

Insights into the forests of Darién, Panama, from the new 10 ha Bacurú Drõa plot established through participatory methods within an Emberá territory.

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Abstract:	Networks of forest plots are a key for documenting how forests are responding to climate change, however very few plots are in inaccessible locations and almost no research is carried out in Indigenous territories. We present the first data from a new forest plot co-developed with the Traditional Emberá Authorities of the Balsa River Collective Lands, Darién, Panama: The Bacurú Drõa plot ("Old Growth Forests" in Emberá). We compare floristic characteristics and conservation status of trees in Bacurú Drõa with those of 53 forest plots established across Panama. In Bacurú Drõa, trees with DBH \geq 10 cm were classified in 290 taxonomic units with 60% of taxa identified to species (174 species), 49 assigned to genera and 22 to families leaving 45 unidentified tree taxa. On a per ha basis, stem density and species richness differed significantly amongst plots and groups of plots, both variables being highest in plots located in the Alto Chagres and lowest in the plots located along the Pacific. Estimates of species number for stem density in 1 ha, however, are significantly higher in Bacurú Drõa. Conservation value, measured through community weighted mean (CWM) range and CWM International Union for Conservation value when compared to the other ForestGEO plots in Panama. We contrasted IUCN values with assigned by the Emberá people, showing that tree species with important cultural values have relatively low IUCN scores. We show that Bacurú Drõa has high biodiversity, many singletons, and many unidentified species, consistent with other plots in the Chocó-Darién Ecoregion, an understudied global biodiversity hotspot. Overall, Bacurú Drõa provides a blueprint on how tropical forest research can value and benefit from the contribution of the Indigenous communities that live and conserve the vanishing intact forests of the world.

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3 Abstract

Networks of forest plots are a key for documenting how forests are responding to climate 4 5 change, however very few plots are in inaccessible locations and almost no research is carried 6 out in Indigenous territories. We present the first data from a new forest plot co-developed 7 with the Traditional Emberá Authorities of the Balsa River Collective Lands, Darién, 8 Panama: The Bacurú Drõa plot ("Old Growth Forests" in Emberá). We compare floristic 9 characteristics and conservation status of trees in Bacurú Drõa with those of 53 forest plots established across Panama. In *Bacurú Drõa*, trees with DBH \geq 10 cm were classified in 290 10 taxonomic units with 60% of taxa identified to species (174 species), 49 assigned to genera 11 12 and 22 to families leaving 45 unidentified tree taxa. On a per ha basis, stem density and species richness differed significantly amongst plots and groups of plots, both variables being 13 highest in plots located in the Alto Chagres and lowest in the plots located along the Pacific. 14 15 Estimates of species number for stem density in 1 ha, however, are significantly higher in Bacurú Drõa. Conservation value, measured through community weighted mean (CWM) 16 range and CWM International Union for Conservation of Nature (IUCN) score revealed 17 Bacurú Drõa to be of high conservation value when compared to the other ForestGEO plots 18 19 in Panama. We contrasted IUCN values with assigned by the Emberá people, showing that 20 tree species with important cultural values have relatively low IUCN scores. We show that 21 *Bacurú Drõa* has high biodiversity, many singletons, and many unidentified species, consistent with other plots in the Chocó-Darién Ecoregion, an understudied global 22 23 biodiversity hotspot. Overall, Bacurú Drõa provides a blueprint on how tropical forest research can value and benefit from the contribution of the Indigenous communities that live 24 25 and conserve the vanishing intact forests of the world.

26 Introduction

27 Indigenous Peoples' lands — areas owned, managed, or used by Indigenous Peoples — are key to large-scale land conservation, and overlap with 37% of remaining natural lands (Garnett 28 et al. 2018). More than 25% of tropical forests are within Indigenous Peoples' lands, and these 29 30 areas have lower deforestation and degradation compared to non-protected areas and similar levels of disturbance to protected areas (Sze et al. 2024). Thus, Indigenous Peoples' lands 31 32 protect biodiversity and provide multiple ecosystem services, including climate regulation and carbon sequestration, while supporting Indigenous Peoples (Watson et al. 2018). The Emberá 33 34 Collective land of the Balsa River in the Darién province of Panama illustrates this perfectly (Figure 1). Old-growth forests cover 98% of this territory with only 1.3% of the land used for 35 sustainable swidden-fallow agriculture (Kunz et al. 2022). The > 125,000 ha Emberá Collective 36 37 Land of the Balsas River has consistently high Forest Landscape Integrity indices (FLII) (FLII values > 9 sensu (Grantham et al. 2020); See Appendix S1). 38

Here, we present the first data from a new forest plot established to fill gaps in tropical 39 40 ecological research; namely that many study areas are located in accessible locations and almost no research is carried out in Indigenous territories (Carvalho et al. 2023). The Bacurú 41 Drõa plot ("Old Growth Forest" in the Emberá language) was co-developed with the 42 Traditional Authorities of the Emberá Collective Lands of the Balsa River, who welcomed the 43 44 scientific team on their territory. This plot forms the heart of a community-driven Old-Growth 45 Forest Observatory implemented following a methodology of participatory action research (PAR) in which the Emberá play a central role in deciding the next steps in the research process 46 (McGregor 2002; Holmes, Potvin, and Coomes 2017). Principles of PAR include the active 47 48 participation of community members and researchers in decision-making, action, and developing critical consciousness for co-constructing knowledge. PAR allows the mobilization 49 50 of multiple knowledge and governance systems that complement western knowledge, resulting

in improved understanding and management of tropical forests (Malmer 2020; Ometto 2022). The biocentric approach (Zanotti and Knowles 2020) of *Bacurú Drõa* plot recognizes that the Emberá are key actors of forest conservation and holders of knowledge. To ground our research in the way of life of Indigenous Peoples' and to respect the connection between cultural and biological diversity (Nemogá, Appasamy, and Romanow 2022), *Bacurú Drõa* considers scientific and traditional knowledge, community development, and Indigenous rights (Appendix S1.2) as core to its methodology.

58 The Emberá Collective Lands of the Balsa River are located in the Chocó-Darién 59 Ecoregion, the second largest intact forest area in the Americas after the Amazon (Potapov et al. 2017) and a global biodiversity hotspot (Myers et al. 2000; Brooks et al. 2002). A time-60 series of maps from 2002 to 2015 show that the best conserved forests of the Chocó-Darién 61 62 Ecoregion are in the Darién region of Panama (Fagua and Ramsey 2019). Scientific interest 63 in establishing a plot in the Balsa territory followed forest inventories reporting some of the highest tree diversity and carbon stocks in the Neotropics (Mateo-Vega, Arroyo-Mora, and 64 65 Potvin 2019; Kunz et al. 2022). The Chocó-Darién flora is derived mostly from Andean immigrants (Pérez-Escobar et al. 2019). Botanist Alwin Gentry suggested that this Ecoregion 66 likely hosted "more vet-to-be-described species than anywhere else in the world" (Gentry 67 1986), and further botanical work in the Chocó-Darién Ecoregion confirmed Gentry's initial 68 69 perception of an unusual and highly diverse flora (Faberlangendoen and Gentry 1991; 70 Quinto-Mosquera, Hurtado, and Alboleda 2019; Quinto Mosquera and Moreno Hurtado 71 2014). Few studies have taken place in Darién as it is remote, difficult to access and has a 72 reputation as inhospitable (Runk 2015); as a result it remains one of the most poorly 73 described regions of the world in terms of botany (Kolanowska 2015).

The scientific value of forest inventory plots has grown with the creation of plot networks
that share common protocols and data (Phillips 2023). For example, networks of forest plots

are a key tool for documenting how forests across the world are responding to climate change
(Moonlight et al. 2021). Panama has been central to the development of forest plot protocols
with the establishment of the 50-hectare (ha) Forest Dynamic Plot (BFDP) on Barro Colorado
Island (BCI) in 1983. Here, we compare floristic characteristics and conservation status of trees
in the new *Bacurú Drõa* plot with those of 53 other forest plots established across Panama by
Smithsonian ForestGEO (formerly the Center for Tropical Forest Study; (Ibáñez et al. 2002;
Condit et al. 2001; Davies et al. 2021).

The forest plots in Panama are at locations varying in rainfall, cloud cover, and elevation, 83 84 and with different levels of historical land use, all of which influence the diversity and biological patterns in the plots (for additional information see Figure 1 and methods), for 85 example forest types across these plots vary from cloud forest (Alto Chagres) to dry forests 86 87 (Pacific). Bacurú Drõa is expected to resemble most closely to the forests studied in the larger Chocó-Darién Ecoregion, which are reported to have similar flora to cloud forests (Gentry 88 1986). These forests, reputed for extremely high rainfall (Quinto Mosquera and Moreno 89 90 Hurtado 2014), are characterised by a high number of singletons (Toasa, Morochz, and Oleas 2020; Quinto Mosquera and Moreno Hurtado 2014; Faberlangendoen and Gentry 1991), high 91 92 biodiversity (Cámara-Leret et al. 2016; Gentry 1986), and many endemic and unidentified species (Gentry 1986; Quinto Mosquera and Moreno Hurtado 2014), as well as the hyper 93 94 dominance of a few families (Gentry 1986; Quinto Mosquera and Moreno Hurtado 2014; 95 Forero 1989).

96 In this paper, we focus on three main questions:

97 1. How does the species composition and the conservation status of trees of the *Bacurú*98 *Drõa* plot compare with those of other forest plots in Panama, given our expectation that sites
99 with higher rainfall and lower fragmentation (like the Darién) will have higher species
100 richness?

2. Are characteristic elements of the Chocó-Darién forests such as high diversity, high
 number of singletons, high family dominance, and many potentially new species or species not
 reported in Panama also observed in this Darién Forest?

104 3. How does the conservation value of tree species as assigned by scientists compare with105 the cultural value assigned by the Emberá?

In his plea to use forest plots as a method to understand our living planet, (Phillips 2023)
states "*Many of the greatest needs and opportunities in tropical forest science are therefore not to be found in space or in silico, but in vivo, with the people, places and plots who*

109 *experience nature directly*". He concludes by calling for a new deal where tropical forest

research will value the contribution of the grassroot communities that live and conserve the

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111 vanishing intact forests of the world. This is *Bacurú Drõa*.

112

113 Methods

114 Bacurú Drõa Plot Establishment

Prior to the establishment of the plot, the research team followed ethical relationship 115 building processes, sensu Levitan 2019, with the communities in the region over the long 116 term (Mateo-Vega et al. 2017). This included following traditional Emberá practices for 117 118 requesting permission to create the plot through the signature of a Cooperation Agreement, sharing the findings with the communities, and consulting on important matters, such as 119 120 treatment of the forest and fair employment practices. Once permission was granted and a 121 plan confirmed, the first 10 ha of the Bacurú Drõa plot were surveyed and censused for trees \geq 10 cm in diameter in 2022 following the ForestGEO (formerly the Center for Tropical 122 Forest Study) standardized methodology (Condit 1998; ForestGEO 2023). The coordinates of 123 the south-western corner of the plot are 7.86007°N, 77.81921°W (+-5m GPS accuracy; 124

125 Figure 1). Seven Emberá technicians (Co-authors A.O., D.C., E.D., E.M., H.F., I.D., W.V.) were initially trained by ForestGEO professionals (Co-authors S.A., D.M. and R.P.) in and 126 near Barro Colorado Island over 9 days. This group formed the core technical team consisting 127 128 of two teams of six Emberá men and women who established the plot, and subsequently 129 mapped and measured the trees. The 10 ha plot is 200 m x 500 m, with the longer edge oriented towards magnetic north. The plot is subdivided into 20 by 20 m quadrats, whose 130 131 boundaries were established using a Ushikata Tracon S-25 optical theodolite and measuring tapes to control for slope. All trees with a diameter at breast height (DBH) ≥ 10 cm were 132 133 tagged, measured, and mapped in 2022.

Once all trees were mapped, measured, and tagged, co-author J.V. alongside 4 youth and 4 134 elders worked on tree identification and collection using both Emberá and scientific 135 taxonomy. Co-author J.V., with the help of ForestGEO professionals R.P. and S.A., identified 136 137 individuals to the lowest possible taxonomic level. The identifications were based on highresolution photographs, field notes, and botanical specimens. Photographs were taken with a 138 Canon PowerShot SX70 HS 4K camera and included buttress roots, stem, leaves, and, where 139 140 possible, reproductive structures. Field notes included information on bark, latex, wood 141 colour, stem branching, and root type. Scientific species identification was aided by 142 published floras: Trees of Panama and Costa Rica (Condit 2011), Trees and Shrubs of Panama (Carrasquilla R. 2006), Árboles Comunes del Yasuní (Villa Muñoz 2015), Manual 143 de Plantas de Costa Rica (Hammel 2007), Flora da Reserva Ducke, Brasil (Ribeiro 1999), 144 145 Guide to the Vascular Plants of Central French Guiana (Mori et al. 2002), a species inventory of a wet forest in Chocó (Galeano 2000), the Panama biota Species Database of the 146 147 Smithsonian Institution (https://panamabiota.org/stri/index.php), and Plants of the World 148 Online (https://powo.science.kew.org/)(POWO 2024). Specimens were compared and 149 verified with those housed at the Universidad de Panama herbarium and the STRI herbarium.

150	Unidentified individuals were classified by means of dendrological characteristics (root,
151	stem, and leaf) into morphospecies and assigned unique morphospecies codes; these
152	morphospecies are being monitored in the field until reproductive structures can be sampled
153	to finalise identification to the species level.

In addition to scientific nomenclature, the Bacurú Drõa plot uses Emberá nomenclature. 154 The Traditional Authorities selected four knowledge holders (Emberá botánicos), who then 155 156 assigned Emberá names to trees they knew. The first 25 quadrats established were surveyed independently by each of the four botánicos enabling assessment of the consistency of 157 assigned Emberá names among the four *botánicos*. Thereafter, each 1 ha subplot was 158 159 surveyed by one of the Emberá botánicos. Working with Emberá names as well as scientific nomenclature ensured that the Emberá youth assisting in identification learned tree names in 160 both Emberá and Latin binomial nomenclatures. Recognising the importance of indigenous 161 162 names is an important step in de-colonising science (Gillman and Wright 2020).

163 *Comparison sites*

We compared floristic characteristics of the *Bacurú Drõa* plot with those of 53 other forest
plots established in Panama by Smithsonian ForestGEO under the leadership of Dr. Richard
Condit and co-authors S.A. and R.P. All forest plots were established following the standard
ForestGEO methodology (Condit 1998). They range between 1 ha and 50 ha in area; the
largest plot is the Barro Colorado Island Forest Dynamic plot (BFDP) located in Central
Panama.

Most of the 53 plots were located in Central Panama (Appendix S1.3), and were
established during an inventory of the Panama Canal watershed in the late 1990s (Ibáñez et
al. 2002). They served to document how forest composition varied with climate and soils,
with forests on the Atlantic slope of Panama being wetter than those on the Pacific slope

(Pyke et al. 2001; Condit et al. 2013). For the purpose of comparisons, we grouped plots with 174 respect to climate and elevation, hereafter referred to as geographical group (see Appendix S3 175 for climate and elevation). To control for plot shape and size, all analyses were based on 176 177 100 x 100 m (1 ha) plots or subplots (the Bacurú Drõa, BFDP, Cocoli and San Lorenzo plots were thus subdivided into 100 x 100 m subplots). We grouped the thirty-two 1 ha plots 178 located in the Central region of the isthmus as "Gamboa" plots, while the five 1 ha plots 179 180 located at higher elevation in the Panama Canal watershed were assigned to the "Alto Chagres" group. On the Atlantic side, the "San Lorenzo" group includes the 5.96 ha San 181 182 Lorenzo plot as well as four additional 1 ha plots. For consistency, only 5 ha of the 5.96 ha of the San Lorenzo plot were included in the analyses. Ten plots located on the Pacific slope 183 were assigned to the "Pacific" group, including a 4 ha plot in Cocolí as well as distant 1 ha 184 185 plots established in the provinces of Coclé and Los Santos (Appendix S1.3). To ensure nomenclature consistency across sites, we verified all scientific names using the 186 Taxonomic Name Resolution Service (TNRS- https://tnrs.biendata.org/). For Bacurú Drõa 187

we report data from the first census in 2022. For all other plots, data were from the most
recent complete inventory and were downloaded from the ForestGEO website
(https://www.forestgeo.si.edu/). Together, these forest plots cover 119 ha of forest, and our
dataset includes 50,368 individual living trees with diameter at breast height (DBH) ≥ 10 cm
representing 824 taxa, of which 653 have assigned scientific names.

193 *Tree diversity, floristic composition, and tree species conservation status*

We analysed floristic composition of the forest plots for trees with diameter at breast height (DBH) ≥ 10 cm. We focus on per ha values to control for differences in plot size (1 to 50 ha), using ANOVAs to evaluate differences among plot groups. The completeness of tree identification varied depending on sites, the *Bacurú Drõa* plot had the highest proportion of taxa identified only to morphospecies (Table 1). We therefore calculated measures of

199 tree diversity based on all species, including named species and morphospecies, hereafter 200 referred to as total species. We include morphospecies in our estimates of total species richness for the Bacurú Drõa and other plots because we expect morphospecies to eventually 201 202 be identified as taxonomically distinct species once reproductive material is collected. Tree densities and total species richness were calculated for each 1 ha plot or subplot. Alpha 203 204 diversity was estimated using Fisher's alpha (F α), an index that takes into account total 205 abundance as well as total species number and is relatively insensitive to sample size (i.e. 206 stem density). We calculated Fisher's alpha for all species combined (named and 207 morphospecies) for each 1 ha plot or subplot using the vegan package in R (Oksanen et al. 2022). We investigated total species compositional variation across plots and subplots using 208 209 Nonmetric Multidimensional Scaling (NMDS) analysis of abundances. After investigating 210 how results varied with the number of NMDS axes (Appendix S4), we report results for a 3-211 axis NMDS run with the vegan package in R (Oksanen et al. 2022). Finally, we evaluated how total species composition varied among plots and subplots with respect to elevation, 212 213 precipitation, mean annual cloud cover and forest fragmentation (See Appendix S3 on environmental explanatory variables) using a partial Redundancy Analysis (RDA). 214 215 Abundance community matrices were Hellinger transformed and the explanatory variables were standardized as continuous variables. The RDA was conditioned on mean distance from 216 217 geographic group centroid (in km) to adjust for varying distances among plots across the 218 groups. The RDA and data transformation was conducted in R using the Vegan package (Oksanen et al. 2022). 219

We assessed the conservation value of named species and compared these across plots.
We quantified conservation value using International Union for Conservation of Nature
(IUCN) status and geographical range (assuming species with smaller ranges have higher
conservation value). Using the IUCN red list (https://www.iucnredlist.org/en) each named

224 species was assigned a number reflecting its IUCN endangerment status: 5 = Critically Endangered, 4 = Endangered, 3 = Vulnerable, 2 = Near Threatened, and 1 = Least Concern. 225 Data Deficient, non-assessed, and morpho- species were assigned NA and excluded from 226 227 quantitative analyses. We obtained range from (Condit, Aguilar, and Pérez 2020) who 228 provides a comprehensive listing of Panamanian trees. Range is calculated as the minimum 229 convex polygon around the Botanical Information and Ecology Network (BIEN) record. For 230 the species not found in (Condit, Aguilar, and Pérez 2020), we extracted range directly from 231 Tropicos (https://www.tropicos.org/) and BIEN (https://bien.nceas.ucsb.edu/bien/) databases. 232 We evaluated how these conservation variables (IUCN score and *range*) varied among plots and subplots using community weighted means and assessing with ANOVAs. 233

234

235 Traditional Emberá use

Co-author A.O. recorded the traditional use and scored the cultural importance of 24
named species on the *Bacurú Drõa* plot. Cultural importance was scored on a scale of 1 to
3, with 3 indicating the highest cultural importance. We compared species' cultural value to
the Emberá with their conservation value as quantified by IUCN status.

240 The Bacurú Drõa plot census was extended in 2023 to include trees 1-10 cm DBH of 241 these 24 species (Appendix S5.1). In total, 787 saplings from these 24 species and sub-242 species were added to the tree census. To obtain a more complete picture of species 243 demography, we evaluated size-class distributions for the species of cultural importance with populations of at least 5 individuals \geq 1 cm DBH. Fourteen species of cultural 244 245 importance were found in other plots as well. For these fourteen species, we compared 246 size distributions among groups to see if there is a size class signature of traditional 247 Emberá use (for example, through a reduction in the number of large individuals for trees used to make dug-out canoes). 248

249 Finally, we estimated spatial variation in the intensity of traditional use across the plot. In 250 each 20 x 20 m quadrat of the Bacurú Drõa plot we counted cut stems of Socratea exorrhiza (Mart.), a culturally important palm species used for the flooring of traditional Emberá 251 252 houses, and the only species that could be easily identified after cutting due to its 253 characteristic stilt roots. 254 255 Results 256 *Tree species composition and diversity* 257 In the 10 ha *Bacurú Drõa* plot, trees with DBH \geq 10 cm were classified in 290 taxonomic units with 174 taxa (60%) identified to species, 49 only to genus, and 22 only to family, 258 259 leaving 45 unidentified tree taxa (Table 1). All taxa not yet fully identified to species were 260 carefully morphotyped by co-authors J.V., S.A. and R.P. to ensure consistency across the data set and are referred to as morphospecies. Some of the morphospecies awaiting full 261 identification in the Bacurú Drõa plot are abundant, e.g. Pouteria sp. 1 with 33 individuals, 262 263 and Lauraceae sp. 1 with 86 individuals. On a per ha basis, mean stem density and tree species richness differed significantly 264 amongst plots and groups of plots. Named species and total species per ha were highest in 265 Gamboa and second highest in Alto Chagres (Table 1). Named species per ha was lowest in 266 the Bacurú Drõa, though it ranks third in total tree species richness per ha, and total species 267 268 per ha was lowest in the Pacific group (Table 1). These differences in species richness in part 269 reflect variation in stem density: stem density was highest in the Alto Chagres and lowest in the Pacific (Figure 4). Interestingly, Bacurú Drõa has high species richness for low stem 270 271 density (Table 1, Figure 4) and estimates of total species per stem in 1 ha are significantly highest in the Bacurú Drõa plot (0.28) while the BFDP and Alto Chagres have similar values, 272 273 0.22 and 0.23 respectively. When comparing Fisher's alpha, a measure of diversity that is

274 relatively invariant with sample size, we found that alpha diversity (including named species and morphospecies) was highest in Alto Chagres and second highest in Bacurú Drõa (Table 275 1, Figure 4). Octave plots combining named species and Morphospecies show that both the 276 Bacurú Drõa plot and Alto Chagres have many singletons (Figure 2). 277 At the family level, Alto Chagres, BFDP, and Bacurú Drõa have the highest diversity and 278 279 Pacific has the lowest, as reflected in family-level Fisher's alpha for $DBH \ge 10$ cm (Table 1). 280 Mean Family Fisher's alpha was not significantly different for Bacurú Drõa, Alto Chagres and BFDP (Table 1). The families with the most species in the *Bacurú Drõa* plot are 281 282 Fabaceae (42 species), Rubiaceae (19 species), Moraceae (18 species), Malvaceae (16 species) and Sapotaceae (15 species) (Appendix S6.5). Plots and groups of plots were broadly 283 similar in the most speciose families, with just 6 families having 5% or more of species in all 284 285 regions (Appendix S6.4). In contrast, family dominance by proportion of individuals showed different patterns across plots, for example 21% of individuals in *Bacurú Drõa* belong to the 286 Fabaceae family, compared to <8% for all other geographic groups (Appendix S6.4). 287 288 Dominant families by number of individuals for Bacurú Drõa were Fabaceae (778 individuals), Moraceae (382 individuals), Urticaceae (358 individuals), Malvaceae (330 289 290 individuals), Lecythidaceae (280 individuals) and Violaceae (235 individuals).

Our analysis of the number of species shared amongst pairs of groups of plots illuminated 291 292 patterns of similarities and differences in the floras (Appendix S6.1; Appendix S6.2). The 293 Alto Chagres group stands out with 138 species found nowhere else. The two most similar 294 floras are those of San Lorenzo and Gamboa with 182 shared species, closely followed by Gamboa-BFDP, with 181 shared species, both representing over half of the species in each 295 296 region (Appendix S6.6). Tree species composition for the Bacurú Drõa plot (174 named species) overlaps most closely with the Gamboa group, with 103 shared species, and is most 297 298 dissimilar to the Pacific group with 52 shared species. The NMDS using tree species

abundance per geographic group highlights the distinctiveness of the *Bacurú Drõa* tree
species assemblage (Figure 3). The 1 ha subplots clustered closely together for the *Bacurú Drõa* 10 ha plot and the BFDP 50 ha plot. NMDS1 appears to segregate the plots based on
rainfall, with wetter plots generally having more negative and drier plots more positive values
on NMDS1.

We conducted an RDA (adjusted R²: 0.11) constrained by spatial position to quantify the 304 degree to which climate and land cover could explain variation in species assemblages among 305 plots or plot groups. The included environmental variables explain 13.97% of the variation in 306 307 species composition across geographic group, while spatial positioning within geographic group explained 11.89% of the variation. Still, 74.14% of the variation remains unexplained. 308 The two most important loading factors on canonical axes 1 are annual cloud cover (0.5608) 309 310 and FFI (Forest Fragmentation Index; 0.3533) while axis 2 is mostly explained by precipitation (-0.6475) and elevation (-0.4361) (see Appendix S3 for environmental 311 explanatory variables and figure). 312

313

314 *Conservation value*

Across the entire data set, 83% of the named species were categorised as least concern by 315 316 the IUCN. The only critically endangered species in the data set, *Dalbergia retusa* Hemsl., is 317 found in a few of the Pacific plots (Achotines, Cocoli, Plot 30) as well as one plot in Gamboa (Plot 21) and explains the high IUCN score for these plots. Four species are classified as 318 319 endangered: Pouteria bracteate T.D. Penn., Pouteria juruana K. Krause, Swietenia macrophylla (King) and Virola surinamensis Rol. ex Rottb. (Warb.). While S. macrophylla is 320 321 found only in Gamboa and the Pacific, the other three species occur in Alto Chagres. 322 Additionally, V. surinamensis is also found in BFDP, Bacurú Drõa, Gamboa and San

323 Lorenzo with 129 individuals DBH \geq 10cm in BFDP. The *Bacurú Drõa* plot harbours many species and individuals with high IUCN scores, for example 147 individuals $DBH \ge 10$ cm of 324 Gustavia nana Pittier classified as vulnerable. Fifty-four of the named species in the dataset 325 326 were not encountered in the IUCN red list and an additional 6 species were listed as data 327 deficient. Finally, seven species are listed under CITES because there are threatened by illegal trade for example *Dipteryx oleifera* Benth, and *Handroanthus chrysanthus* (Jacq.) 328 329 S.O.Grose, the latter found only in the *Bacurú Drõa* plot (Appendix S6.3). We evaluated the conservation value at the 1 ha plot level by calculating the community 330 331 weighted mean (CWM) for global range and IUCN score (Figure 4). The Bacurú Drõa plot

had significantly lower CWN global range than the BFDP and Pacific, while the CWM IUCN 332 score of the Bacurú Drõa plot was significantly higher than the BFDP, Pacific, and Gamboa 333 Lieu 334 plots (Figure 4).

335

Traditional use and cultural value 336

337 A key difference among the different plots compared in this study is the historical custody 338 of land, where the Darién forests are the Indigenous peoples. According to co-author A.O., 22 339 tree species and 2 sub-species present in the *Bacurú Drõa* plot are important to Emberá livelihoods and culture (Appendix S5.1). Uses for these species include material for 340 341 traditional house construction, tool making, dug-out canoe construction, medicinal use as well as providing foods for animals and thus providing important hunting grounds. Most trees 342 have more than one use, for example the trunks of *Hieronyma alchornoides* Allemão 343 (Emberá name: Pantano) are used to build houses but also to make *pilón* for rice, while the 344 345 fruits of both sub-species of Pouteria torta (Mart.) Radlk. (Emberá: Mamey Pa and Nensara 346 Jo) are eaten by people and animals while the wood is used to build houses. Cultural value

was not correlated with IUCN status (Figure 5), as most of the species important to the 347 Emberá are assigned "Least Concern" by the IUCN. The exceptions are Gustavia nana subsp. 348 Rhodantha (Emberá: Baga), which is of intermediate cultural importance for its role in 349 350 feeding animals and hence helping hunters, and Vitex masoniana (Emberá: Cujao Torro), which can be used in building houses but is rated low in cultural importance. 351 352 Eighteen species of cultural importance were represented by at least 5 individuals ≥ 1 cm 353 DBH, of which 14 were also found in other geographic groups. Six of these 18 species lack both larger size classes (trees in the top 40% of the DBH range for their species in the 354 355 dataset) in the Bacurú Drõa plot (Appendix S5.2): Beilschmiedia tovarensis (Klotzsch & H.Karst. ex Meisn.) Sachiko Nishida, Chrysophyllum argentum Jacq., Guarea guidonia (L.) 356 Sleumer, Platypodium elegans Vogel, Pouteria calistophylla (Standl.) Baehni, and Pouteria 357 358 *reticulata* (Engl.) Eyma. Emberá uses however do not target large trees for four of the six species. P. reticulata (Emberá: Manguillo) is used to extract latex to be used as glue, a non-359 destructive usage. C. argentum (Emberá: Dosarrejo), G. guidonia (Emberá: Rapadillo), and 360 361 P. elegans (Emberá: Bosain) are used a little for house building but are of moderate importance and have other uses which target smaller individuals (e.g. fishing pole for G. 362 363 guidonia) or do not damage individuals (e.g. fruit and hunting for C. argenteum). B. 364 tovarensis (Emberá: Sigua) and P. calistophylla (Emberá: Kira), however, are used in 365 construction or to make dugout canoes. The abundance of S. exorrhiza (Emberá: Jira), prized 366 by the Emberá for its use in building floors, is lower in *Bacurú Drõa* (7.6 ha⁻¹) than in San Lorenzo (37 ha⁻¹), Alto Chagres (17 ha⁻¹), and Gamboa (10 ha⁻¹), but higher than in BFDP 367 368 (5.3 ha⁻¹) and Pacific (0 ha⁻¹); a pattern that aligns with the regional precipitation gradient. 369 Size distributions for S. exorrhiza were similar across groups of plots (Appendix S5.2), even 370 though we found evidence of its harvest across the Bacurú Drõa plot (Appendix S5.3; Appendix S5.4). 371

372 Discussion

Our knowledge of tropical diversity is highly uneven across regions (Gatti et al. 2022); the 373 Chocó-Darién Ecoregion is one of the most biodiverse and threatened regions on earth 374 375 (Cámara-Leret et al. 2016) and is a "neglected biodiversity hotspot" (Pérez-Escobar et al. 2019). By co-developing the Bacurú Drõa plot with the people of the Emberá territory of the 376 Balsa River, we were able to study the forests of Darién in greater depth than ever before. 377 378 The flora of the Bacurú Drõa plot shares characteristics with the Alto Chagres plots. Tree species richness reported for the Bacurú Drõa and Alto Chagres plots, 108 and 139 total 379 380 species ha-1 respectively, are higher than in other Panamanian plots and fall in the low 381 range of other hyper-diverse forests in the tropics (Faberlangendoen and Gentry 1991). The Alto Chagres plots are located in wet mid elevation forests, which are known to 382 383 have a high number of endemic species (Tokarz and Condit 2021), and these plots in particular have a high stem density, both of which contribute to their high species richness. It 384 is noteworthy that the *Bacurú Drõa* plot has high species richness for a significantly low stem 385 density, giving it a significantly higher estimate of species per stem density than any other 386 plots or group of plots. The highest tree richness value reported for the Chocó-Darién 387 388 Ecoregion is 300 species ha⁻¹ for trees \geq 10 cm DBH in the Colombian Chocó (Quinto-Mosquera, Hurtado, and Alboleda 2019) and the lowest, 93 species ha⁻¹ in an Ecuadorian 389 390 Chocó forest (Toasa, Morochz, and Oleas 2020).

Species abundance distributions for the *Bacurú Drõa* plot and the Alto Chagres group
follow a lognormal distribution, driven by a high number of singletons. Such species
abundances distributions are typical for highly diverse tropical forests, e.g., in the
Amazon (Duque et al. 2017). Undeniably the number of singletons is a function not only of
rarity but also of sampling effort (Gatti et al. 2022). However, similar sampling intensity in *Bacurú Drõa*, San Lorenzo and the Pacific groups suggests that the observed high number of

397	singletons is more than a sampling bias. Furthermore, high numbers of singletons is a
398	consistent characteristic of the Chocó-Darién forests as reported by (Toasa, Morochz, and
399	Oleas 2020; Quinto Mosquera and Moreno Hurtado 2014) and (Faberlangendoen and Gentry
400	1991); these authors all indicated that most species encountered in their studies were
401	represented by a single individual (out of 93 species in 1 ha \geq 10cm DBH, 174-233 species
402	$DBH \ge 10$ cm in five 1 ha plots, and 250 sp. ≥ 10 cm DBH ha ⁻¹ in 1.5 ha respectively). The
403	similarities in flora between Alto Chagres and the Bacurú Drõa plot echoes (Gentry 1986),
404	who stated that many features of the Chocó Forest seem more characteristic of a cloud forest
405	than a lowland forest, possibly because the Chocó is known as one of the wettest places in
406	the world (Quinto Mosquera and Moreno Hurtado 2014). Inferred precipitation at the Bacurú
407	Drõa plot shows intermediate rainfall (2400 mm year) (Kunz et al. 2022; Appendix S3),
408	however, annual mean cloud cover, however, is above 90% (Kunz et al. 2022; Appendix S3),
409	possibly explaining similarities with the premontane plots of Alto Chagres.
410	Forests of the Colombian Chocó (Gentry 1986; Quinto Mosquera and Moreno
411	Hurtado 2014; Forero 1989) are characterized by the dominance of a few families, a
412	characteristic encountered in the Bacurú Drõa plot despite family diversity being similar to
413	that of other Panamanian forests. We see, for example, a higher representation of Fabaceae
414	both in terms of individuals and species in the Bacurú Drõa plot compared to other plots.
415	There is also a high proportion of Urticaceae and Violaceae in Bacurú Drõa that is not seen
416	in plots from other groups. Furthermore, in the Bacurú Drõa plot the prevalence of species
417	belonging to the Malvaceae subfamily Bombacoideae appears characteristic of the humid
418	forests of the Colombian and Ecuadorian Chocó (Forero 1989).

Around 30-60% of the named tree species found in the *Bacurú Drõa* plot are also present
in other Panamanian plots, and similarity appears to be inversely correlated with distance
between the Darién and the other groups of plots. This might reflect the role of Darién as a

422 land bridge between South and Central America. Despite these similarities, the Bacurú Drõa plot contains a large number of morphospecies and species not reported in Panama, including 423 some potentially yet to be described species. Unidentified species also occur in other plots; 424 425 the Santa Rita plot in Alto Chagres was established 26 years ago and still has 3 taxa identified only to morphospecies (Table 1), in part because of the difficulty of encountering fertile 426 427 specimens. It is therefore not surprising that the Bacurú Drõa plot floristic composition remains partially unresolved. However, it remains that the Bacurú Drõa plot has significantly 428 429 more unidentified and potentially new species than the other geographic groups, a 430 characteristic of the Chocó-Darién Ecoregion noted by (Gentry 1986). For example, after encountering flowers and fruits, we are currently describing a new species of *Pachira* 431 (Malvaceae) close to *P. speciosa* (Valdes et al. in preparation). 432 433 Overall, results from the *Bacurú Drõa* plot confirms that this forest shares many botanical characteristics with other forests of the Chocó-Darién Ecoregion and highlights the 434 differences in composition between this region and the ForestGEO plots elsewhere in 435 Panama. Our study highlights the Darién forests as a unique site to study and preserve for its 436 high diversity and likelihood for new species discovery and highlights the value of adding the 437 438 Bacurú Drõa plot to the Panamanian and international networks of tropical forest plots. The idea of conservation value is prevalent in the conservation literature and has been 439

used to prioritize protected areas or to assess threatened species status (Capmourteres and
Anand 2016; Harnik, Simpson, and Payne 2012). Building on Drinan et al. 2013, who
assigned a species-quality-score to each species of an assemblages based on their abundance,
we considered species *range* as well as IUCN status as key elements of conservation value.
The *Bacurú Drõa* plot had CWM values that indicate smaller ranges and higher IUCN scores
on average than the other plots in Panama.

446 Our comparisons of the conservation value metrics with valuation by the Emberá people of Balsa, showed that tree species with important cultural values have relatively low standard 447 conservation value. These species have multiple roles in Emberá lives, providing materials 448 449 for building houses and dugout canoes, etc., as well as food for humans or animals. A study of traditional Emberá knowledge focusing on palms in the Colombian Chocó showed that 450 451 construction usages were most valued (Cámara-Leret et al. 2016) which is coherent with the 452 ranking made by co-author A.O. These results reflect the reality that the IUCN status does 453 not consider provision of ecosystem services. Overall, the divergence in ranking values for 454 conservation and cultural use confirms the importance of adopting a biocultural framework to adequately consider the importance of species that sustain the livelihoods of local 455 456 communities when prioritising for conservation (Nemogá, Appasamy, and Romanow 2022). 457 The Chocó-Darién is facing pressures from mining (Valois-Cuesta and Martínez-Ruiz 2016), logging, and deforestation (Cuenca and Echeverria 2017; Fagua, Baggio, and Ramsey 458 459 2019; Luna et al. 2020) as well as pressure from illicit activity in a geopolitical location of 460 great importance including arm, drug and human trafficking (Panesso et al. 2019; Carneiro, Reolon, and Portela 2019; Gabster et al. 2021). These threats and illegal activities greatly 461 reduce accessibility and prevent research and conservation activities in the region. In Darién, 462 the livelihoods of the resident Indigenous population remains affected by illegal activities, 463 464 with limited options for legal sources of income while simultaneously experiencing 465 unresolved claims to their ancestral lands (van Uhm and Grigore 2021). The Bacurú Drõa plot offers a novel perspective on the value of forest plots. Our case 466 study of full partnership allows increased knowledge of tree diversity in a neglected 467 468 biodiversity hotspot while addressing three essential social needs: support of traditional knowledge, education, and opportunities for community development and employment 469 (Appendix S1.2). In 2023, the project gave employment to 52 men and 82 women. Bacurú 470

471	Drõa's socio-ecological vision complements other plots in the ForestGEO network opening
472	an avenue to study one of the least botanically explored regions of the world; one that is
473	remote, intact and under indigenous custody, thus filling the gaps in current tropical forest
474	research. Bacurú Drõa emphasizes the need for indigenous stewardship and involvement in
475	science and provides a blueprint to do so.
476	
477	Supporting Information
478	Additional supporting information may be found in the online version of the article at the
479	publisher's website.
480	Appendix S1: Location and characteristics of the Emberá Collective lands of Balsa
481	Appendix S2: Notable published observations on the forests of the Chocó-Darién region
482	Appendix S3: Environmental explanatory variables and RDA
483	Appendix S4: NMDS stress justification and Shephard plot
484	Appendix S5: Traditional Emberá use of the Bacurú Drõa plot and cultural values
485	Appendix S6: Supplemental information on the species and families found in the dataset
486	and across the geographic groups
487	
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Tables and Figures 773

- **Table 1.** Floristic characteristics of the six different plot or plot groups for trees >= 10cm 774
- DBH; mean values are means and standard deviations for 1 ha plots or subplots. ^{1,2} 775

	Alto Chagres	Bacurú Drõa	BFDP	Gamboa	Pacific	San Lorenzo	F, p ANOVA
Number of plots	5	1	1	32	10	5	
Total area (ha)	5	10	50	32	13	9	
Total individu als	3,102	3,797	20,832	14,656	3,750	4,231	
Total named + morpo- species	368	290	219	374	188	224	
Named species	332	174	217	360	184	212	
Total number of families	68	50	54	62	50	54	
Mean number of named species (ha ⁻¹)	129 ± 35.2 a	81.0± 10.9 bc	89.6 ± 8.09 b	73.3 ± 16.0 c	43.8 ± 13.1 d	73.1 ± 9.32 c	40.51 ***

¹ The significance level of the ANOVA comparing the six geographical groups is indicated (*** p < 0.001). ² Means followed by different letters are significantly different as per Tukey a posteriori test

Mean number of morpho species (ha ⁻¹)	9.8 ± 4.97 b	26.6± 5.10 a	0.04 ± 0.198 c	0.844 ± 1.30 c	0.615 ± 0.650 c	1.78 ± 1.86 c	384.4 ***
Mean named + morpho- species richness (ha ⁻¹)	139 ± 36.2 a	108 ± 12.1 b	89.6 ± 8.02 c	74.1 ± 16.3 d	44.5 ± 13.1 e	74.9 ± 9.17 d	50.86 ***
Mean stem density (ha ⁻¹)	620 ± 78.1 a	380 ± 36.2 b	417 ± 41.5 bc	458 ± 89.3 c	288 ± 82.1 d	470 ± 68.5 c	23.7 ***
Mean Fisher's alpha (ha ⁻¹) (named + morpho species)	59.2 ± 26.7 a	50.4 ± 7.90 a	35.4 ± 4.73 b	25.9 ± 7.84 c	15.5 ± 6.09 d	25.5 ± 4.90 c	40.85 ***
Mean Fisher's alpha (ha ⁻¹) (Family)	11.3 ± 1.05 a	9.58 ± 1.10 ab	9.74 ± 0.748 a	7.86 ± 1.82 c	5.50 ± 1.39 d	8.19 ± 0.861 bc	32.69 ***

778 Figure 1: Location of the Bacurú Drõa permanent plot within the Darién region of eastern Panama (bottom right). Overview map of the Collective Lands of the Balsa River (left) and 779 detailed map of the location of the 10-ha plot within the study region (top right). Major rivers 780 are shown in blue and labelled according to Emberá names. Pink dots show very large trees 781 identified by remote sensing (RS) from Kunz et al. (2022). Coloured terrain is based on the 782 30-meter digital elevation model for Panama, derived from ALOS Global Digital Surface 783 Model 30m (JAXA DEM, STRI). Terrain contours are plotted in 25 m intervals. 784





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789 Figure 2: Species abundance distributions for different geographical groups, visualized using octave plots showing the number of species (named and morphospecies) in 790 abundance classes when combining all plots within groups (Trees \geq 10cm DBH). The 791 792 lighter color shows the number of morphospecies, and the darker color the number of named species. The abundance classes are a geometric series (doubling classes), also known 793 794 as octaves: class 1 includes singletons (abundance = 1), class 2 species abundance 2 individuals, class 3 species abundance = 3-4 individuals, class 4 species abundance 5-8795 individuals, and so forth, all the way up to class 13 (abundances = 2049-4096). 796



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Figure 3: Species compositional variation across the plots or subplots as quantified
by nonmetric multidimensional scaling (NMDS) with three axes. Trees ≥ 10cm



801 DBH. Stress = 10%.

818 Figure 4: Boxplots for diversity measures (Fisher's Alpha, Species per Stem) and

819 Community Weighted Means of conservation value metrics (IUCN score, range) estimated at

the 1ha level for forest plots or groups of plots. All metrics were calculated using data for





Figure 5: Comparison of the Cultural score (1 low - 3 high) and IUCN status for the 837 species of importance for the Emberá for trees ≥ 1 cm DBH encountered in the *Bacurú* 838 Drõa plot. Twenty-four species of cultural values are listed in Table S1. Both subspecies 839 840 of Pouteria torta present in Table S1 are here grouped as Pouteria torta. Species names are written both in Emberá and Latin. 841



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