1

1   Type: Research Paper

2   Title: The utility of visual estimation of cover for rapid assessment of graminoid abundance

3   in forest and grassland habitats in studies of animal foraging

4

5   Author names: Hansraj Gautam, G. G. Potdar & T.N.C. Vidya

6

7   Author addresses: Gautam, H. (hansrajgautam@jncasr.ac.in)[1], Potdar, G. G.

8   (girishpotdar@gmail.com)[2], Vidya, T. N. C. (Corresponding author,

9   tncvidya@jncasr.ac.in)[1,*]

10

11   [1]Evolutionary and Organismal Biology Unit, Jawaharlal Nehru Centre for Advanced

12   Scientific Research, Bengaluru, India.

13   [2] Department of Botany, Yashwantrao Chavan College of Science, Karad, Maharashtra,

14   India.

15   * Corresponding author

16   Address for correspondence:

17   T.N.C. Vidya

18   Evolutionary and Organismal Biology Unit

19   Jawaharlal Nehru Centre for Advanced Scientific Research

20   Jakkur, Bengaluru – 560 064, India.

21   Email: tncvidya@jncasr.ac.in

22   Phone: +91-80-22082968

23   Fax: +91-80-22082766

24

25   Running head: Rapid assessment of graminoid abundance by visual estimation

26

27 **The utility of visual estimation of cover for rapid assessment of graminoid abundance in**

28 **forest and grassland habitats in studies of animal foraging**

29

30 **Abstract:**

31 **Questions:** To assess the feasibility of using visually-estimated cover in rapid assessment of

32 herbivore food species abundance in the grass layer, we asked the following questions: 1)

33 What is the relationship between total graminoid cover and biomass in forests, and does

34 height improve the prediction of biomass from cover? 2) How does total cover relate to

35 biomass in a grassland habitat? 3) How does elephant food species graminoid cover relate to

36 individual species biomass? 4) How well does species diversity of forest understorey grass

37 layer, calculated from cover data, mirror that calculated from biomass data? **Location:**

38 Nagarahole National Park, India. **Methods:** We estimated the abundance of graminoids

39 through visual estimation of cover and weighted harvested biomass in forest and grassland

40 plots. In forests, two estimates of total graminoid abundance, total graminoid cover and sum

41 of species covers, were used. In the grassland, only total graminoid abundance was measured.

42 We examined the relationship between cover estimates and biomass, and the additional utility

43 of height in predicting biomass, using multiple regressions and AIC-based model selection.

44 We also assessed similarity in cover- and biomass-based Simpson's and Shannon-Wiener

45 diversity indices using regressions. **Results:** Graminoid cover explained a large portion of

46 variation in total graminoid biomass in forest and grassland habitats. The sum of species

47 covers was better than total cover in estimating total graminoid biomass in the forest. The

48 benefit of including height to estimate total biomass was moderate in forests but substantial in

49 grassland. Cover estimates were good proxies of food species biomass, and the addition of

50 height did not yield better models for most species. Species diversity indices calculated from

51 cover largely matched those based on biomass. **Conclusions:** Visual estimation of species

52 cover is a good alternative to biomass harvesting for rapid assessment of abundance of

53 graminoids consumed by generalist herbivores, like elephants.

54 **Key words:**

55 Elephant food species, graminoids, forage distribution, vegetation abundance, rapid

56 assessment methods, visual estimation of cover, species diversity, tropical forests, grasslands.

57

3

58   **Author contribution:** HG and TNCV planned the work, performed statistical analyses and

59   wrote the manuscript, HG did field sampling, GP did species identification and all the authors

60   critically revised the manuscript.

61

Introduction

63   Ecologists estimate vegetation abundance in order to study various structural and functional

64   attributes of plant communities (e.g. Hermy 1988, Guo and Rundel 1997, Chiarucci et al.

65   1999, Henschel et al. 2005, Lavorel et al. 2008), the productivity of animals' habitats (e.g.

66   Hutto 1990, Säid et al. 2005, Pettorelli et al. 2011, Iversion et al. 2014) and its effect on

67   foraging behaviour (e.g. Wilmshurst et al. 1999), and the impact of animal activities on

68   vegetation (e.g. Pekin et al. 2015). While studies of plant community structure and function

69   may require intensive measurements of species abundance or traits (e.g. Chiarucci et al. 1999,

70   Lavorel et al. 2008), assessment of resource availability for animals often necessitates

71   sampling over large spatial scales (see Pettorelli et al. 2011), which would, therefore, benefit

72   from rapid methods of estimating species abundance. The estimation of forage abundance is a

73   pre-requisite in studies of ecological and behavioural aspects of foraging ecology (Hutto

74   1990, Säid et al. 2005), but the collection of detailed forage abundance data may be very

75   demanding in terms of effort, time, and resources, which are limitations for most field

76   biologists. Different methods of estimating vegetation abundance vary in their sensitivity to

77   vegetation structure, accuracy, precision, practicality, time and manpower required, and

78   destructive nature (Harmoney et al. 1997, reviewed in Wilson 2011), and no single method is

79   clearly superior in all these respects. Given the apparent trade-off in methods between

80   accuracy and speed, it has been suggested that the choice of method should be based on the

81   objective of the study and after consideration of the advantages and limitations of each

82   method (Elzinga et al. 1998, Lavorel et al. 2008, Wilson 2011, Redjadj et al. 2012).

83   The diet of the animal and the vegetation structure in its habitat will together determine

84   whether the measurement of forage abundance should be carried out on all components of the

85   vegetation or only on a portion of the vegetation (such as specific plants or plant parts). For

86   example, all the vegetation of a largely monocultural grassland may be considered for

87   quantifying the food abundance of a grazing herbivore, whereas many components of

88   vegetation (herbs, shrubs, and tree species) in a forest or woodland may not be part of the

89   same animal's diet, and only the food component of the vegetation should be measured.

4

90   Second, in studies of foraging, ecologists are also often interested in studying whether an
91   animal shows selectivity at the species level during feeding (e.g. Owen-Smith and Chafota
92   2012) and whether it maintains species diversity in its diet (e.g. Marsh et al. 2006). It is,
93   therefore, also important for the method of estimation of forage abundance to provide
94   species-level detail. Given the considerations above, several methods of abundance
95   estimation become impractical or too time-consuming to implement in diverse habitats,
96   primarily because the vegetation layers that are not relevant to foraging may dominate the
97   biomass in forests with rich biodiversity. Unlike other estimation methods, the biomass
98   harvest method (e.g. Drew 1944, Hermy 1988), and the visual estimation of cover (Kennedy
99   and Addison 1987) can be applied even when a selected portion of vegetation is to be
100   quantified. However, biomass-harvesting can be time-consuming if species have to be
101   weighed separately, as this requires sorting of individuals into different species by hand
102   (Harmony et al. 1997, Lavorel et al. 2008). In this regard, the use of visual estimation of
103   cover may be advantageous, as it allows for rapid assessment of portions of vegetation and is
104   also non-destructive.

105

106   #Fig. 1 approximately here#

107

108   We, therefore, tested the utility of the visual estimation method in predicting biomass in
109   the context of forage availability for herbivores in general and for Asian elephants in a
110   tropical forest in southern India in particular. Elephants are considered generalist herbivores,
111   but primarily feed on grasses in the lower vegetation strata, in addition to stems and bark of
112   woody species in the upper strata (Owen-Smith 1988, Sukumar 1990, Baskaran et al. 2010).
113   Although their diet consists of numerous species, in species-rich tropical forests, this number
114   may be a small proportion (Blake 2002, HG and TNCV unpubl. data) of all the species
115   present. The estimation of abundance of woody species is simple as it involves the counting
116   of trees and measurements of tree-girth which can be done rapidly since the number per plot
117   is usually low. However, elephant foods in understorey vegetation are represented by
118   numerous individuals that are difficult to count within limited time. Moreover, most of the
119   vegetation represented by herbs and shrubs is not consumed by elephants (in our study area,
120   the abundance of food species as a percentage of all species in the respective vegetation strata
121   during the wet and dry seasons, respectively, was about 23% and 10% for herbs, 18% and

122   16% for shrubs and 80% and 85% for graminoids, HG and TNCV unpubl. data). Therefore,

123   in such habitats, the focus should be on estimating the abundance of only food plant species

124   in the lower strata of the forest. The dominance of grasses in Asian elephant diet (Baskaran

125   et al. 2010) makes its quantification crucial, and we explored the utility of the visual

126   estimation method in assessing graminoid biomass. Since other herbivores in similar

127   deciduous forests are also primarily grazers (Ahrestani et al. 2012), if the visual method could

128   be used to reliably estimate biomass, our results would also have implications for the

129   quantification of resource abundance for such herbivores. Therefore, we assessed the utility

130   of visually estimated cover in explaining elephant food graminoid biomass, as well as total

131   graminoid biomass, which would establish the generality of the method, for use in other

132   species. We investigated the utility of this rapid method at the community level, as well as at

133   the more detailed species level. We also examined the additional utility of height, another

134   variable which can be rapidly measured, in modelling graminoid biomass in two types of

135   habitats, forest and grassland. Such questions regarding biomass of graminoids have been

136   rarely addressed in forest habitats (eg. Andariese and Covington 1986), especially in the

137   context of forage availability for wildlife.

138   Previously, studies have found strong correlations between visual estimates and biomass

139   (Hermy 1988, Guo and Rundel 1997, Chiarucci et al. 1999, Henschel et al. 2005, Axmanová

140   et al. 2012) but were not carried out in the context of sampling food availability for wildlife.

141   On the other hand, studies on foraging ecology have sometimes used visual estimation for

142   assessment of forage distribution (e.g. Noyce and Coy 1990, Blake 2002, Rebollo et al. 2013,

143   Iversion et al. 2014), but the relationship between visual estimates and biomass of relevant

144   foods has seldom been tested rigorously in a complex habitat (but see Noyce and Coy 1990

145   for bear foods), which is important before making inferences about the relationship between

146   resource distribution and forage selection.

147   The questions we addressed in this paper were the following:

148   1. What is the relationship between visually-estimated total graminoid cover and total

149   graminoid biomass (measured through the standard biomass-harvest method) in forest

150   habitats, and does the inclusion of height or using the visually-estimated sum of species

151   covers improve the prediction of total graminoid biomass? This question would help find out

152   if the visual estimation method can be used in general in a forest with multiple strata, in

153   studies of foraging by grazing herbivores.

6

154   2.   Does the relationship between visually-estimated total graminoid cover and total

155   graminoid biomass (as seen from the results of question 1) also hold in a grassland habitat,

156   and does the inclusion of height improve the prediction of total graminoid abundance?

157   3.   How do visually-estimated species covers of individual graminoid food species of

158   elephants relate to their respective species biomass measurements in forest habitats? Since the

159   proportion of food graminoid species represents only a small fraction of all species in the

160   herbaceous stratum of the vegetation in the forest sampled (HG and TNCV unpubl. data), if

161   there was a high correlation between visually-estimated species cover and species biomass,

162   visually estimated cover could be used to assess food species abundance and also estimate

163   proportional abundance of different species.

164   4.   How accurately do species diversity indices of the grass layer in forest habitat,

165   measured by visual estimates, reflect the diversity indices obtained from biomass data? It

166   would be desirable to obtain good diversity estimates in order to study selectivity of species

167   and selection of different kinds of vegetation patches by herbivores.

168

169   **Study area**

170   The study was carried out in Nagarahole National Park (644 km^2, 11.85°–12.26° N, 76.00°–

171   76.28° E), which is a part of the larger contiguous Nilgiris-Eastern Ghats landscape in

172   southern India (Figure 2). The forest is tropical deciduous, comprising several strata, and is

173   home to several herbivores, including Asian elephants, on which a long-term study based on

174   individually identified elephants is currently ongoing (see Vidya et al. 2014). Along the

175   southern boundary of the park flows the river Kabini, on which a dam was constructed during

176   the 1970s to create a reservoir that extends along the southern boundary of the park. During

177   the dry season, when the waters of the reservoir recede, the exposed area forms a grassland

178   consisting mostly of just two short grass species (*Cynodon dactylon* and *Sporobolus* sp.,

179   which are also found in the forest, see Supporting Information 1) and attracts a large number

180   of elephants, deer, and gaur. The graminoids in the grassland are shorter (mean height 5.7

181   cm) and more continuously distributed compared to those in the forests (mean weighted

182   average of species heights 24.6 cm), where they are more sparsely distributed. Both the

183   grassland and the forest habitat are used by elephants, and data on graminoid abundance were

184   collected from both types of habitats, as described below.

7

185   **Data sampling and analysis**

186   Forest data

187   Data collection in forests was done from November to December 2013. Based on a forest

188   type classification map of the region developed by Pascal (1982), Nagarahole National Park

189   was divided into the three major forest types: dry deciduous forest, moist deciduous forest,

190   and teak plantations. We had previously divided the area into a 2 km × 2 km grid and placed

191   60 1-km line transects in randomly selected cells in order to map the distribution of elephant

192   food resources. During the present study, 23 of these transects in the southern and central

193   parts of the park and 17 additional transects, at least half a km away from each other and at

194   least 100 m away from forest roads, were chosen for sampling. Care was taken to adequately

195   represent all three forest types (based on their availability) in the sampling sites. Sampled

196   locations are mapped in Figure 2.

197

198   #Fig. 2 approximately here#

199

200   Sampling was carried out in 20 m × 5 m plots at the start or end of each of the 40 1-km

201   transects. In each of these 20 m × 5 m plots, three 1 m × 1 m quadrats were sampled,

202   equidistant along a straight diagonal line (except one plot, in which only two quadrats could

203   be sampled due to the presence of dense *Lantana* thickets). This resulted in 119 quadrats

204   sampled. We sampled all graminoid plants, including *Poaceae* (grasses), *Juncaceae* and

205   *Cyperaceae*. Graminoid abundance was measured at two levels: total graminoid abundance

206   (all the graminoid species present) and species-level abundance. First, total graminoid cover

207   was visually estimated by a single observer (HG) as the percentage of quadrat area covered

208   by all graminoids (Figure 1). Second, species cover for each graminoid species was visually

209   estimated, independent of the cover of other species. Cover was estimated to the closest 5%

210   or in interval bin of 5% (for low values such as 0 to 5% cover), in which case, the middle

211   value of the interval was chosen as the cover value. Values of less than 5% were applied in

212   the case of rare species that were represented by only one or two individuals in the quadrat.

213   Four individuals (except in the case of rare species, in which fewer than four individuals were

214   available) of each species were arbitrarily selected, their natural standing heights (i.e. without

215   straightening the plant) were measured, and the average of these was used as the height for

8

216 that species. The total graminoid (fresh) biomass was measured in the field using a digital

217 weighing balance (with 1 gram precision) after harvesting all the graminoids from the ground

218 level. Individuals were then hand-sorted into the respective species, and the biomass of each

219 species was measured.

220 At the level of the graminoid community, two measures of visually-estimated overall

221 graminoid abundance were used: total graminoid cover as described above, and the sum of

222 species cover (the sum of individual graminoid species covers; the value might exceed 100%

223 since each species was assessed independently; see Figure 1). Total graminoid biomass was

224 normally distributed whereas individual species biomass data were non-normal and were,

225 therefore, log-transformed for the analyses. However, the analyses were also performed on

226 untransformed data to evaluate the robustness of the results. We first used homogeneity of

227 regression slopes test (Zar 1974) to inspect the effect of forest type (dry deciduous, moist

228 deciduous and teak forests) on the relationship between total graminoid biomass and overall

229 graminoid cover. Similar relationships between total biomass and overall cover in different

230 forest types would result in a homogeneity of slopes. We then performed multiple regressions

231 of biomass on both estimates of overall graminoid cover to assess the utility of both measures

232 in predicting total graminoid biomass. We also used the weighted average of graminoid

233 species heights (weighted according to species cover) as an additional explanatory variable

234 and performed multiple regressions to test the utility of height in improving total biomass

235 estimates. Akaike information criterion with small sample correction (*AICc*; Hurvich and

236 Tsai 1989) was used for selection from the regression models including and excluding height.

237 Although there was a homogeneity of slopes (see Results) and plots from all forest types

238 could be combined for further analyses, we used forest type as a factor to account for the off-

239 chance that pooling the data would affect the results. In order to include the information on

240 forest type in multiple regressions, two dummy categorical variables were generated:

241 deciduous (category 1) or not (category 0 representing teak plantation), and moist deciduous

242 (1) or not (0 representing dry deciduous forest when the previous categorical variable had

243 value 1). These two variables were included in all regression analyses of data from the forest

244 habitats. At the level of individual species, multiple regressions (including the variables for

245 forest type) of species cover on species biomass were carried out for 10 common species (the

246 other species were present in fewer than 10 plots) all of which happened to be elephant food

247 species. We also checked whether multiple regressions that included the individual species'

248 height explained variation in individual species' biomass better compared to regressions

9

249   lacking this information. Model selection from the two types of regression models was done

250   on the basis of *AICc*. All the regressions described above were carried out on data from two

251   spatial scales: a) 1 m × 1 m quadrat level on which the measurements were originally made,

252   and b) 20 m × 5 m plot level, such that the plots were spatially independent. Values of

253   different variables in 1 m × 1 m quadrats were averaged to obtain values for the 20 m × 5 m

254   plots.

255   We also carried out multiple regressions to find out how closely species diversity

256   calculated using visually assessed cover data matched that calculated using biomass data. We

257   calculated two commonly used measures of species diversity, Simpson's diversity index and

258   Shannon-Wiener index of diversity (see Southwood and Henderson 2009)). We calculated

259   diversity of a) all the graminoid species and b) only elephant food species. Diversity index

260   values from the three quadrats of every plot were averaged, and analyses were carried out

261   using the average index value for each plot. Forest type variables were used as described

262   above in all multiple regressions.

263

264   Grassland data

265   Seven large stretches (called zones) across the length of the grassland were sampled. A zone

266   would, therefore, be somewhat analogous to the 20 × 5 m plots in the forest, within which

267   quadrats were sampled, although zones were much larger and quadrats within zones were

268   randomly placed. Within each zone, 20 independent quadrats (1 m × 1 m) were marked, each

269   chosen by walking from the centre of the zone up to a randomly chosen distance and along a

270   randomly chosen direction (distance and angle obtained from a random number generator).

271   Visual estimation of total graminoid cover was carried out in these quadrats and graminoid

272   heights were measured before harvesting the above-ground biomass. Species-level data were

273   not sampled since the only two grass species present could not be differentiated in their non-

274   flowering states. Both these grasses are fed upon by elephants. The data were collected

275   during four 30-day periods between mid-February and mid-June 2015 with equal numbers of

276   random quadrats sampled in each period. Biomass measurements for 10 quadrats could not be

277   performed because of heavy rain, which might have affected the weight significantly.

278   General regression models were used to analyse data from grassland quadrats. Total

279   graminoid biomass was used as a dependent variable, total graminoid cover as an

10

280   independent variable, and month and zone as categorical predictors to control for the effect of

281   variation due to time and location, respectively. The analysis was done both with and without

282   graminoid height as a continuous predictor.

283   Analyses were performed using Statistica 8 (StatSoft 2007).

284   **Results**

285   *Relationship between visually-estimated total graminoid cover and total graminoid biomass*

286   *in forest habitat*

287   Based on the analysis of data from the 40 plots sampled in the three forest types, the mean

288   graminoid biomass was 0.204 kg (95% CI: 0.165 to 0.241 kg). We found no effect of forest

289   type on the relationship between total biomass and total cover, between total biomass and the

290   sum of species covers, or between total biomass and weighted average of species heights (see

291   Table 1). The statistics for regressions tests of how well the graminoid biomass is explained

292   by cover and height are shown in Table 2. We found that both total graminoid cover and the

293   sum of graminoid species cover were able to explain a large amount of variation in total

294   biomass, with the sum of species cover showing a slightly higher coefficient of determination

295   than the total cover (scatter-plots shown in Figure 3). Inclusion of weighted average of

296   species heights to the multiple regression increased the coefficient of determination slightly

297   in the case of sum of species cover and total cover compared to the respective models without

298   the inclusion of height (Table 2). The small difference in *AICc* in both cases suggested that

299   the models including height were not significantly better.

300

301   #Table 1 approximately here.

302

303   #Table 2 approximately here.

304

305   #Fig. 3 approximately here#

306

11

307   *Relationship between visually-estimated species covers of graminoid food species of*

308   *elephants and their respective species biomass in forest habitat*

309   Analyses of species-wise abundance at the plot level showed strong relationships between

310   biomass and visually-estimated species cover for all the common (which were present in 10

311   or more plots) graminoid species (R^2=0.63 to 0.98; Table 3). Multiple regressions using

312   species average height as an additional predictor variable also yielded high R^2 values

313   (R^2=0.69 to 0.98; Table 3), although average height had a significant effect in the regression

314   only in the case of *Oplismenus compositus* and *Digitaria* sp.2 at the plot level (Table 3). With

315   the exception of *Oplismenus compositus*, the *AICc* values for all other species tested were

316   smaller when height was not included in the model to estimate biomass compared to the

317   model when height was included along with cover. However, the differences in *AICc* values

318   between the respective models were small, indicating that the models with and without

319   heights largely performed equally well. At the quadrat level also (Table 4), high regression

320   coefficients were obtained from the regression models that used species cover (R^2=0.68 to

321   0.90) and the regressions that used both species cover and height (R^2=0.68 to 0.90), with

322   height having a significant effect in the case of *Cyrtococcum accrescens*, *Cyrtococcum*

323   *oxyphyllum*, *Cyrtococcum patens*, *Oplismenus compositus*, and *Oryza sativa*. The *AICc*

324   values were smaller in the models that included height in these species but none of the

325   species showed large differences (>10) in AICc that would suggest an overwhelming

326   advantage to adding height in regression models (Table 4).

327

328   #Table 3 approximately here.

329

330   #Table 4 approximately here.

331

332   *Relationship between diversity indices calculated from visually-estimated species covers and*

333   *the respective species biomass in forest habitat*

334   The average number of graminoid species per 1 m × 1 m quadrat was 4.7 (95% CI: 4.02–

335   5.38) out of which the average number of food species per quadrat was 3.74 (95% CI: 3.24–

336   4.24). Species diversity calculated using visually-estimated cover explained a large

337   proportion of variance in the diversity calculated using biomass data, at both the plot level

338   (20 m × 5 m) and quadrat level, and when diversity was measured by either the Simpson's

339   diversity index or the Shannon-Wiener diversity index (H') (Figure 4, Table 5). Similar

340   regressions of biomass-based diversity on visual cover-based diversity using only elephant

341   food graminoid species, rather than all graminoid species, also showed strong relationships

342   (Table 5).

343

344   #Table 5 approximately here

345

346   #Fig. 4 approximately here#

347

348   *Relationship between visually-estimated total graminoid cover and total graminoid biomass*

349   *in grassland habitat*

350   Based on data from 550 quadrats, the mean graminoid biomass was calculated to be 0.684 kg

351   (95% CI: 0.655–0.712 kg). Visual estimation of total graminoid cover, along with month and

352   zone ID as categorical predictors, explained total graminoid biomass to a large extent

353   (General regression model, test of SS Whole Model vs. SS Residual: $R = 0.78$, $R^2 = 0.61$, $F[3,$

354    $54] = 281.64$, $P < 0.001$, $AICc = -1687.49$). The effects of total graminoid cover and month

355   were significant ($\text{beta}_{\text{total graminoid cover}} = 0.51$, $\text{beta}_{\text{month}} = 0.41$), whereas zone did not have a

356   significant effect. The addition of average height improved the R^2 value (Test of SS Whole

357   Model vs. SS Residual: $R = 0.83$, $R^2 = 0.69$, $F[4, 544] = 306.84$, $P < 0.001$, $AICc = -1819.85$),

358   with significant effects of total graminoid cover, height, and month, but not zone, on biomass

359   ($\text{beta}_{\text{total graminoid cover}} = 0.44$, $\text{beta}_{\text{height}} = 0.30$, $\text{beta}_{\text{month}} = 0.41$).

360

361   **Discussion**

362   We found that visual assessment of cover, which allows for rapid sampling, performed very

363   well in assessing forage availability in forest and grassland habitat. Using this method, we

364   were able to obtain fairly accurate estimates of biomass of graminoids in general and food

365   graminoids of Asian elephants in particular. The biomass harvest method has been suggested

13

to be an ideal measure of abundance (Wilson 1991, Chiarucci et al. 1999) of herbaceous vegetation, but can be time-consuming if species have to be hand-sorted and weighed separately (Harmony et al. 1997, Lavorel et al. 2008). Biomass harvesting also has limitations with respect to permits in critical wildlife areas because of its destructive nature, unlike visual estimation of cover. We found that visually estimated cover, which does not suffer from these drawbacks, was a good proxy for biomass of individual food species, as well as total graminoid biomass, in complex forest habitats. Such estimation of individual species or portions of the vegetation (in our study area, herbs are more abundant than graminoids) is not feasible with other non-destructive methods (discussed in Radloff and Mucina 2007, Redjadj et al. 2012, Walter et al. 2015). An objection to the visual estimation of species covers had been that the "sum of species covers" as a measure of total cover would give "non-sense number"s that exceeded 100% (Wilson 2011). Wilson (2011) had argued that there was no particular reason why between-species leaf overlaps would be helpful while within-species overlaps would not be important. However, empirically, the sum of species covers performed better at explaining total graminoid biomass in our study, and, perhaps, this is because it incorporates at least some (between-species) overlap component (see Figure 1), unlike the total graminoid cover that does not include any overlap. The sum of graminoid species covers may perform better than total graminoid cover when the within-species leaf overlap is smaller than the between-species leaf overlap. We speculate that this might be true of forests with multiple strata, in which individuals in the lower strata avoid self-shading and individuals of the same species are not very close to one another in order to reduce competition. Since the sum of graminoid species cover better represents total biomass compared to total cover (as discussed above) and since species-level cover estimates are highly related to species biomass, one can obtain good estimates of the proportional abundance of foods by dividing the sum of food species covers by the sum of all species covers. This would be useful for studies on foraging ecology in tropical forests with high diversity where food species are a small fraction of the total number of species present.

The inclusion of height in regression models yielded mixed results. In the forests, total graminoid biomass and sum of species biomass were explained adequately by cover and most models that included height were not substantially better than those that did not include height (small differences in *AICc*). The effect of height was not significant at the individual species-level also for most food species. On the other hand, the relationship between cover and total graminoid biomass was improved by the inclusion of average height in the grassland

14

399 habitat. This pattern may result from higher variability in total cover (average total graminoid
400 cover=54.85%, CV total graminoid cover=42.33%) than in height (average weighted
401 height=24.63cm, CV weighted height=32%) in forest habitat. As cover by graminoids
402 saturates (total cover estimate has an upper limit of 100% whereas biomass and height are not
403 limited) and relative variability in cover decreases vis-à-vis height, for example, in grasslands
404 or swamps, the explanatory power of height with respect to that of cover is expected to
405 increase. Thus, in the grassland habitat, where cover is closer to saturation and less variable
406 (average total graminoid cover: 87.27%, CV for total graminoid cover: 19.17%; average
407 height=5.71cm, CV for height: 46.84%) the effect of height relative to that of graminoid
408 cover ($beta_{total\ graminoid\ cover}$=0.44, $beta_{height}$ =0.30, $P<0.05$ for both) was greater than that in the
409 forest habitat ($beta_{total\ graminoid\ cover}$ =0.78, $beta_{weighted\ average\ of\ species\ heights}$=0.21, $P<0.05$ for both).
410 We thus found that there was no overwhelming benefit to including height in forest habitat,
411 while it might be worthwhile measuring height in grassland habitat. The improvement in
412 biomass estimation models after inclusion of height has also been reported in other grassland
413 habitats like tussock-grasslands in alpine Andes (Oliveras et al. 2013) and rangelands in
414 Argentina (Guevara et al. 2002). In forest habitats, such relationships have been rarely
415 studied for graminoids, although in one study in pine forests of Arizona, height did not result
416 in substantial improvement to predictive power of models that used only cover (Andariese
417 and Covington 1986). In habitats where cover is near saturation value (100%), we suggest
418 that measurement of height can substantially improve biomass estimates, as seen in grassland
419 habitat in our study. The limited predictive power of cover in plots with high cover values
420 (above 80%) has also been discussed in Axmanová et al. (2012) for wet meadows of
421 temperate Central Europe. One caveat is that we do not know if graminoid height itself
422 affects selection of foraging sites by animals.

423 We also found that the species diversity of graminoids as calculated from cover data
424 explained large variations in the diversity indices measured from biomass data when used
425 along with forest type as a categorical variable. This similarity in community characteristics
426 from the two methods further support the utility of visual estimation as a rapid assessment
427 method in foraging ecology since ecologists may also be interested in assessing the diversity
428 of foraging sites in order to test whether an animal selects a few food items or feeds on a
429 wide range of species from the available plant species (e.g. Owen-Smith and Chafota 2012).
430 Apart from selectivity, since prolonged feeding on a few plant species may result in
431 accumulation of specific secondary metabolites which can be difficult to detoxify by the

432   mechanism for those metabolites, it is hypothesised that feeding on a wide range of species

433   allows multiple counter pathways to share the load of detoxification of multiple types of

434   secondary metabolites (reviewed in Marsh et al. 2006). Some generalist feeders may thus

435   adopt a strategy of feeding on a variety of plants, thereby increasing their feeding rates.

436   Quantification of species diversity may thus be useful in addressing such proximal aspects of

437   foraging which affect patch selection. Such proximate mechanisms have been invoked to

438   explain the relation between the diet of African elephants and tree diversity in the habitat

439   (Cordon et al. 2011).

440

441   One possible limitation of this study is that we measured fresh rather than dry biomass.

442   Fresh biomass has a component of leaf water content, which can change temporally based on

443   environmental conditions. Therefore, the cover-biomass relationship that we recovered based

444   on fresh biomass measurement may not be the same as that based on dry biomass

445   measurement. However, it is often of interest to measure fresh biomass in studies of foraging

446   because that is the weight of food that an animal would consume. We addressed the issue of

447   observer bias associated with the visual method (Tonteri 1990) to some extent by having a

448   single observer (HG) carry out the cover estimation from all sites. As observer-related errors

449   can cumulatively become large if many observers are involved in data collection (Tonteri

450   1990, Klimeš 2003), it would be necessary to consider the error across observers before the

451   final estimation.

452   In summary, we find that the visual estimation method performs very well in assessing

453   forage availability in a tropical forest and a grassland habitat, and can, therefore, be used in

454   studies of elephant habitat and forage selection. This will save time and allow for sampling a

455   larger number of sites. Our study was carried out in tropical deciduous forests, which

456   constitute more than 65% of the total forest area in India (Reddy et al. 2015) and about one-

457   sixth of the forest cover in South-east Asia (Wohlfart et al. 2014). It is likely that the positive

458   relationship between cover and biomass will hold in similar forests, although the strength of

459   the relationship may vary geographically. We do not imply that the relationships we find are

460   completely transferable to other locations and suggest independent assessments in order to

461   develop site-specific cover-to-biomass models. However, since we show that visual estimates

462   of cover can be very useful in studies of foraging, this opens up the method for use by various

463   researchers, who may have otherwise been deterred from using this based on a few previous

464 studies. Moreover, since other sympatric ungulates like *Axis axis* and *Bos gaurus* are also

465 primarily grazers (Ahrestani et al. 2012), the visual estimation method should also work well

466 for quantifying the resource distribution for these generalist ungulates in our study site and

467 similar deciduous forests.

468

Acknowledgements

477

References

479 Ahrestani, F.S., Heitkönig, I.M. and Prins, H.H. 2012. Diet and habitat–niche relationships

480 within an assemblage of large herbivores in a seasonal tropical forest. *Journal of Tropical

481 Ecology* 28: 385–394.

482 Andariese, S.W. and Covington, W.W. 1986. Biomass estimation for four common grass

483 species in northern Arizona ponderosa pine. *Journal of Range Management* 39: 472-473.

484 Axmanová, I., Tichý, L., Fajmonová, Z., Hájková, P., Hettenbergerová, E., Li, C.F.,

485 Merunková, K., Nejezchlebová, M., Otýpková, Z., Vymazalová, M. and Zelený, D. 2012.

486 Estimation of herbaceous biomass from species composition and cover. *Applied Vegetation

487 Science* 15: 580-589.

488 Baskaran, N., Balasubramanian, M., Swaminathan, S. and Desai, A.A. 2010. Feeding ecology

489 of the Asian elephant *Elephas maximus* Linnaeus in the Nilgiri Biosphere Reserve, southern

490 India. *Journal of the Bombay Natural History Society* 107: 3-13.

491 Blake, S., 2003. *The Ecology of Forest Elephant Distribution and its Implications for

492 Conservation*. PhD thesis, University of Edinburgh, Edinburgh, UK.

493 Chiarucci, A.J.B.W., Wilson, J.B., Anderson, B.J. and Dominicis, V. 1999. Cover versus
494 biomass as an estimate of species abundance: does it make a difference to the conclusions?
495 *Journal of Vegetation Science* 10: 35-42.

496 Codron, D., Lee-Thorp, J.A., Sponheimer, M., Codron, J., De Ruiter, D. and Brink, J.S. 2007.
497 Significance of diet type and diet quality for ecological diversity of African
498 ungulates. *Journal of Animal Ecology* 76: 526-537.

499 Drew, W.B., 1944. Studies on the use of the point-quadrat method of botanical analysis of
500 mixed pasture vegetation. *Journal of Agricultural Research* 69: 289-297.

501 Elzinga, C.L., Salzer, D.W. and Willoughby, J.W. 1998. *Measuring and Monitoring Plant*
502 *Populations*. Bureau of Land Management, Denver, Colorado.

503 Guevara, J.C., Gonnet, J.M. and Estevez, O.R. 2002. Biomass estimation for native perennial
504 grasses in the plain of Mendoza, Argentina. *Journal of Arid Environments* 50: 613-619.

505 Guo, Q. and Rundel, P.W. 1997. Measuring dominance and diversity in ecological
506 communities: choosing the right variables. *Journal of Vegetation Science* 8: 405-408.

507 Harmoney, K.R., Moore, K.J., George, J.R., Brummer, E.C. and Russell, J.R. 1997.
508 Determination of pasture biomass using four indirect methods. *Agronomy Journal* 89: 665-
509 672.

510 Henschel, J.R., Burke, A. and Seely, M. 2005. Temporal and spatial variability of grass
511 productivity in the central Namib Desert. *African Study Monographs* 30: 43-56.

512 Hermy, M., 1988. Accuracy of visual cover assessments in predieting standing crop and
513 environmental correlation in deciduous forests. *Vegetatio* 75: 57-64.

514 Hurvich, C.M. and Tsai, C.L. 1989. Regression and time series model selection in small
515 samples. *Biometrika* 76: 297-307.

516 Hutto, R. L. 1990. Measuring the availability of resources. *Studies in Avian Biology* 13: 20-
517 28.

518 Iversen, M., Fauchald, P., Langeland, K., Ims, R. A., Yoccoz, N. G. and Bråthen, K. A. 2014
519 Phenology and cover of plant growth forms predict herbivore habitat selection in a high
520 latitude ecosystem. *PLoS One* 9: 1-11.

18

521   Kennedy, K.A. and Addison, P.A. 1987. Some considerations for the use of visual estimates
522   of plant cover in biomonitoring. *Journal of Ecology* 75: 151-157.

523   Klimeš, L. 2003. Scale-dependent variation in visual estimates of grassland plant
524   cover. *Journal of Vegetation Science* 14: 815-821.

525   Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrough, J., Berman,
526   S., Quétier, F., Thébault, A. and Bonis, A. 2008. Assessing functional diversity in the field -
527   methodology matters! *Functional Ecology* 22: 134-147.

528   Marsh, K.J., Wallis, I.R., Andrew, R.L. and Foley, W.J. 2006. The detoxification limitation
529   hypothesis: where did it come from and where is it going? *Journal of Chemical Ecology* 32:
530   1247-1266.

531   Noyce, K. V. and Coy, P. L. 1990. Abundance and productivity of bear food species in
532   different forest types of northcentral Minnesota. In *Bears: Their Biology and Management*,
533   Vol. 8, A Selection of Papers from the Eighth International Conference on Bear Research and
534   Management, Victoria, British Columbia, 1990, pp. 169-181.

535   Oliveras, I., Eynden, M., Malhi, Y., Cahuana, N., Menor, C., Zamora, F. and Haugaasen, T.
536   2014. Grass allometry and estimation of above-ground biomass in tropical alpine tussock
537   grasslands. *Austral Ecology* 39: 408-415.

538   Owen-Smith, N. and Chafota, J. 2012. Selective feeding by a megaherbivore, the African
539   elephant (*Loxodonta africana*). *Journal of Mammalogy* 93: 698-705.

540   Owen-Smith, R. N. 1988. *Megaherbivores: The Influence of Very Large Body Size on*
541   *Ecology.* Cambridge University Press, Cambridge, UK.

542   Pascal, J. P. 1982. *Bioclimates of the Western Ghats: Maps 1-2*. French Institute of
543   Pondicherry, Pondicherry, India.

544   Pekin, B.K., Endress, B.A., Wisdom, M.J., Naylor, B.J. and Parks, C.G. 2015. Impact of
545   ungulate exclusion on understorey succession in relation to forest management in the
546   Intermountain Western United States. *Applied Vegetation Science* 18: 252-260.

547   Pettorelli, N., Ryan, S.J., Mueller, T., Bunnefeld, N., Jedrzejewsk, B., Lima, M. and Kausrud,
548   K., 2011. The Normalized Difference Vegetation Index (NDVI): unforeseen successes in
549   animal ecology. *Climate Research* 46: 15-27.

550 Radloff, F.G.T. and Mucina, L. 2007. A quick and robust method for biomass estimation in
551 structurally diverse vegetation. *Journal of Vegetation Science* 18: 719-724.

552 Rebollo, S., Milchinas, D. G., Stapp, P., Augustine, D. J. and Derner, J. D. 2013.
553 Disproportionate effects of non-colonial small herbivores on structure and diversity of
554 grassland dominated by large herbivores. *Oikos* 122: 1757-1767.

555 Reddy, C.S., Jha, C.S., Diwakar, P.G. and Dadhwal, V.K. 2015. Nationwide classification of
556 forest types of India using remote sensing and GIS. *Environmental Monitoring and*
557 *Assessment* 187: 1-30.

558 Redjadj, C., Duparc, A., Lavorel, S., Grigulis, K., Bonenfant, C., Maillard, D., Saïd, S. and
559 Loison, A. 2012. Estimating herbaceous plant biomass in mountain grasslands: a comparative
560 study using three different methods. *Alpine Botany* 122: 57-63.

561 Saïd, S., Pellerin, M., Guillon, N., Débias, F. and Fritz, H. 2005. Assessment of forage
562 availability in ecological studies. *European Journal of Wildlife Research* 51: 242-247.

563 Southwood, T.R.E. and Henderson, P.A., 2009. *Ecological methods*. John Wiley & Sons.

564 StatSoft, Inc. 2007. Statistica (data analysis software system), Version 8.0. www.statsoft.com

565 Sukumar, R. 1990. Ecology of the Asian elephant in southern India. II. Feeding habits and
566 crop raiding patterns. *Journal of Tropical Ecology* 6: 33-53.

567 Tonteri, T. 1990. Inter-observer variation in forest vegetation cover assessments. *Silva*
568 *Fennica* 24: 189-196.

569 Vidya, T.N.C., Prasad, D. and Ghosh, A. 2014. Individual identification in Asian
570 elephants. *Gajah* 40: 3-17.

571 Walter, C.A., Burnham, M.B., Gilliam, F.S. and Peterjohn, W.T. 2015. A reference-based
572 approach for estimating leaf area and cover in the forest herbaceous layer. *Environmental*
573 *Monitoring and Assessment* 187: 1-9.

574 Wilmshurst, J.F., Fryxell, J.M. and Colucci, P.E. 1999. What constrains daily intake in
575 Thomson's gazelles? *Ecology* 80: 2338-2347.

576 Wilson, J.B. 1991. Methods for fitting dominance/diversity curves. *Journal of Vegetation*
577 *Science* 2: 35-46.

20

578   Wilson, J.B. 2011. Cover plus: ways of measuring plant canopies and the terms used for

579   them. *Journal of Vegetation Science* 22: 197-206.

580   Wohlfart, C., Wegmann, M. and Leimgruber, P. 2014. Mapping threatened dry deciduous

581   dipterocarp forest in South-east Asia for conservation management. *Tropical Conservation*

582   *Science* 7: 597-613.

583   Zar, J.H. 1974. *Biostatistical Analysis*. Prentice-Hall, NJ.

584

585

21

586 **Tables**

587 **Table 1**: Results from homogeneity of slopes test to examine the effect of forest type on the

588 regression slopes of graminoid biomass on three continuous predictors: 1) sum of species

589 covers, 2) total cover, and 3) weighted average of species heights.

	Sum of species cover	Total cover	Weighted heights
Effect of forest type on slope	$F[2, 33] = 0.35$, $P = 0.704$	$F[2, 33] = 0.43$, $P = 0.652$	$F[2, 33] = 1.13$, $P = 0.336$
Effect of continuous predictor	$F[1, 33] = 57.21$, $P < 0.001$	$F[1, 33] = 35.34$, $P < 0.001$	$F[1, 33] = 1.07$, $P = 0.308$

590

591

592

593

594

595

596

597

598

599

600

601

602

603

604

22

605   **Table 2**: Results of regressions to examine how visual estimates of cover explain total
606   graminoid biomass in forest habitat, and the additional utility of weighted average of species
607   heights in improving the total biomass estimates. $P < 0.05$ for all beta coefficient values.
608   *AICc* can be used to compare the regressions with and without average species height. The
609   difference between a model with the lowest *AICc* and other models are not considered
610   significant if the difference in *AICc* is less than two. The model with the lowest *AICc* is
611   moderately better than the other models if the difference in *AICc* is between 4 and 7, and
612   model with the lowest *AICc* is considerably better than the other models if the difference in
613   *AICc* is >10.

614

Level of analysis	Continuous predictors	R, R²	F test results	beta	AICc
Plot level (20 x 5m)	Total cover	0.80, 0.63	$F[3,35]=20.11$, $P<0.001$	$beta_{\text{total graminoid cover}} = 0.76$	-198.24
	Total cover + Weighted height	0.82, 0.68	$F[4,34]=17.78$, $P<0.001$	$beta_{\text{total graminoid cover}} = 0.78$, $beta_{\text{weighted ave. of species heights}} = 0.21$	-200.70
	Sum of species cover	0.84, 0.70	$F[3,35]=27.36$, $P<0.001$	$beta_{\text{sum of graminoid species covers}} = 0.82$	-206.25
	Sum of species cover + Weighted height	0.86, 0.74	$F[4,34]=24.00$, $P<0.001$	$beta_{\text{sum of graminoid species covers}} = 0.83$, $beta_{\text{weighted ave. of species heights}} = 0.20$	-208.97
Quadrat level (1 x 1m)	Total cover	0.78, 0.61	$F[3,111]=58.66$, $P<0.001$	$beta_{\text{total graminoid cover}} = 0.76$	-535.55
	Total cover + Weighted height	0.80, 0.64	$F[4,110]=48.55$, $P<0.001$	$beta_{\text{total graminoid cover}} = 0.73$, $beta_{\text{weighted ave. of species heights}} = 0.16$	-541.15
	Sum of species	0.85,	$F[3,111]=92.7$	$beta_{\text{sum of graminoid species}}$	-570.64

23

cover	0.71	9, $P<0.001$	$_{covers}=0.84$	
Sum of species cover + Weighted height	0.86, 0.74	$F[4,110]=79.0$ 1, $P<0.001$	$beta_{sum of graminoid species}$ $_{covers}=0.81$, $beta_{weighted ave. of}$ $_{species heights}=0.17$	-579.89

615

616

617

618

619

620

621

622

24

623   **Table 3**. Results for plot-level regressions of graminoid species biomass on 1) visually-
624   estimated species cover, and 2) visually-estimated species cover and measured average
625   species height, in forest habitat. Details of the regressions are shown based on analysis of log-
626   transformed data along with R^2 untransformed data (shown as R^2 (untr.)). *P* values for the
627   regressions are not shown separately, except for *Digitaria* sp.2, because all the other *P* values
628   (for transformed and untransformed data) were smaller than 0.001. #Effect of habitat in
629   multiple regression was significant. **Effect of height was significant. See Table 2 for
630   interpretation of *AICc* differences.

631

Species	Species cover						Species cover and avg. species height					
	F	df_1, df_2	R	R^2	AICc	R^2 (untr.)	F	df_1, df_2	R	R^2	AICc	R^2 (untr.)
Axonopus compressus	22.36	3,15	0.90	0.82 #	-57.69	0.71	15.77	4,14	0.90	0.82 #	-54.56	0.71
Chloris dolichostachya	73.62	3,14	0.97	0.94 #	-58.16	0.93 #	56.32	4,13	0.97	0.95 #	-56.40	0.94 #
Cynodon dactylon	58.58	3,10	0.97	0.95	-42.22	0.83	39.93	4,9	0.97	0.95	-38.30	0.85
Cyrtococcum accrescens	38.47	3,22	0.92	0.84	-65.74	0.67 #	29.80	4,21	0.92	0.85	-64.67	0.69
Cyrtococcum oxyphyllum	56.99	3,16	0.96	0.91	-58.39	0.87	41.34	4,15	0.96	0.92	-55.79	0.88
Cyrtococcum patens	113.81	3,8	0.99	0.98	-40.45	0.89	82.59	4,7	0.99	0.98	-36.97	0.89
Digitaria sp.2	4.03	3,7;*P*=0.059	0.80	0.63	-23.69	0.74	3.33	4,6;*P*=0.092	0.83	0.69	-20.29	0.90**
Kyllinga monocephala	82.01	3,15	0.97	0.94	-48.02	0.89	57.55	4,14	0.97	0.94	-44.81	0.89
Oplismenus compositus	74.09	3,33	0.93	0.87	-100.10	0.79	64.40	4,32	0.94	0.89**	-103.38	0.84**
Oryza sativa	21.02	3,10	0.93	0.86	-36.39	0.86	16.17	4,9	0.94	0.88	-33.94	0.87

632

633

634

25

635 **Table 4**. Results for quadrat-level regressions of graminoid species biomass on visually-
636 estimated species cover, and of species biomass on visually-estimated species cover and
637 measured average species height for forest habitat. Details of the regressions are shown based
638 on analysis of log-transformed data along with R^2 untransformed data (shown as R^2 (untr.)).
639 P<0.001 for multiple regressions. #Effect of habitat in multiple regression was significant.
640 **Effect of height was significant. See Table 2 for interpretation of *AICc* differences.

641

Species	Species cover						Species cover and avg. species height					
	F	*df₁, df₂*	*R*	*R²*	AICc	*R²* (untr.)	*F*	*df₁, df₂*	*R*	*R²*	AICc	*R²* (untr.)
Axonopus compressus	25.84	3,26	0.87	0.75	-61.57	0.76	19.79	4,25	0.87	0.76	-60.24	0.76
Chloris dolichostachya	36.68	3,32	0.88	0.77	-83.80	0.88	27.18	4,31	0.88	0.78	-81.81	0.88
Cynodon dactylon	55.33	3,21	0.94	0.89	-67.24	0.83	45.49	4,20	0.95	0.90	-67.53	0.83
Cyrtococcum accrescens	50.27	3,41	0.89	0.79 #	-98.43	0.53	39.72	4,40	0.89	0.80	-98.76	0.61**
Cyrtococcum oxyphyllum	59.39	3,38	0.91	0.82	-100.92	0.70	52.63	4,37	0.92	0.85**	-105.28	0.72
Cyrtococcum patens	42.47	3,16	0.94	0.89	-55.75	0.74	31.50	4,15	0.95	0.89	-53.53	0.81**
Digitaria sp.2	10.69	3,15	0.83	0.68	-26.19	0.81	7.48	4,14	0.83	0.68	-22.94	0.81
Kyllinga monocephala	81.55	3,28	0.95	0.90	-78.76	0.81	63.29	4,27	0.95	0.90	-78.17	0.82
Oplismenus compositus	91.64	3,82	0.88	0.77	-170.46	0.73	73.76	4,81	0.89	0.78**	-173.8	0.74**
Oryza sativa	24.31	3,14	0.92	0.84	-43.74	0.85	27.39	4,13	0.94	0.89**	-47.90	0.89**

642

643

644

645

646

26

647   **Table 5**: Results from multiple regressions to examine the relationship between diversity
648   indices calculated using biomass data and cover data. $P < 0.001$ in all cases.

649

Scale	All graminoid species		Food graminoid species	
	Simpson's index (1-D)	Shannon-Wiener index (H')	Simpson's index (1-D)	Shannon-Wiener index (H')
Plot Level	$R=0.93$, $R^2=0.87$, $F[3,36]=79.92$	$R=0.85$, $R^2=0.72$, $F[3,36]=30.12$	$R=0.92$, $R^2=0.85$, $F[3,36]=67.42$	$R=0.95$, $R^2=0.89$, $F[3,36]=101.44$
Quadrat Level	$R=0.89$, $R^2=0.80$, $F[3,115]=150.47$	$R=0.93$, $R^2=0.86$, $F[3,115]=232.56$	$R=0.88$, $R^2=0.78$, $F[3,115]=132.86$	$R=0.92$, $R^2=0.84$, $F(3,115)=205.55$

650

651

652

653

654

655

656

657

658

659

660

661

662

663

664

27

665 **Figures**

666 **Figure 1:** Illustration of a 1 m × 1 m sampling quadrat, showing estimates of total cover,
667 individual species covers of four species (shown as different combinations of shape and
668 colour), and sum of species cover. The sum of species cover is higher than total cover
669 primarily because of between-species overlaps.

670

671

28
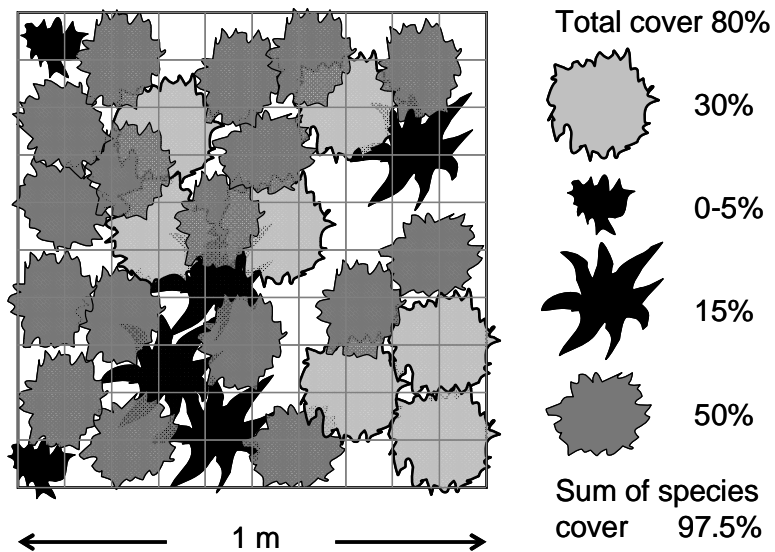
672   **Figure 2:** Locations of sampling sites in the study area. The forest type classification is based

673   on Pascal (1982). Inset: map of southern India showing the location of Nagarahole National

674   Park.

675

676

677

29
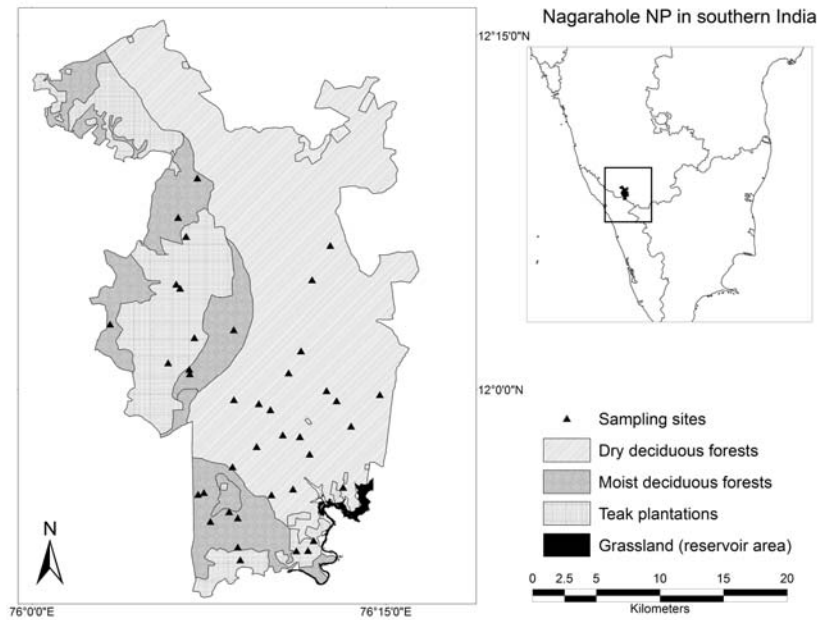
678   **Figure 3:** Scatter plots for the plot-level graminoid abundance data from the forest plots,

679   showing the relation between a) visually-assessed total graminoid cover and total graminoid

680   biomass and b) the sum of visually-assessed individual graminoid species cover and total

681   graminoid biomass.

682

a) $y = -0.0216 + 0.00410x$ b) $y = 0.01824 + 0.00247x$


683

684

685

30
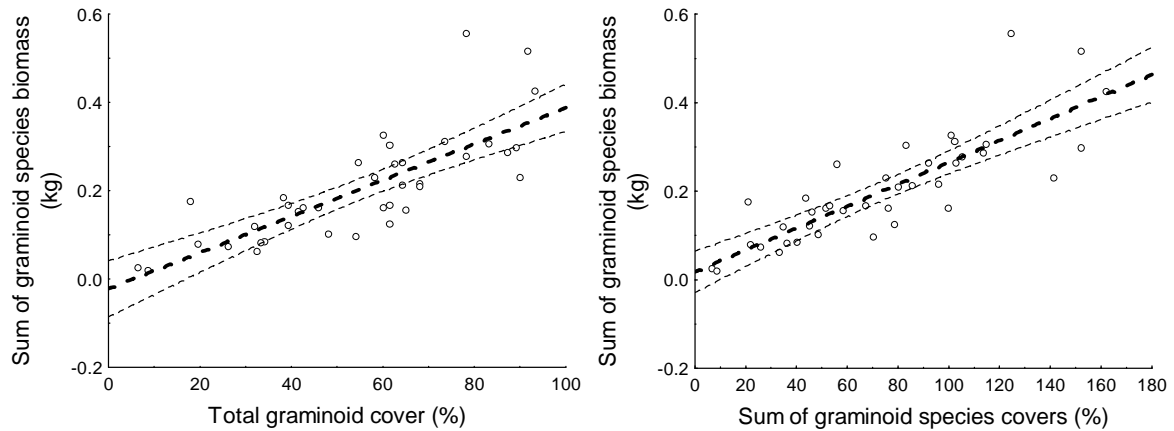
686 **Figure 4:** Scatter plots for the plot-level graminoid abundance data from the forest plots,
687 showing the relationships between Simpson's diversity indices (1-*D*) calculated from cover
688 and biomass data (a, c) and Shannon-Wiener diversity indices (*H'*) calculated from cover and
689 biomass data (b, d). All graminoid species are included in a) and b), while only elephant food
690 species are included in c) and d).

691
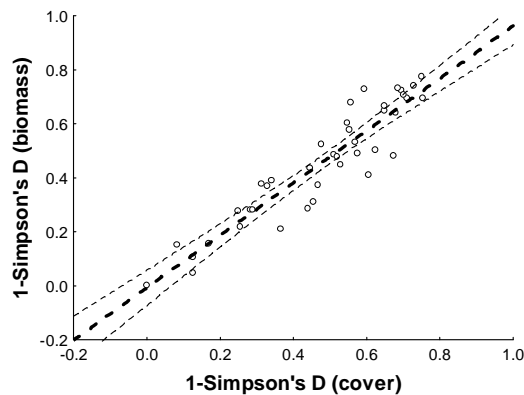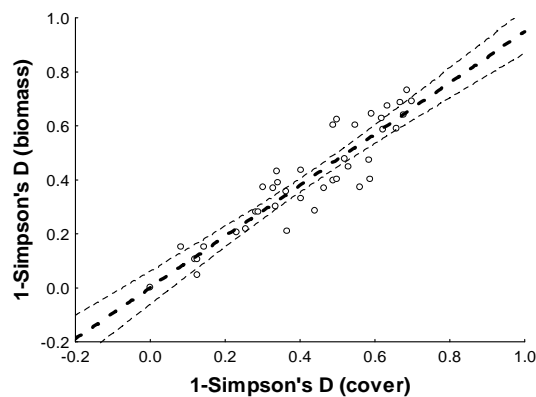
a) y = -0.0068 + 0.97050x   b) y = -0.0484 + 0.96844x
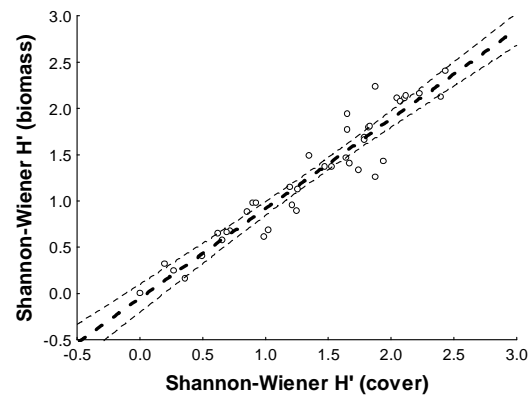
c) y = 0.00123 + 0.94883x   d) y = -0.0295 + 0.96124x

692

693