

1 **WHERE TO NEST? ECOLOGICAL DETERMINANTS OF CHIMPANZEE NEST**
2 **ABUNDANCE AND DISTRIBUTION AT THE HABITAT AND TREE SPECIES SCALE**

3 **Ecological Determinants of Chimpanzee Distribution**

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19 **ABSTRACT**

20 Conversion of forests to anthropogenic land-uses increasingly subjects chimpanzee populations
21 to habitat changes and concomitant alterations in the plant resources available to them for nesting
22 and feeding. Based on nest count surveys conducted during the dry season, we investigated nest
23 tree species selection and the effect of vegetation attributes on nest abundance of the western
24 chimpanzee, *Pan troglodytes verus*, at Lagoas de Cufada Natural Park (LCNP), Guinea-Bissau, a
25 forest-savannah mosaic widely disturbed by humans. Further, we assessed patterns of nest height
26 distribution to determine support for the anti-predator hypothesis. A zero-altered generalized
27 linear mixed model showed that nest abundance was negatively related to floristic diversity
28 (exponential form of the Shannon index) and positively with the availability of smaller-sized
29 trees, reflecting characteristics of dense-canopy forest. A positive correlation between nest
30 abundance and floristic richness (number of plant species) and composition indicated that
31 species-rich open habitats are also important in nest site selection. Restricting this analysis to
32 feeding trees, nest abundance was again positively associated with the availability of smaller-
33 sized trees, further supporting the preference for nesting in food tree species from dense forest.
34 Nest tree species selection was non-random, and oil palms were used at a much lower proportion
35 (10%) than previously reported from other study sites in forest-savannah mosaics. While this
36 study suggests that human disturbance may underlie the exclusive arboreal nesting at LCNP,
37 better quantitative data are needed to determine to what extent the construction of elevated nests
38 is in fact a response to predators able to climb trees. Given the importance of LCNP as refuge for
39 *P. t. verus* our findings can improve conservation decisions for the management of this important
40 umbrella species as well as its remaining suitable habitats.

41

- 42 *Key-words:* Guinea-Bissau; hurdle models; nest tree species selection; nesting patterns;
- 43 vegetation attributes; western chimpanzee.

44 INTRODUCTION

45 Over large geographic scales distribution patterns of primates are shaped by historical
46 biogeography and environmental constraints [Lehman and Fleagle, 2006; Kamilar, 2009], and
47 communities living in close geographic proximity and under the same environmental conditions
48 should exhibit similar species composition [Lehman, 2006; Kamilar, 2009]. The distribution of
49 primates can additionally be influenced by human disturbance along a gradient of geographic
50 scales [Rovero and Struhsaker, 2007; Potts, 2011].

51 At small spatial scales, primate distribution is determined by topographical features and
52 vegetation attributes [Furuichi and Hashimoto, 2004; Ndimuligo, 2007]. Vegetation attributes
53 such as floristic richness, diversity and composition, tree size and density, and fruit abundance,
54 are commonly used predictor variables in studies assessing correlates of primate abundance
55 [Furuichi and Hashimoto, 2004; Wieczkowski, 2004; Cristóbal-Azkarate et al., 2005; Rovero
56 and Struhsaker, 2007; Stevenson, 2011; Linder and Lawler, 2012]. These attributes also reflect
57 the distribution of the tree species preferentially selected for nesting and feeding [Furuichi and
58 Hashimoto, 2004; Ogawa et al., 2007]. Most of these studies have contributed significant
59 information regarding patterns of habitat preference, but few have quantitatively assessed
60 vegetation correlates of primate abundance and distribution [Hanya and Chapman, 2013],
61 including for chimpanzees [Balcomb et al., 2000; Hernandez-Aguilar, 2006].

62 Most mammals spend a large time of their lives sleeping or resting in building burrows,
63 caves, dens, nests, or other shelters [Eisenberg, 1983], which provide protection from
64 environmental challenges [Stewart et al., 2011]. We use the term "nest" throughout the paper
65 when referring to the sleeping platforms constructed by chimpanzees, although they differ
66 fundamentally from those of other nest-building animals in terms of their function [see Samson

67 and Hunt, 2012]. Since great apes, in contrast to all other nonhuman primates [Anderson, 2000],
68 build a nest every night for sleeping or resting during the day, nest abundance has been a useful
69 surrogate for estimating densities and population sizes as well as for assessing their home range
70 [Fruth and Hohmann, 1996; Buij et al., 2003; Devos et al., 2008; Carvalho et al., 2013]. Nest site
71 distribution may also inform about the distribution of food resources [Furuichi and Hashimoto,
72 2004].

73 Although for some study sites it has been documented that chimpanzees build their nests
74 on the ground [Furuichi and Hashimoto, 2000; Hicks, 2010; Koops et al., 2012b; Last and Muh,
75 2013], arboreal nest building is most frequent and its function has been explained through the
76 following non-mutually exclusive hypotheses: antipredation [Baldwin et al., 1981; McGrew,
77 2004; Pruetz et al., 2008; Hernandez-Aguilar et al., 2013], antipathogen [Fruth and Hohmann,
78 1996; Anderson, 1998], thermoregulation [McGrew, 2004; Koops et al., 2012a; Samson and
79 Hunt, 2012], and promotion of mental health [Fruth and Hohmann, 1996; Anderson, 1998]. In
80 this context, many studies suggest that nest height and canopy cover, among other variables, are
81 important determinants of arboreal nesting patterns, in line with the predation avoidance
82 hypothesis [Goodall, 1962; Baldwin et al., 1981; Pruetz et al., 2008].

83 Several studies have documented that chimpanzees only use a subset of the total floristic
84 richness available at a site for nest building and, among those tree species used, only select a few
85 in greater proportions [Furuichi and Hashimoto, 2004; Ndimuligo, 2007; Stanford and O'Malley,
86 2008; Koops et al., 2012a]. Nest tree species selection is not an exclusive behaviour of
87 chimpanzees, and has also been reported for other great apes [Fruth and Hohmann, 1996;
88 Rothman et al., 2006; Cheyne et al., 2013]. Whereas some studies have reported a preference of
89 the western chimpanzee, *Pan troglodytes verus*, for nesting in oil palms [Barnett et al., 1996;

90 Sousa et al., 2011], others found no such evidence [Seringbara (Guinea), Humle and Matsuzawa,
91 2004], and the underlying causes for such preference remain generally understudied, highlighting
92 the need for more data across the species geographic distribution range to understand this
93 preference.

94 *Pan t. verus* has been classified as Endangered on the IUCN Red List since 1988 [IUCN,
95 2014] and has suffered a loss of 11% in the area of suitable environmental conditions since 1986
96 [Torres et al., 2010; Junker et al., 2012], anthropogenic causes being the main driver of this
97 decline. In this paper, we provide a quantitative assessment of vegetation correlates of western
98 chimpanzee nest abundance in a protected but highly human-modified landscape in Guinea-
99 Bissau. We also assess patterns of nest height distribution to evaluate the anti-predation
100 hypothesis. Finally, we investigate patterns of nest tree species selection to further our
101 understanding of how this behavior varies geographically across the species' range.
102 Understanding cultural, environmental and ecological factors that shape distribution patterns of
103 *P. t. verus* at small geographic scales will improve future management strategies to ensure its
104 long-term conservation at the westernmost margin of its geographic distribution.

105

106 **METHODS**

107 **Study Site**

108 The study was conducted in Lagoas de Cufada Natural Park (LCNP, between 11°34' and
109 11°51' N and 14°49' and 15°16'W), a protected area in Guinea-Bissau that covers 890 km²
110 [IBAP, 2008] (Fig. 1). Its climate is characterized by an average temperature of about 26°C
111 during both the dry and rainy season. Annual rainfall averages 2200 mm, which mostly falls in
112 the rainy season between June and October, with almost no precipitation (<100 mm) in the

113 pronounced dry season between November and May [Catarino et al., 2002;
114 <http://sdwebx.worldbank.org/climateportal/index.cfm>; IBAP, 2008]. LCNP is a Ramsar
115 Convention site characterized by an extensive network of rivers, streams, and lagoons whose
116 water levels fluctuate strongly depending on rainfall, with some rivers and streams drying up
117 towards the end of the dry season [IBAP, 2008]. The park topography is relatively flat, reaching
118 a maximum of 39 m of altitude, and soil composition and its depth varies, which defines and
119 limits the presence of plant species [Catarino et al., 2006a].

120 LCNP is characterized by a mosaic of different habitats at different stages of degradation
121 and early regeneration as a consequence of human disturbance [Catarino et al., 2006a]. The
122 habitat types suitable for chimpanzee nest building are dense and open canopy forests, and
123 savannah-woodland. Other habitats such as herbaceous savannah, swamp forest and mangrove
124 have no suitable trees for nesting. Dense-canopy forest is structurally and compositionally
125 similar to the multi-storeyed forests of Sierra Leone and Liberia (FAO 1995). This forest type is
126 characterized by high canopy coverage (ca. 90%) and a typically poorly developed understory.
127 The most common species are *Azelia africana*, *Albizia* spp., *Antiaris toxicaria*, *Ceiba*
128 *pentandra*, *Chlorophora* spp., *Detarium senegalense*, *Dialium guineense*, *Elaeis guineensis*,
129 *Erythrophleum guineense*, *Malacantha alnifolia*, *Parkia biglobosa*, *Parinari excelsa*, and
130 *Spondias mombin* (FAO 1995, Catarino et al. 2006b). Open-canopy forest (60-70% canopy
131 cover) is dominated by *Borassus aethiopicum*, *Daniellia oliveri*, *P. biglobosa*, and *Piliostigma*
132 *thonningii*. Open forest and savannah-woodland have some tree species in common, due to their
133 occurrence on similar soil types [Catarino et al., 2006a]. Other tree species are, however,
134 restricted to savannah-woodland (about 20-40% canopy cover): *Albizia zygia*, *Crossopteryx*

135 *febrifuga*, *Lophyra lanceolata*, *P. thonningii*, *Pterocarpus erinaceus*, *Terminalia albida*, as well
136 as some species of *Combretum* and *Ficus*. For more details see Catarino et al. [2006a; b].

137 The relative proportions of these habitat types in LCNP (dense forest: 9%, open forest:
138 35%, savannah-woodland: 54%; [Amaro, 2011]) roughly correspond to their total occurrence
139 countrywide (dense forest: 3%, open forest: 25%, savannah-woodland: 48%; [Oom et al., 2009]).

140

141 **Chimpanzee Nest Surveys**

142 This research adhered to the American Society of Primatologists (ASP) principles for the
143 ethical treatment of primates as well as to the legal requirements of the governmental agency that
144 manages the protected areas in Guinea-Bissau (*Instituto da Biodiversidade e das Áreas*
145 *Protegidas*).

146 Due to the difficulty of observing chimpanzees themselves nests were recorded as
147 indirect evidence of their presence. The sampling design was initially defined for an application
148 of line transect distance sampling, with repeated visits to eleven systematically placed linear
149 transects to estimate chimpanzee densities [Carvalho et al., 2013]. Transects were walked at a
150 steady speed of about 1 km /h and all nests visible from the transect line were recorded, using
151 binoculars when necessary. Nest counts were conducted during the dry seasons of 2010 and 2011
152 (4 visits between February and April 2010 and 5 visits between February and May 2011, in
153 biweekly sampling intervals). Total survey effort comprised 302.4 km. Nest trees were tagged
154 with a rope to avoid double counting and the number of nests encountered during each visit was
155 recorded. However, as we did not record nest position and also have no information on the reuse
156 of old nests, nest counts may constitute slight underestimates. For the purpose of this study, we
157 pooled nests of all ages. For each nest, the habitat type in which it was observed, tree species,

158 and nest height (measured from the ground to the base of the nest by using a laser range finder,
159 Bushnell Yardage Pro Sport 450) were recorded.

160

161 **Habitat Description**

162 A qualitative and quantitative assessment of the vegetation was conducted from October
163 to December 2009 along 5 linear transects randomly chosen from among the 11 used during nest
164 surveys (2.5 m to each side, approximately 3 km in length, 15.2 km total survey effort). Habitat
165 boundaries were geo-referenced to determine the proportion of each habitat along these transects.
166 Each transect comprised a variable number of units of habitat types (hereafter referred to as
167 sampling units, SU). All plant species >10 cm diameter at breast height (dbh, measured at a
168 height of 1.5 m) were identified and counted, and the corresponding dbh measured using a tape
169 measure. Where two trunks originated from the same base each was measured independently and
170 the average of these was taken as the overall measurement for that tree. Plant species
171 identification was done with the help of the park guards and other locals. When necessary,
172 samples were collected for later identification at the herbarium of the *Instituto de Investigação*
173 *Científica e Tropical* (Lisboa, Portugal).

174

175 **Data Analysis**

176 All analyses were conducted in R version 3.0.2 [R Development Core Team, 2013].

177 Reported values are mean \pm 1SE unless otherwise noted.

178 To test for a habitat effect on nest height a generalized linear mixed model (GLMM) was
179 performed using the package *lme4* [Bates et al., 2012], using a Gaussian distribution and identity
180 link function and including tree species as a random factor.

181 Vegetation attributes - floristic richness, diversity and composition, plant density (plant
182 abundance /0.1 ha), and total basal area (m^2 /0.1 ha) - were calculated for each SU, considering
183 only native species (i.e. agricultural species were excluded). Because the SUs differed in size and
184 number of species, we standardized the data by (1) converting abundances into relative densities,
185 i.e. the abundance of each species was standardized to 0.1 ha and weighted by the total density
186 obtained for each SU, and by (2) using sample-based rarefaction to calculate the number of
187 species expected in a subset of individuals selected at random from a larger sample [Gotelli and
188 Colwell, 2010]. Sample-based rarefaction was computed using EstimateS software [Colwell,
189 2013]. Comparisons of rarefied species richness among habitats were made at 5 samples, the
190 maximum number of SUs in common across habitat types. Vegetation attributes were calculated
191 based on the relative density of native species in 18 SUs of 0.1 ha, considering either the entire
192 floristic assemblage (N=93 species) or only plant species known to be consumed by LCNP
193 chimpanzees during the dry season (N=22 species; see Table SI). The floristic diversity of each
194 SU was measured using the exponential form of the commonly used Shannon entropy index (e^H)
195 [Jost, 2006]. To assess statistical differences among SUs in plant density and diversity, and total
196 basal area, the non-parametric Kruskal-Wallis test was employed. Linear regression was used to
197 test for a correlation between average nest height and mean dbh of tree species used for nesting
198 (using dbh data from the vegetation surveys as a proxy for nest tree dbh).

199 To compare community-level patterns of floristic composition across habitats non-metric
200 multidimensional scaling (NMDS) was used. NMDS is a robust, non-linear ordination technique
201 considered an efficient method to analyse ecological community data [McCune and Grace,
202 2002]. The goodness of fit of the final ordination is evaluated by the stress, a measure of how
203 good the m -dimensional configuration is [see Zuur et al., 2007]. Statistical significance of the

204 variation of floristic composition among habitats was investigated with a permutational
205 multivariate ANOVA (PERMANOVA), which consists in assessing differences between *a*
206 *priori*-defined groups of community samples based on a (dis)similarity matrix [Clarke, 1993]. To
207 interpret the ordination, plant species and total basal area were added to the plot using vector
208 fitting, i.e. plotting arrows that represent the direction of the variables gradient and the
209 correlation between ordination axes and these variables [Oksanen et al., 2012]. For plotting, the
210 axes were scaled by the square root of the square correlation coefficient (R^2) and P-values were
211 computed based on 999 permutations. NMDS and PERMANOVA were performed using the
212 package *vegan* [Oksanen et al., 2012], based on a Bray-Curtis distance matrix.

213 Appropriate statistical approaches to deal with the high frequency of zeroes often found
214 in ecological count data should be applied as these can influence the predictive performance of
215 models and ecological inference [Martin et al., 2005; Linder and Lawler, 2012]. In ecological
216 data two types of zero counts are often encountered: true zeroes, when a species or indirect signs
217 of its presence are absent from the survey area, and false zeroes, when an animal or indirect
218 evidences are present but the observer failed to record them [see Zuur et al., 2009]. We
219 accounted for the presence of excess zeroes by fitting zero-inflated (ZI) models and hurdle or
220 zero-altered (ZA) models [Zuur et al., 2012] to the nest abundance data. ZI and ZA models have
221 one important distinction in how they interpret and analyze zero counts [Zamani and Ismail,
222 2013]. A ZI model, also known as a mixture model, does not “know the truth” about a zero being
223 false or true, and distinguishes two different origins for the probability of zero observations:
224 coming from a count process and from a binomial (in fact strictly Bernoulli, i.e. binary) process
225 [Zuur et al., 2009]. On the other hand, a ZA model is a modified count model explicitly
226 composed of two parts: one generating the positive values (i.e. non-zeroes), usually a truncated-

227 at-zero count model, and one generating the zeroes, a binary response model [Cameron and
228 Trivedi, 1998].

229 We modelled nest abundance as a function of the aforementioned vegetation attributes
230 (floristic richness, diversity and composition, plant density and total basal area) in a GLMM
231 framework, specifying transects and visits to transects as random factors, and the area of each
232 SU and previous estimates of habitat-specific nest detectability [Carvalho et al., 2013] as an
233 offset. For ZI models, a Poisson distribution or negative binomial distribution was used for nest
234 count data, and a binomial distribution with a logit link for presence/absence data [Martin et al.,
235 2005; Zuur et al., 2009]. For ZA models, a Poisson distribution or negative binomial distribution
236 was used to model the non-zero counts, and a binomial distribution with a logit link for fitting
237 zeroes [Martin et al., 2005; Zuur et al., 2009]. Collinearity among the explanatory variables was
238 not severe: the maximum variance inflation factor (VIF) obtained was smaller (4.81) than the
239 rule of thumb for the cut-off value (5) suggested by Neter et al. [2004]. The small sample size
240 version of Akaike's Information Criterion (AICc) was used for model selection [Burnham and
241 Anderson, 2002]. We present only the parameter estimates and model diagnostics for the most
242 parsimonious model. The analyses were performed using the R packages *glmmADMB* [Fournier
243 et al., 2012; Skaug et al., 2012] and *MuMIn* [Bartón, 2013].

244 To determine whether chimpanzee tree species choice for nesting deviates significantly
245 from random we implemented a randomization test in R. We compared samples of tree species
246 randomly selected from those available (random trees: RT) with those actually used for nest
247 building (nest trees: NT, N=459). RT samples (N=459 trees, corresponding to the NT sample
248 size) were selected by random sampling with replacement from the tree abundance data
249 (N=1,963 trees, including 10 individuals of unidentified tree species). This procedure was

250 repeated 1000 times to evaluate how far from the expected proportion at random (p_{RT}) each
251 observed proportion was (p_{NT}). Thus, for each tree species, we obtained the distribution of the
252 proportion of use if that species were chosen at random (p_{RT}). Plotting the expected p_{RT}
253 distribution as a function of observed p_{NT} allows one to easily distinguish preferred tree species
254 ($p_{NT} > p_{RT}$) from those avoided ($p_{NT} < p_{RT}$), depending on whether the distribution lies entirely
255 below or above the 1:1 line, respectively. If the randomization distribution p_{RT} overlaps the 1:1
256 line this indicates that the observed p_{NT} might be observed as a result of random choice.

257

258 **RESULTS**

259 **Chimpanzee Nest Surveys**

260 Only arboreal nests were found and mostly in dense forest (N=239), whereas fewer nests
261 were observed in the two habitats with less canopy coverage: open forest (N=114) and savannah-
262 woodland (N=106) [see Carvalho et al., 2013]. Most of the nests were built in tree species
263 belonging to the two legume subfamilies Caesalpinioideae and Mimosoideae, and Palmae. Of the
264 23 tree species recorded with chimpanzee nests (Table I), at least 12 provide fruits eaten by
265 LCNP chimpanzees during the dry season (Table SI) and 90% of the nests were built in those
266 species.

267 Nest height averaged 14.60 ± 0.01 m across the full range of observed nest tree species
268 (N=459), and 14.01 ± 0.01 m when excluding nests in oil palms (N=413), which due to their
269 physiognomic distinctiveness often harbored nests higher on the trunk compared to other tree
270 species (Table I). The greatest mean nest height was observed in savannah-woodland ($16.71 \pm$
271 0.04 m), followed by dense forest (14.11 ± 0.02 m) and open forest (13.66 ± 0.05 m), however,
272 differences were not significant (GLMM: $\chi^2 = 3.00$, $df=2$, $P=0.22$) (Fig. 2). A positive

273 correlation was found between average nest height and mean dbh of tree species used for nesting
274 based on the vegetation surveys ($R^2=0.27$, $F=7.232$, $P<0.05$), although this relationship had low
275 explanatory power (Table I; Table SI).

276

277 **Habitat Description**

278 A total of 2,005 individual plants were recorded, belonging to 85 tree (N=1,966) and 8
279 liana species (N=39) (Table SI). Datasets standardized by sample-based rarefaction confirmed
280 that savannah-woodland was significantly more species-rich than either forest type, which
281 showed similar levels of species richness (Fig. S1).

282 The two-dimensional NMDS ordination clearly separated savannah-woodland from open
283 and dense forest plant communities along axis 1 which were more similar in floristic
284 composition as indicated by the fairly tight clustering of SUs compared with the more
285 heterogeneous floristic composition of savannah-woodland which showed considerable spread
286 along axis 2 (Fig. 3; Table SII). PERMANOVA confirmed significant compositional variation
287 among habitat types ($R^2=0.25$, $F=2.455$, $P<0.001$). The nest trees *D. guineense*, *E. guineensis*
288 and *A. africana* showed a positive association with dense and open forests along axis 1, and *D.*
289 *senegalense* and *P. biglobosa* were the nest trees associated negatively and positively,
290 respectively, with savannah-woodland along axis 2 (Fig. 3). For more details see Supporting
291 Material (Fig. S2).

292 Considering only plant species known to be eaten by LCNP chimpanzees, the same
293 patterns were found for floristic richness, diversity and composition, as for the whole
294 assemblage. For more details see Supporting Material (Fig. S3; Table SI and Table SII).

295

296 **Nest Abundance and Vegetation Attributes**

297 Considering the entire floristic assemblage, a zero-altered negative binomial (ZANB)
298 GLMM was the best-fitted model based on AICc (Table SIII). The ZANB GLMM that contained
299 all explanatory variables (i.e. floristic richness, diversity and composition, and total basal area)
300 except plant density was the one best supported for nest counts (Table II). Chimpanzee nest
301 abundance was negatively correlated with floristic diversity (e^H) and total basal area, whereas
302 positive associations were found with floristic richness and both NMDS axes summarizing
303 floristic composition (Table III). Regarding the binary component of the model, significant
304 parameter estimates were only obtained for e^H and plant density, suggesting that the probability
305 of finding a zero decreases with increasing floristic diversity, but slightly increases with plant
306 density (Table III).

307 Restricting the analysis only to food plant species, a ZANB GLMM again fitted our data
308 best (Table SIII). For nest counts, the best model contained only total basal area of food tree
309 species, showing a negative correlation between this predictor and nest abundance (Table II and
310 III). This model further included floristic richness, e^H , NMDS2, and total basal area as important
311 variables for explaining the occurrence of zeroes, suggesting that the probability of finding a
312 zero increases with an increase in floristic richness, NMDS2, and total basal area, but decreases
313 with e^H (Table III).

314

315 **Nest Tree Species Choice**

316 Chimpanzees used 23 out of a total of 89 available tree species for nest building, which
317 comprised, in addition to the tree species found during the vegetation surveys, five species that
318 were only recorded during nest surveys (Fig. S4; compare Table I and Table SI). The tree species

319 most chosen for nesting, *D. guineense* (52.7%), was also the most abundant (23.1%) in the study
320 area (Fig. S4; Table I and Table SI). Comparing the proportions of tree species used for nesting
321 and tree availability, *D. guineense*, *A. africana*, *D. senegalense*, *E. guineensis*, *P. biglobosa* and
322 unidentified species 39 were clearly selected more often than expected by chance, hence being
323 preferred tree species (i.e. located below the 1:1 line, see Fig. 4A1-2). In contrast, 17 species
324 were used less frequently than expected based on their availability (i.e. found above the 1:1 line,
325 see Fig. 4A1-2) and thus appear to be avoided for nesting. Based on the resampling procedure,
326 for most trees used for nesting the proportions of randomly selected trees did not cross the 1:1
327 line, confirming a non-random choice of nest tree species by chimpanzees (Fig. 4B).

328

329 **DISCUSSION**

330 This paper reports the first detailed quantitative data on nesting patterns of LCNP
331 chimpanzees. During the dry season, chimpanzees built nests preferentially in dense forest
332 [Carvalho et al., 2013], similar to what has been reported for other West African sites [Baldwin
333 et al., 1981; Pruetz et al., 2008; Fleury-Brugiere and Brugiere, 2010; Sousa et al., 2011]. At their
334 easternmost limit of distribution in Issa (Tanzania), despite no evident preference for forest or
335 woodland, most nests were found in woodland even during the dry season [Hernandez-Aguilar,
336 2009]. Estimates of chimpanzee density at LCNP show an inverse relationship with habitat
337 availability [Carvalho et al., 2013], highlighting that dense forest, although the least available
338 habitat type in the park, offers the most suitable nesting conditions. Such conditions could
339 include the availability of materials adequate for nest building [Koops et al., 2012a], the
340 distribution and availability of food resources [Furuichi and Hashimoto, 2004], and a lower
341 incidence of human disturbance in dense forest compared to other habitat types [Last and Muh,

2013]. While we do not have data to evaluate the role of the first two factors, a negative influence of human disturbance on chimpanzee distribution at LCNP was demonstrated based on the distances between nests or habitat types and proxies of human disturbance (i.e. settlements, roads and rivers), suggesting that human disturbance is lower in dense forest relative to the other habitat types [Carvalho et al., 2013]. Nesting conditions in dense forest may also be more suitable due to the greater year-round availability of water, in contrast to savannah-woodland where most water sources dry up during the dry season [IBAP, 2008].

Chimpanzee nest abundance was negatively related to floristic diversity and tree basal area, reflecting the preference for dense forest, the habitat characterized by comparatively lower diversity and a greater availability of smaller-sized trees. The positive correlation between nest abundance and floristic richness and composition, however, highlights that the other more open and species-rich habitats also play an important role in chimpanzee nest building. Studies on atelid [Cristóbal-Azkarate et al., 2005; Stevenson, 2011] and cercopithecoid monkeys [Rovero and Struhsaker, 2007; Linder and Lawler, 2012] found that primate abundance is positively associated with floristic diversity and total basal area, in contrast with our findings, and with floristic richness and composition, in line with our results. To the best of our knowledge, there are no comparable studies on chimpanzees that have related nest abundance with the comprehensive set of vegetation characteristics explored herein. Plant density was not a significant predictor of chimpanzee nest abundance in our study, in line with findings from Kalinzu Forest (Uganda) [Furuichi and Hashimoto, 2004], where other predictors such as fruit abundance and vegetation type best explained chimpanzee nest abundance. Human activities have been contributing to the change in floristic richness, diversity, and composition in LCNP, as is typical for other African forests such as Kibale (Uganda) [Mitani et al., 2000], which have

365 been recovering from decades or centuries of human disturbance. LCNP is a forest-savannah
366 mosaic widely disturbed by humans and consequently current patterns of floristic richness,
367 diversity, and composition are strongly shaped by everyday life activities and agro-ecological
368 management by the park residents [IBAP, 2008], as also reported from Kissidougou (Republic of
369 Guinea) [Fairhead and Leach, 1996]. Over the last decades, the social, economic, and
370 demographic changes in Guinea-Bissau have altered the extent to which sustainable land use has
371 been practiced. Nowadays, dense forest is not well protected but often replaced by extensive
372 monocultures of cashew [Barry et al., 2007; Carvalho et al., 2013]. Thus, present-day
373 distribution patterns of chimpanzees may reflect an adaptation to past human activities.

374 Typically, primate surveys have less than 100% detection probability, which leads to a
375 possibly high frequency of zero counts. In our case, the probability of recording a zero was
376 associated with a number of predictor variables (floristic diversity and plant density) suggesting
377 that some nests, specifically in dense forest, may not have been observed due to reduced
378 visibility. Thus, the number of nests observed in dense forest and the preference for building
379 nests in this type of habitat is likely even more pronounced than our nest count data indicate.

380 Our analysis restricted to food plant species showed that total basal area was negatively
381 correlated with chimpanzee nest abundance, congruent with a preference for nesting in dense
382 forest. In contrast, total basal area of food species was a positive predictor for *Cercocebus*
383 *galeritus* abundance at Tana River Primate National Reserve (Kenya) [Wieczkowski, 2004].
384 Most nests (90%) at LCNP were built in feeding trees, similar to the proportion of nests (93%) at
385 Bwindi National Park (Uganda) [Stanford and O'Malley, 2008]. Similar to our study, no data
386 were collected on whether nest trees had ripe fruit at the time of observation or on physical
387 characteristics of nest trees. According to Stanford and O'Malley (2008), chimpanzees may be

388 selecting nest trees due to certain physical characteristics, such as tree height, maturity, among
389 others, and not because they are feeding trees. Further research is clearly needed to determine
390 whether tree physical characteristics in LCNP are having an effect on tree species selection for
391 nesting.

392 We identified 23 tree species harboring chimpanzee nests at different proportions, of
393 which *D. guineense*, *A. africana*, *D. senegalense*, *E. guineensis*, *P. biglobosa*, and one
394 unidentified species (unidentified 39) were selected more often than expected by chance. In line
395 with previous findings [Kalinzu Forest (Uganda), Furuichi and Hashimoto, 2004], chimpanzees
396 also nested in other ubiquitous tree species when preferred tree species were not available.
397 Selectivity in the choice of nest tree species was also reported from other sites in Guinea,
398 Uganda, and Tanzania [Furuichi and Hashimoto, 2004; Ndimuligo, 2007; Stanford and
399 O'Malley, 2008; Koops et al., 2012a]. In Cantanhez National Park (CNP) in southern Guinea-
400 Bissau, chimpanzees build nests preferentially (92%) in oil palms (*E. guineensis*) during the dry
401 season [Gippoliti and Dell'Omo, 1996; Sousa et al., 2011], in contrast to LCNP where it was the
402 second most preferred species, albeit at a much lower proportion (10%). Other tree species such
403 as *D. guineense* and *P. excelsa* [Sousa et al., 2011] are used for nesting by chimpanzees in both
404 areas. Oil palm preference was also documented in Kounounkan Massif (Guinea) [Barnett et al.,
405 1996], and in Bossou (Guinea) and Yealé (Ivory Coast) [Humle and Matsuzawa, 2004]. In
406 contrast, no evidence for this was found at another Guinean site, Seringbara [Humle and
407 Matsuzawa, 2004]. Humle and Matsuzawa [2004] found that differences in oil-palm use between
408 Bossou, Yealé and Seringbara could not be explained by environmental differences, but instead
409 argued that patterns of oil-palm preference may be culturally determined. Since Yealé is a
410 forested site, the findings of these authors are in contrast to Barnett et al.'s [1996] suggestion that

411 oil palm preference could be an exclusive behaviour of marginal chimpanzee populations in
412 West Africa that live in forest-savannah mosaics. Clearly, more data on oil palm use for nesting,
413 particularly on oil palm density, from a greater range of study sites are necessary to be able to
414 draw solid conclusions.

415 Based on our data, we cannot distinguish between two possible causes underlying the
416 observed tree species preference. On the one hand, it could be a consequence of suitable habitat
417 conditions offered by dense forest, for instance, in terms of resource availability, topographical
418 features, or climatic conditions [Furuichi and Hashimoto, 2004; Stanford and O'Malley, 2008;
419 Koops et al., 2012a]. On the other hand, it could reflect the fact that chimpanzees preferentially
420 select certain physical characteristics of trees [Baldwin et al., 1981; Pruetz et al., 2008;
421 Hernandez-Aguilar et al., 2013] and those are predominantly found in tree species of dense
422 forest.

423 Average nest height including *E. guineensis* or not was very similar (14.60 m and 14.01
424 m, respectively), and no significant differences were found among habitat types, although LCNP
425 chimpanzees built nests higher in savannah-woodland than in forest habitats. Of the top two tree
426 species preferentially used for nesting, *D. guineense* harbored nests at lower heights and at lower
427 tree dbh than *E. guineensis*. If one considers the positive correlation found between nest height
428 and tree dbh, nest tree species selection may be a consequence of different tree physiognomies.
429 However, for several reasons this needs to be interpreted with caution. First, we used nest tree
430 dbh as a proxy to infer nest tree height. However, the relationship between dbh and height is not
431 always constant and comparison of tree dbh across study sites may not reflect a proportional
432 difference in tree height [Hernandez-Aguilar et al., 2013]. Secondly, nest height is better
433 understood if compared to height distributions of trees with and without nests, as proposed by

434 Pruetz et al. [2008] who found that chimpanzees select taller trees for nesting than expected
435 based on the mean heights of available trees. Finally, variables such as nest tree height and the
436 height of the lowest branch, among other characteristics, seem to better explain chimpanzee nest
437 height, however, these data are currently only available for a few study sites [Hernandez-Aguilar
438 et al., 2013]. We therefore advocate that such information be more routinely collected in future
439 studies.

440 Irrespective of whether nests in *E. guineensis* were included or not, on average, we found
441 that nest height at LCNP was considerably lower than what has been reported for CNP (14.6 m
442 vs. 19.7 m) [Sousa et al., 2011], but higher compared with reports from other countries across the
443 subspecies' geographic range [see Hernandez-Aguilar et al., 2013]. Lacking data on nest tree
444 height or other tree physical characteristics for LCNP, we can only speculate whether the
445 elevated nest height is actually a response to predator pressure in this park. Evidence that non-
446 human predators still occur in Guinea-Bissau at abundances high enough to be considered a
447 relevant threat to chimpanzees is limited, even though the presence of leopards is reported both
448 for LCNP [IBAP, 2008] and CNP [Gippoliti and Dell'Omo, 1996]. In CNP, nests in oil palm
449 were located at the forest edge (i.e. in open-canopy habitats), reflecting, at least in part, that
450 chimpanzees in this park are not directly persecuted by humans and generally do not avoid areas
451 of human activity [Sousa et al., 2011; Hockings and Sousa, 2012]. The physiognomic
452 characteristics and distribution of oil palms, which provide protection from predators (e.g.
453 leopards), easier communication among group members, a wider view of the surrounding
454 landscape, and proximity to specific resources for chimpanzees, were qualitatively attributed as
455 the main causes for this preference in CNP [Gippoliti and Dell'Omo, 1996; Sousa et al., 2011].

456 Arboreal nesting is generally interpreted as a strategy to avoid predation [Baldwin et al.,
457 1981; McGrew, 2004; Pruetz et al., 2008; Hernandez-Aguilar et al., 2013]. However, in our case
458 exclusive arboreal nesting could be related to human disturbance, similar to findings by Last and
459 Muh [2013] who attributed the lack of ground nesting at one of their study sites to increased
460 human pressure. Due to a local taboo, chimpanzees in Guinea-Bissau are supposedly not hunted
461 owing to their similarities with humans [Gippoliti and Dell’Omo, 2003]. Nevertheless, LCNP
462 residents reported that females are sometimes killed to sell their babies as pets, a scenario which
463 has also been documented for the southern region of Tombali [Cá, 2008]. In Guinea-Bissau,
464 body parts of chimpanzees have also recently been found to be used in traditional medicine [Sá
465 et al., 2012]. While this lends some support to the idea that exclusive arboreal nesting at LCNP
466 may be a consequence of human disturbance, better quantitative data on non-human predators
467 are needed to determine to what extent the construction of elevated nests is indeed a response to
468 predators that can climb trees.

469 We are aware that our data only cover the dry season. Since an effect of seasonality on
470 nesting patterns was documented for other West African sites (Assirik and Fongoli [Baldwin et
471 al., 1981; Baldwin et al., 1982; Pruetz et al., 2008]) characterized by similar climatic conditions
472 to those of LCNP, it would be important for future research to extend our work to include also
473 the wet season to determine if patterns observed in this study hold over the full annual cycle.

474

475 **Implications for Conservation**

476 As shown, *D. guineense* is a key resource for LCNP chimpanzees, playing a central role
477 in their nest building behavior. In 2011 we learned about a future local project that intends large-
478 scale exploitation of this tree species for commercial timber harvesting (Nelson Dias, personal

479 communication). As the remaining patches of dense forest in which this tree species occurs and
480 suitable habitat conditions for chimpanzees are restricted to southern Guinea-Bissau, our results
481 underline the importance of implementing effective conservation measures to mitigate the
482 negative impacts of such exploitation on these forests, and consequently on one of the most
483 threatened coastal chimpanzee populations.

484 Natural regeneration has been recommended following agricultural abandonment to
485 recover forest structure and floristic composition [Aide et al., 2000]. It is crucial that this
486 traditional practice is maintained in this protected area as a low-cost strategy to restore dense
487 forests. However, slash-and-burn agriculture needs to be regulated to enable colonization of seed
488 sources from adjacent mature forests and to prevent soil degradation [Fairhead and Leach, 1996;
489 Aide et al., 2000]. While these conservation efforts are foreseen in the forest law of Guinea-
490 Bissau (Decree No. 4-A/91) an effective control by strengthening and enforcing the existing law
491 will be important for these measures to succeed.

492

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506

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697 TABLES

698

699 Table I. Relative Proportion, Total Number, and Mean Nest Height (\pm SE) of Chimpanzee

700 Nests Observed in 23 Tree Species, Along With the Corresponding Tree Family.

Tree species (abbreviation)	Family	Nests observed (%)	Nests (total)	Nest height (m)
<i>Dialium guineense</i> (D.guin)	Legum./Caesalp.	52.72	242	13.10 (0.02)
<i>Elaeis guineensis</i> (E.guin)	Palmae	10.02	46	19.93 (0.08)
<i>Detarium senegalense</i> (D.sene)	Legum./Caesalp.	5.66	26	17.66 (0.20)
<i>Afzelia africana</i> (A.afri)	Legum./Caesalp.	4.58	21	15.78 (0.17)
<i>Parkia biglobosa</i> (P.bigl)	Legum./Mimos.	4.36	20	16.34 (0.21)
<i>Parinari excelsa</i> (P.exce)	Chrysobalanaceae	3.70	17	15.15 (0.26)
<i>Daniellia oliveri</i> (D.oliv)	Legum./Caesalp.	3.49	16	14.50 (0.24)
Unidentified 39 (unid.39)	-	3.49	16	9.15 (0.22)
<i>Pterocarpus erinaceus</i> (P.erin)	Legum./Papil.	2.18	10	13.34 (0.28)
<i>Khaya senegalensis</i> (K.sene)	Meliaceae	1.96	9	16.76 (0.52)
<i>Ceiba pentandra</i> (C.pent)	Bombacaceae	1.31	6	21.25 (0.37)
Unidentified 41 (unid41)	-	1.31	6	21.23 (0.76)
<i>Erythrophleum suaveolens</i> (E.suav)	Legum./Caesalp.	1.09	5	14.65 (0.79)
<i>Antiaris toxicaria</i> subsp. <i>welwitschii</i> (A.toxi)	Moraceae	0.87	4	21.98 (0.82)
<i>Newbouldia laevis</i> (N.laev)	Bignoniaceae	0.65	3	15.33 (2.54)
<i>Terminalia macroptera</i> (T.macr)	Combretaceae	0.65	3	13.98 (0.38)
<i>Cola cordifolia</i> (C.cord)	Sterculiaceae	0.44	2	11.15 (0.35)
<i>Spondias mombin</i> (S.momb)	Anacardiaceae	0.44	2	12.65 (0.00)
<i>Acacia macrostachya</i> (A.macr)	Legum./Mimos.	0.22	1	4.65
<i>Allophylus africanus</i> (Al.afri)	Sapindaceae	0.22	1	11.65
Unidentified 5 (unid5)	-	0.22	1	7.65
Unidentified 22 (unid22)	-	0.22	1	13.65
Unidentified 40 (unid40)	-	0.22	1	16.75

701 Tree (sub) family: Legum. – Leguminosae; Caesalp. – Caesalpinioideae; Mimos. – Mimosoideae; Papil. –

702 Papilionoideae.

703 **TABLE II. Results of AICc-Based Model Selection of GLMM Zero-Altered Negative**
 704 **Binomial Regression (ZANB) Models for the Effects of Vegetation Attributes on**
 705 **Chimpanzee Nest Abundance. Note that Results are Reported Considering Both the Entire**
 706 **Floristic Assemblage and Only Plant Species Known to be Eaten by LCNP Chimpanzees**
 707 **(see Table SI).**

Sample	Parameter type	Variables	AICc	Δ AICc*		
Entire floristic assemblage	Nest counts	FR, e ^H , NMDS1, NMDS2, BA	168.87	0.00		
		Full model	174.71	5.84		
		FR, PD, e ^H , NMDS1, NMDS2	174.73	5.86		
		FR, PD, e ^H , NMDS1, BA	180.27	11.40		
		FR, PD, e ^H , NMDS2, BA	181.88	13.01		
		PD, e ^H , NMDS1, NMDS2, BA	184.21	15.34		
		FR, PD, NMDS1, NMDS2, BA	185.63	16.76		
	Zeroes	PD, e ^H , NMDS1, BA	138.61	0.00		
		FR, PD, e ^H , NMDS1, NMDS2	141.89	3.28		
		FR, PD, e ^H , NMDS1, BA	142.35	3.74		
		PD, e ^H , NMDS1, NMDS2, BA	142.80	4.19		
		FR, PD, e ^H , NMDS2, BA	143.79	5.18		
		Full model	144.13	5.52		
		FR, e ^H , NMDS1, NMDS2, BA	144.35	5.74		
		FR, PD, NMDS1, NMDS2, BA	145.48	6.87		
		Food plant species	Nest counts	BA	166.73	0.00
				FR, e ^H , NMDS1, NMDS2, BA	182.27	15.54
FR, PD, NMDS1, NMDS2, BA	182.27			15.54		
FR, PD, e ^H , NMDS1, BA	182.27			15.54		
PD, e ^H , NMDS1, NMDS2, BA	182.28			15.55		
FR, PD, e ^H , NMDS2, BA	182.93			16.20		
FR, PD, e ^H , NMDS1, NMDS2	187.66			20.93		
Full model	188.12		21.39			
Zeroes	FR, PD, e ^H , NMDS2, BA		131.27	0.00		
	FR, e ^H , NMDS1, NMDS2, BA		133.18	1.91		
	Full model	133.46	2.19			
	FR, PD, e ^H , NMDS1, NMDS2	138.05	6.78			
	PD, e ^H , NMDS1, NMDS2, BA	137.50	6.23			
FR, PD, NMDS1, NMDS2, BA	137.96	6.69				
FR, PD, e ^H , NMDS1, BA	143.48	12.21				

708 *reported values correspond to the comparison with the best model.

709 Vegetation attributes: FR- floristic richness; PD- plant density; e^H – exponential form of Shannon’s entropy index;
 710 NMDS1/2- first/second NMDS axis summarizing floristic composition; BA- total basal area.

711 **TABLE III. Summary of GLMM Zero-Altered Negative Binomial Regression (ZANB)**
 712 **Models for Effects of Vegetation Attributes on Chimpanzee Nest Abundance, Considering**
 713 **the Entire Floristic Assemblage and Plant Species Known to be Eaten by LCNP**
 714 **Chimpanzees (see Table SI). Parameter Estimates (β) and Respective Standard Error**
 715 **(SE), z-Statistic and P-Value, are Shown Only for the Best-Ranked Models as Given in**
 716 **Table II.**

Sample	Parameter type	Variable	β	SE	z	P-value
Entire floristic assemblage	Nest counts	FR	0.333	0.083	4.02	<0.001
		e ^H	-0.970	0.243	-3.99	<0.001
		NMDS1	0.964	0.189	5.09	<0.001
		NMDS2	4.917	1.218	4.04	<0.001
		BA	-0.006	0.001	-5.18	<0.001
	Zeroes	Intercept	5.805	0.876	6.62	<0.001
		PD	0.085	0.034	2.49	<0.05
		e ^H	-0.350	0.121	-2.88	<0.01
		NMDS1	0.602	0.369	1.63	0.103
		Intercept	-1.063	1.968	-0.54	0.59
Food plant species	Nest counts	BA	-0.463	0.196	-2.36	<0.05
		Intercept	2.303	0.379	6.08	<0.001
	Zeroes	FR	0.518	0.163	3.18	<0.01
		PD	-0.056	0.029	-1.90	0.057
		e ^H	-0.657	0.228	-2.89	<0.01
		NMDS2	2.848	0.884	3.22	<0.01
		BA	1.058	0.410	2.58	<0.01
		Intercept	-3.813	1.128	-3.38	<0.001

717 Vegetation attributes: FR- floristic richness; PD- plant density; e^H – exponential form of Shannon's entropy index;
 718 NMDS1/2- first/second NMDS axis summarizing floristic composition; BA- total basal area.
 719

720 **FIGURE LEGENDS**

721

722 Figure 1. Location of the Republic of Guinea-Bissau in West Africa and the study area *Lagoas*
723 *de Cufada* Natural Park (LCNP). Nest locations along the transects sampled inside LCNP are
724 shown. Environmental digital data were provided by the CARBOVEG project ([http://carboveg-](http://carboveg-gb.dpp.pt/)
725 [gb.dpp.pt/](http://carboveg-gb.dpp.pt/)).

726

727 Figure 2. Boxplots comparing nest height among nest tree species and habitat types. See Table I
728 for species names and abbreviations.

729

730 Figure 3. Ordination of sampling units along non-metric multidimensional scaling axes for the
731 entire native floristic assemblage (stress=0.11). Also shown are five of the six tree species
732 preferred for nesting (unidentified species 39 was not recorded during vegetation surveys). Tree
733 species: see Table I.

734

735 Figure 4. Expected proportions of trees with nests, if selection was random, as a function of
736 observed proportions of nest tree species: (A1) considering all tree species or (A2) excluding *D.*
737 *guineense*; and (B) distribution of expected proportions based on random sampling with
738 replacement (1000x). Tree species: see Table SI.

739

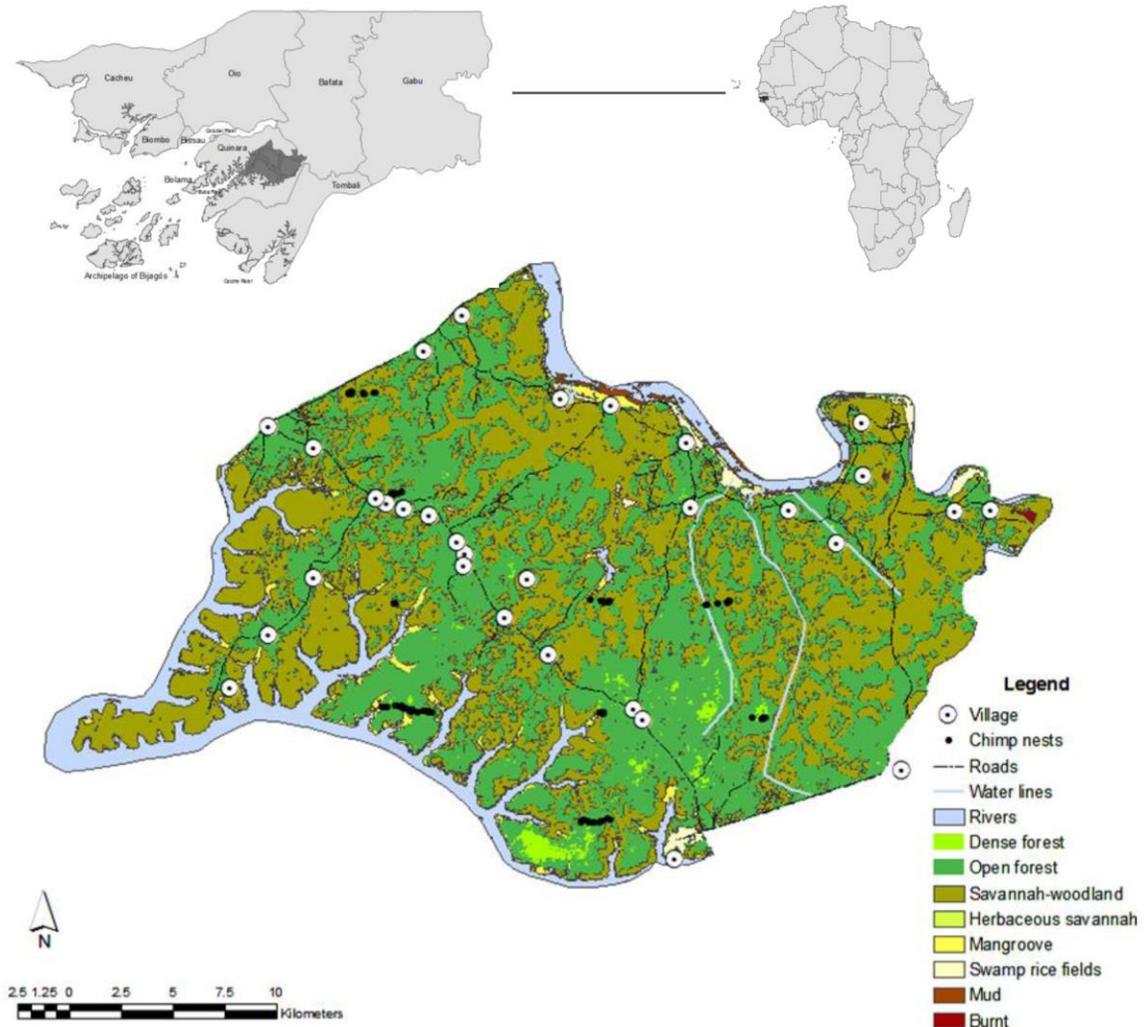


Figure 1. Location of the Republic of Guinea-Bissau in West Africa and the study area *Lagoas de Cufada* Natural Park (LCNP). Nest locations along the transects sampled inside LCNP are shown. Environmental digital data were provided by the CARBOVEG project (<http://carboveg-gb.dpp.pt/>).

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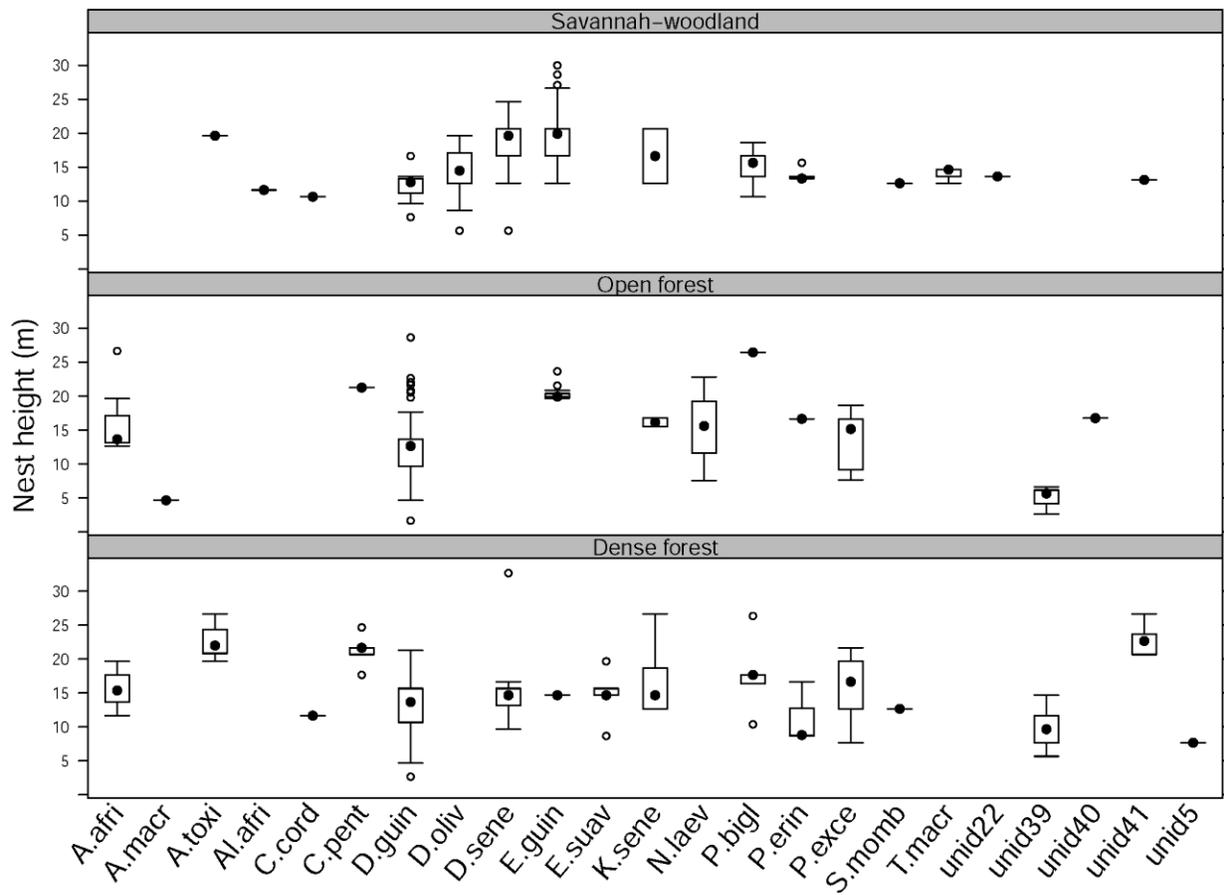


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743

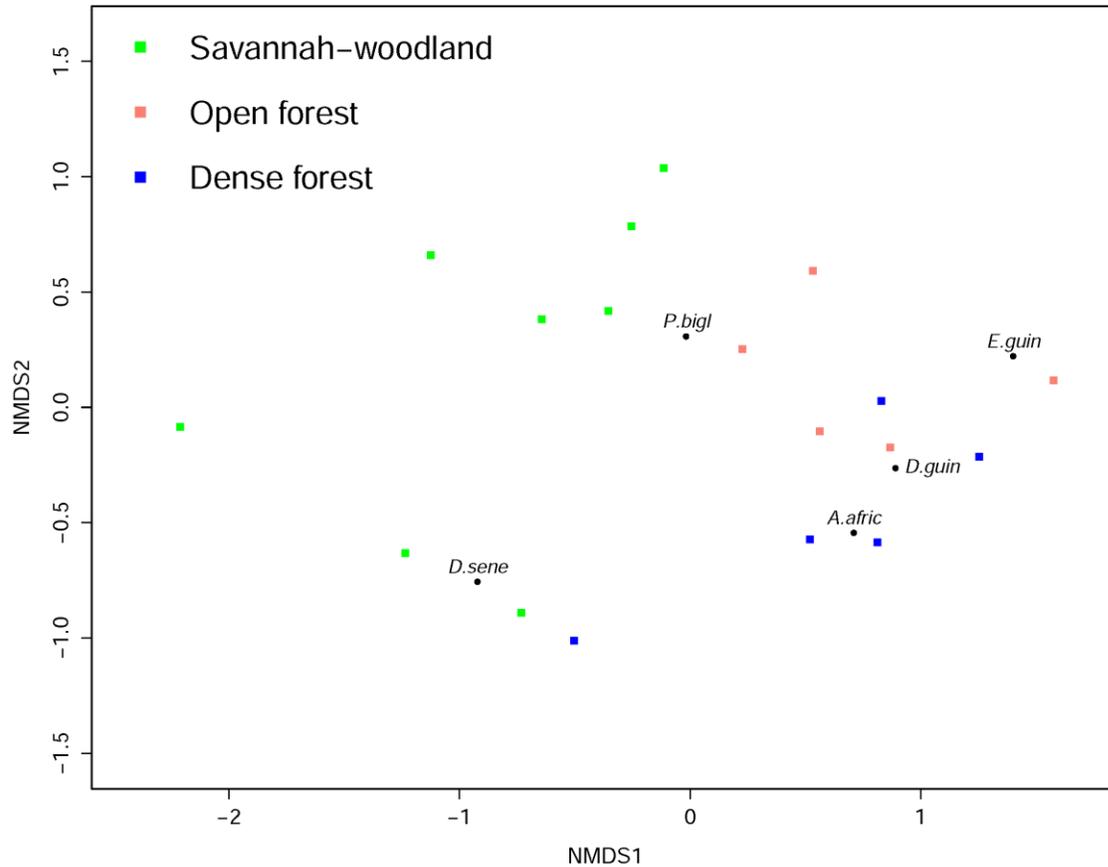


Figure 3. Ordination of sampling units along non-metric multidimensional scaling axes for the entire native floristic assemblage (stress=0.11). Also shown are five of the six tree species preferred for nesting (unidentified species 39 was not recorded during vegetation surveys). Tree species: see Table I.

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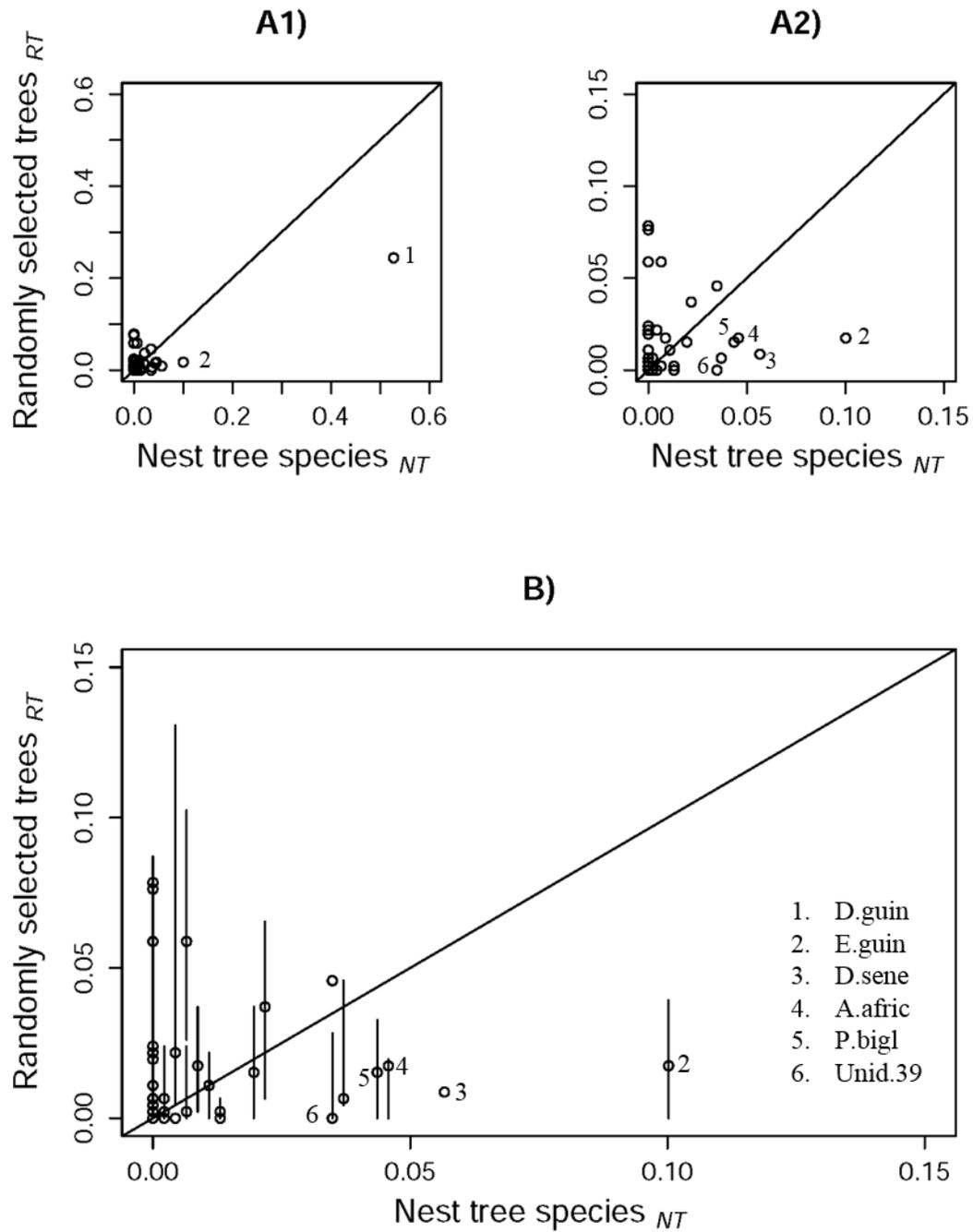


Figure 4. Expected proportions of trees with nests, if selection was random, as a function of observed proportions of nest tree species: (A1) considering all tree species or (A2) excluding *D. guineense*; and (B) distribution of expected proportions based on random sampling with replacement (1000x). Tree species: see Table SI.