (± 2.3)	32.3 (± 3.3)	42.6 (± 2.7)	36.2 (± 2.6)	46.4 (± 5.5)
Canopy cover (%)	39.6 (±2.2)	14.1 (±2.9)	48.6 (±2.4)	45.4 (±1.3)	46.5 (±2.6)	50 (±1.5)
Number of cut stems per plot	15.8 (± 3.3)	24.7 (± 3.3)	6.2 (± 1.3)	2.2 (± 1.3)	5.0 (± 1.1)	10 (± 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)	<i>p</i>
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) ( $\geq 10$  cm GBH) and climatic water  
 738 deficit and land-use categories. Pseudo  $R^2 = 0.33$ .

Predictor variable	Estimate (95% CI)	<i>p</i>
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

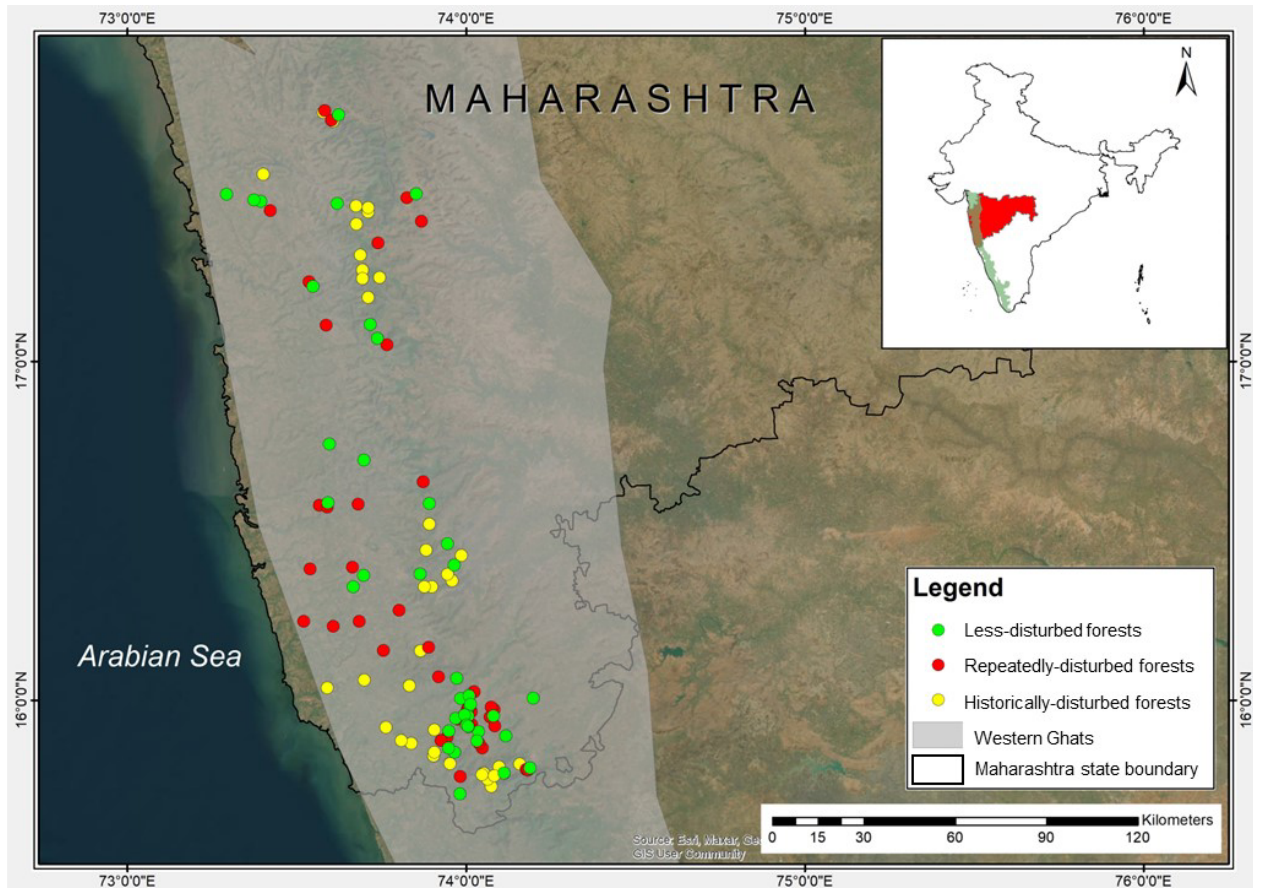
740 **Table S7.** Treatment contrast table showing coefficient estimates and associated 95% CI for the  
 741 Generalized linear model with Poisson error structure that examined the relationship between the

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)	<i>p</i>
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

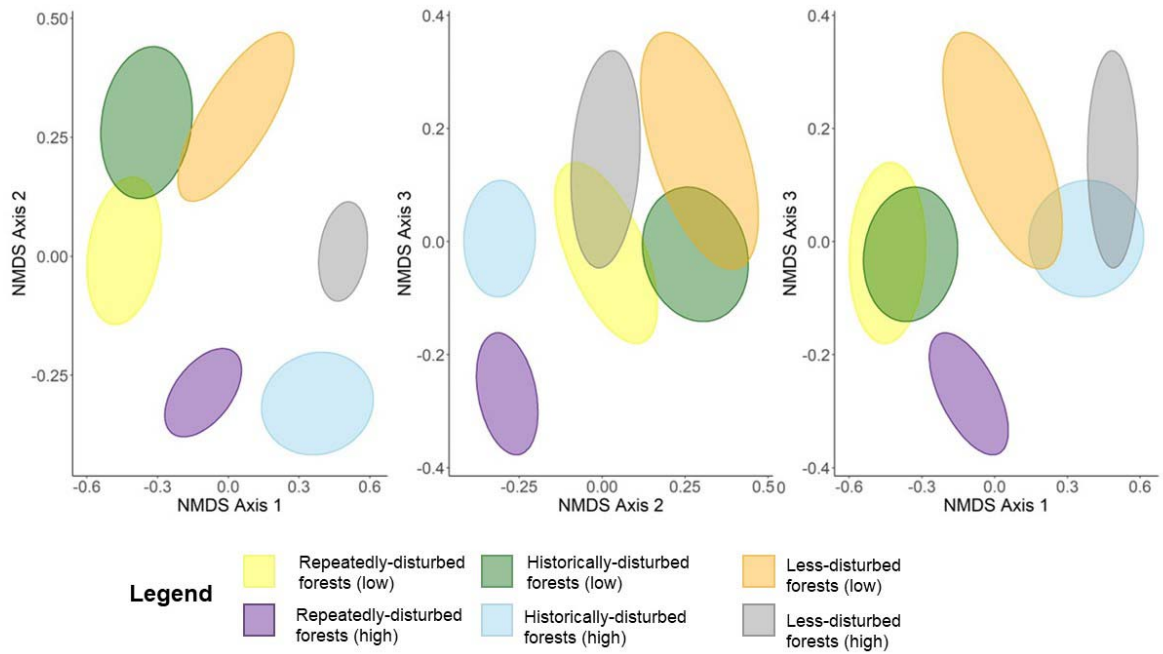
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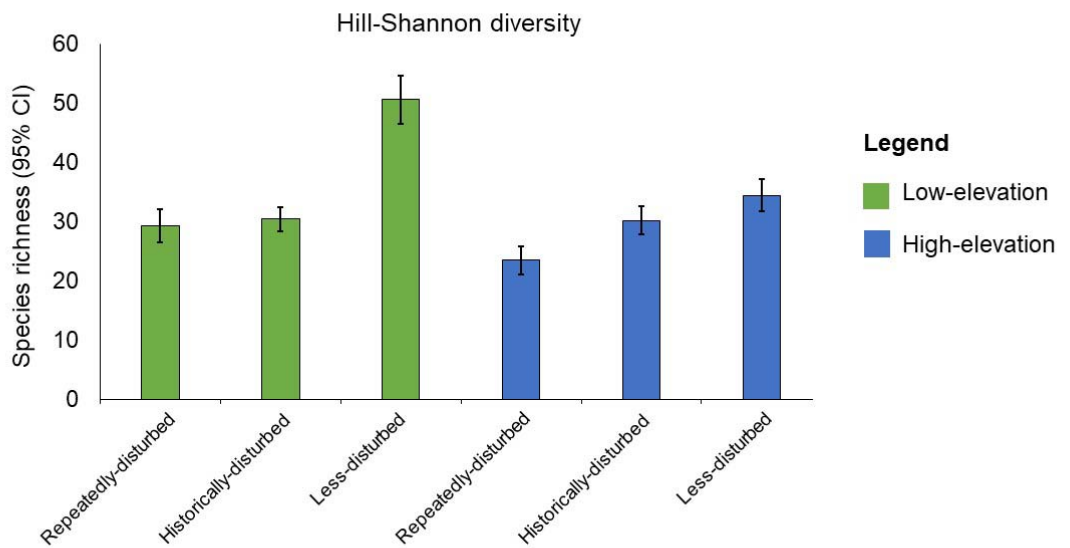
746

747 **Figure S1.** Map showing the vegetation plots distributed in our study region in Maharashtra state  
748 in India. The three forest categories are spread across low (8–514 m ASL) and high elevations  
749 (577–1054 m ASL).



750

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

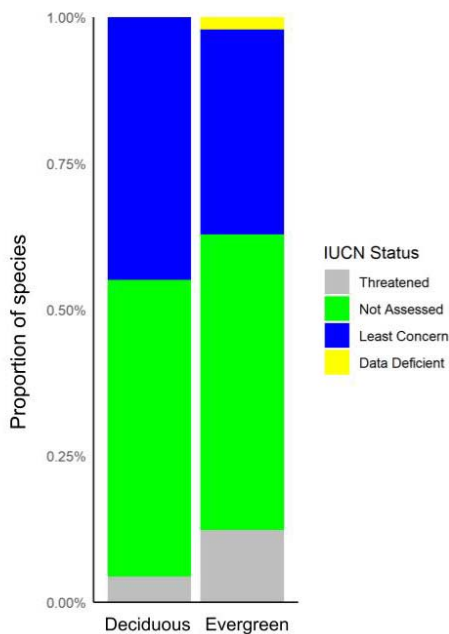


753



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-assessed, Data Deficient and Threatened species for the region.