# Spatial and temporal analysis of beta diversity in the Barro Colorado Island forest dynamics plot, Panama

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Running headline: Temporal beta diversity analysis

17    **Abstract**

18    **1. Background:** Ecologists are interested in assessing the spatial and temporal variation in
19    ecological surveys repeated over time. This paper compares the 1985 and 2015 surveys of the
20    Barro Colorado Forest Dynamics plot (BCI), Panama, divided into 1250 (20 m × 20 m) quadrats.

21    **2. Methods, spatial analysis:** Total beta diversity was measured as the total variance of the
22    Hellinger-transformed community data throughout the BCI plot. Total beta was partitioned into
23    contributions of individual sites (LCBD indices), which were tested for significance and mapped.

24    **3. Results, spatial analysis:** LCBD indices indicated the sites with exceptional community
25    composition. In 1985, they were mostly found in the swamp habitat. In the 2015 survey, none of
26    the swamp quadrats had significant LCBDs. What happened to the tree community in the
27    interval?

28    **4. Methods, temporal analysis:** The dissimilarity in community composition in each quadrat
29    was measured between time 1 (1985) and time 2 (2015). Temporal Beta Indices (TBI) were
30    computed from abundance and presence-absence data and tested for significance. TBI indices can
31    be decomposed into $B$ = species (or abundances-per-species) losses and $C$ = species (or
32    abundances-per-species) gains. B-C plots were produced; they display visually the relative
33    importance of the loss and gain components, through time, across the sites.

34    **5. Results, temporal analysis:** In BCI, quadrats with significant TBI indices were found in the
35    swamp area, which is shrinking in importance due to changes to the local climate. A published
36    habitat classification divided the BCI forest plot into six habitat zones. Graphs of the $B$ and $C$
37    components were produced for each habitat group. Group 4 (the swamp) was dominated by
38    species (and abundances-per-species) gains whereas the five other habitat groups were dominated
39    by losses, some groups more than others.

40    **6. Conclusions:** We identified the species that had changed the most in abundances in the swamp
41    between T1 and T2. This analysis supported the hypothesis that the swamp is drying out and is
42    invaded by species from the surrounding area. Analysis of the $B$ and $C$ components of temporal
43    beta diversity bring us to the heart of the mechanisms of community change through time: losses
44    ($B$) and gains ($C$) of species, losses and gains of individuals of various species. TBI analysis is
45    especially interesting in species-rich communities where we cannot examine the changes in every
46    species individually.

47    **Keywords**: Beta diversity, B-C plots, BCI forest dynamics plot, space-time analysis, temporal
48    beta diversity

## Background

49

50 Whittaker (1972) defined beta diversity as spatial differentiation, or the variation in species
51 composition among sites within a region of interest. Different ways of measuring beta have been
52 proposed by Whittaker himself and by other authors. Several authors have argued that the
53 variance of a community composition data table (sites x species) is an appropriate measure of
54 beta diversity across the sites (Koleff et al. 2003, Legendre et al. 2005, Anderson et al. 2011). It
55 has also been shown that the total variance can be computed from a dissimilarity matrix **D**
56 obtained from an appropriately chosen dissimilarity index *D*. Legendre & De Cáceres (2013)
57 described properties of dissimilarity indices that are necessary for beta diversity studies and
58 identified 11 indices that were appropriate for such studies; two more indices were added to that
59 list by Legendre (2014) and Legendre & Borcard (2018).

60 The concept of beta diversity can be extended to time. It was called temporal beta diversity
61 by Legendre and Gauthier (2014) and by Shimadzu et al. (2015). Temporal beta variation can be
62 the result of gradual or abrupt changes in environmental conditions, including man-induced
63 alterations such as the ongoing worldwide climate warming. Research on temporal variation in
64 communities is conducted, for example, at hundreds of research sites affiliated to the
65 International Long Term Ecological Research (ILTER) network (https://www.ilter.network/), and
66 in the dynamics forest plots affiliated with the Forest Global Earth Observatory (ForestGEO; see
67 https://forestgeo.si.edu/).

68 A statistical method for the analysis of temporal beta diversity has recently been described
69 by Legendre (2019). The objective is to compare observations made during two separate surveys
70 through time, involving several sites. The method has two distinct parts: (1) estimate the change
71 in each geographic sampling unit (site) between time 1 (abbreviated T1) and time 2 (T2), using
72 an appropriate dissimilarity index, called a temporal beta-diversity index (TBI), and test the
73 significance of that change to identify the sites where the change has been exceptionally
74 important; these sites may be worth examining to identify the causes of the differences. And (2)
75 partition the dissimilarity information into finer indices of losses and gains of species, or of
76 abundances-per-species, which may tell us something about the processes at work in the system,
77 which may have generated these changes. Applications of that method have already been
78 published in palaeoecology (Winegardner et al., 2017) and in the study of freshwater (Kuczynski
79 et al., 2018) and marine animal communities (Legendre & Salvat 2015). Three other ecological
80 applications of the method are presented in the Legendre (2019) paper.

81 The TBI method will be illustrated in this paper by an analysis of a 50-ha permanent forest
82 dynamics plot. The precise questions we will try to answer about the plot are the following: (1) Is
83 there a region in the plot where the changes in community composition have been especially
84 important between 1985 and 2015? (2) If there is such an area, what happened in the community?
85 Was the change characterized by species (or abundances-per-species) losses or gains? (3) And
86 finally, what are the species that changed more strongly? If the change was mostly a gain of
87 species, was this the result of a migration or an invasion, and where did these species come from?

88 **Methods**

89 **Plot and censuses**

90 The Barro Colorado Forest Dynamics plot (BCI) in Panama was established in 1981 by Robin
91 Foster and Stephen Hubbell (Hubbell and Foster 1983). Data from this plot have been used in
92 many scientific papers, including a recent one by Condit et al. (2017b) in this journal, where the
93 plot and the survey method are described. Some statistics about the plot are provided in Table 1.
94 This 50-ha plot has been subjected to 8 detailed surveys since its inception: in 1982+, 1985,
95 1990, 1995, 2000, 2005, 2010 and 2015. The present paper is the first application of the TBI
96 method of analysis to the data of a permanent forest dynamics plot. It will serve as a model for
97 the analysis of other forest plots. At the moment, the ForestGEO network includes some 70 such
98 forest plots throughout the world. The census data can be downloaded from Condit et al. (2012,
99 2017a).

100 The BCI data were divided into 1250 quadrats of size (20 m × 20 m) before analysis; this
101 was deemed the most appropriate scale of study to answer the ecological questions addressed in
102 the present paper, which compares the surveys conducted in 1985 and 2015. The union of the
103 species identified in the 1985 and 2015 surveys was 328. Fig. 1 shows a habitat classification
104 map of the BCI forest proposed by Harms et al. (2001).

105 **Statistical methods for spatial analysis**

106 A preliminary spatial analysis of the forest plot will be done first. Total beta diversity, computed
107 as the total variance of the Hellinger-transformed multivariate community composition data
108 throughout the BCI plot, will be partitioned into *Local Contributions to Beta Diversity* (LCBD
109 indices) in order to determine where the quadrats are found that are the most different from the
110 multivariate centroid of all quadrats. LCBD indices can be tested for significance. The
111 computation method and interpretation have been described by Legendre & De Cáceres (2013).
112 Calculations were done using the beta.div function of the *adespatial* package in R (Dray et al.
113 2019).

114 **Statistical methods for temporal analysis**

115 The main part of the paper will consist in a temporal beta diversity analysis focussing on the
116 three questions listed at the end of the Introduction. The methods are the following.

117 *Space-time interaction*

118 For censuses repeated through time, as it is the case in Forest Dynamics Plots, the interaction
119 between space (S) and time (T) is of great interest. A significant interaction would indicate that
120 the spatial structure of the response data has changed through time, and conversely, that the
121 temporal variations differed significantly among the sites (quadrats), indicating, for example, an
122 effect of climate change. The space-time interaction (STI) can be tested on univariate or
123 multivariate data using the method proposed by Legendre et al. (2010), despite the lack of
124 replicated observations. That method is implemented in function stimodels() of the *adespatial*
125 package in R (Dray et al. 2019). The community data were transformed using the Hellinger
126 transformation (Legendre & Gallagher 2001) before this analysis.

127 *Temporal beta diversity indices (TBI)*

128 The dissimilarity in community composition was measured for each of the 1250 quadrats of the
129 BCI plot between time 1 (T1 = 1985 survey) and time 2 (T2 = 2015 survey). The analysis was
130 repeated separately for the 30 quadrats of group 4 (the swamp).

131 The index used for community composition data will be the percentage difference (or
132 %difference; Odum 1950), also known as the Bray-Curtis index. The Sørensen index will be used
133 for occurrence (presence-absence) data; this is the binary form of the percentage difference index
134 (Legendre & Legendre 2012). In the context of a comparison through time, these indices are
135 called *Temporal Beta Indices* (TBI). These indices can be tested for significance, as shown in
136 Legendre (2019). Each index, which compares data from a quadrat at T1 and T2, is composed of
137 two parts: $B$ = species (or abundances-per-species) losses and $C$ = species (or abundances-per-
138 species) gains.

139 The $B$ and $C$ statistics will be used to produce B-C plots, with $B$ (losses per quadrat) in the
140 abscissa and $C$ (gains per quadrat) in the ordinate, as described in Legendre (2019). B-C plots
141 display visually the relative importance of the loss and gain processes in a study area, informing
142 researchers about details of the processes of biodiversity losses and gains across the sites, through
143 time, in space-time surveys. B-C plots will be shown for the whole BCI forest plot and for six
144 separate habitats within the plot.

145 The mean of the differences between the $B$ and $C$ statistics is also computed across all sites
146 in a study. A positive value of $(C - B)$ indicates that the study area was dominated by gains,
147 whereas a negative value indicates overall losses of species or abundances-per-species. The $(C -$
148 $B)$ difference across all quadrats was tested for significance using a paired *t*-test computed for the
149 $C$ and $B$ statistics from all sites in the study. The calculation involves the mean of the differences
150 $(C/den - B/den)$ at all sites; in the present study, *den* was the denominator of Odum's percentage
151 difference index, $(2A + B + C)$.

152 The calculations are implemented in the TBI() and draw.BC() functions, available in the R
153 package *adespatial* (Dray et al. 2019).

154 *Changes in species composition from T1 to T2*

155 In order to understand in more detail the demographic changes at BCI in the quadrats of the
156 swamp habitat in the 1985–2015 interval, we analysed the changes in the 209 species found in
157 the swamp from 1985 to 2015, across its 30 quadrats, using paired *t*-tests. The tests were carried
158 out with 9999 random permutations of the values, in each quadrat, between T1 and T2. A Holm
159 (1979) correction for multiple testing (209 simultaneous tests had been conducted) was applied to
160 the computed p-values. The calculations are implemented in function paired.t.test.spec(),
161 available in the R package *adespatial* (Dray et al. 2019).

162 # Results

163 **1. Preliminary spatial analysis**

164 The quadrats that have high and significant LCBD indices (quadrats with red rims in Fig. 2a) are
165 the most different in species composition from a hypothetical quadrat found at the multivariate
166 centroid of a PCA ordination. The significant quadrats are found mostly in the central portion of
167 the map, in an area called *the swamp* by Harms et al. (2001). This is an old forest habitat where

168   water accumulates during the rainy season and which harbours a different flora than the rest of
169   the BCI plot. The oil palm, *Elaeis oleifera* (Kunth) Cortés, is a conspicuous indicator species of
170   the swamp community (Plate 1).

171       Comparison of Figs. 2a and 2b shows that no quadrat with a red rim remained in the
172   swamp area in the 2015 survey data. This preliminary analysis allows us to ask a new question:
173   Why is it that quadrats with highly significant LCBD indices are no longer found in the swamp in
174   2015?

**2. Temporal beta diversity analysis**

176   The number of stems declined substantially during that period 1985-2015 (Fig. 3): there was a net
177   loss of 35 638 stems between 1990 and 2005, representing about 15% of the stems that were
178   found in 1990 (244 015 stems).

*Space-time interaction*

180   A significant space-time interaction was reported across 4 censuses (from 1982-83 to 1995) by
181   Legendre et al. (2010) for the whole community of 315 species in the (20 × 20 m) quadrats and
182   for 43% of the individual species tested separately.

183       We checked that this was still the case for the seven censuses conducted between 1985 and
184   2015. Indeed, a significant space-time interaction was detected for the (20 × 20 m) quadrats. This
185   significant interaction means that the spatial structure of the multivariate data has changed
186   significantly among the censuses. We will now study these differences in more detail between
187   censuses #2 (1985) and #8 (2015) for the whole plot, then for each habitat type separately, using
188   temporal beta diversity indices and B-C plots.

*Temporal beta diversity indices (TBI)*

190   The results for the group 4 quadrats, abundance data, are mapped in Fig. 4; the TBI() function
191   output is shown in Supporting information, Appendix S1. Two quadrats had significant TBI
192   indices at the 0.05 significance level after correction for 30 simultaneous tests (underscored
193   values in output vector $p.adj, Appendix S1); 3 more swamp quadrats were significant at the
194   same level before correction for multiple tests. These 5 swamp quadrats had the highest TBI
195   values among the 1250 quadrats of the BCI forest plot, indicating that they were the most
196   different in composition between the 1985 and 2015 surveys.

197       The mean of the differences between of *C*/*den* (losses) and *B*/*den* (gains) over the entire
198   BCI forest plot was negative, indicating dominance of losses across all 1250 quadrats (detailed
199   output file not shown). The test of significance of that difference was highly significant. In the
200   separate analysis of the group 4 data (detailed output file in Appendix S1), this same comparison
201   showed a positive difference of the mean of (*C*/*den* – *B*/*den*) over the swamp quadrats, indicating
202   that gains of individuals-per-species had dominated group 4 in the time interval under study; see
203   output element $t.test_B.C in Appendix S1. The test of significance of that difference was also
204   highly significant.

*B-C plots*

206   A first B-C plot is shown in Fig. 5 for the 1250 quadrats of the BCI forest. In this overall plot, the
207   green line is above the red line, materializing in a figure the statistical result found in the previous

208 subsection: losses of abundances-per-species dominated the changes in the entire BCI forest from
209 1985 to 2015.

210    Separate B-C plots were then produced for habitat groups 1 to 6, abundance data (Fig. 6).
211 In all habitat types except group 4, the green line is above the red line, indicating that species
212 losses dominated gains. In group 4 (the swamp), however, the red line is above the green line,
213 indicating that gains dominated losses in this habitat. The same result was found when analysing
214 occurrence data in the 6 habitat types; see Supporting information, Appendix S2.

### *Changes in species composition from T1 to T2*

216 The paired *t*-tests computed separately for the 209 species of group 4 (the swamp) over its 30
217 quadrats showed that 7 species had significant increases in abundances (number of stems) in
218 these quadrats from 1985 to 2015 (Table 2a) whereas one, *Bactris major,* decreased in
219 abundance. The species that increased in abundances also increased in occurrences, and
220 conversely.

221    For comparison, six of the seven species that increased in group 4 also increased in
222 abundances in group 1 (Table 2b). Only *Trichilia tuberculata* decreased in group 1 while
223 increasing in group 4.

224    Of course, these 209 individual tests are not proper paired *t*-tests of comparison of means
225 because the data are from contiguous quadrats, hence they are strongly autocorrelated. Yet, the
226 tests allowed us to identify the species where the differences in abundances between T1 and T2
227 were the strongest in group 4 (Table 2a). *B. major* decreased in abundance and in occurrences in
228 both habitats.

229    The species we were looking for here are those that changed the most in the T1-T2 interval.
230 This is different from the search for indicator species of the six habitat groups. For example, we
231 mentioned above that the oil palm, *Elaeis oleifera*, was a most conspicuous indicator species of
232 the swamp habitat. This species has not noticeably changed in abundance in the swamp between
233 1985 and 2015, going from 16 to 17 individuals.

## Discussion and conclusion

235 Results of the individual analyses presented in the previous section combine into a coherent story
236 of what happened in the BCI forest plot.

### *Preliminary spatial analysis*

238 Analysis of the local contributions to beta diversity (LCBD) at the quadrat level showed that in
239 1985, the swamp area (habitat group 4) had a highly distinctive community, with many quadrats
240 significantly different from the other habitat types of the BCI plot. In 2015, this community was
241 still different in composition but the importance of the difference had subsided. This observation
242 called for a more detailed analysis of the difference between the 1985 and 2015 surveys in the
243 swamp area.

### *Temporal beta diversity analysis*

245 At BCI, the period 1982–1992 included several extreme dry seasons; since then, there have been
246 few such drought events. High tree growth rates and death rates were observed during the

247    drought but not since then (Condit 2017b). A simple indicative statistic is the loss of 36761 tree
248    stems between 1990 and 2010, or 15% of the stems surveyed in 1990 (Fig. 3).

249         The annual amount of rain has a strong influence on tropical forest composition. It
250    determines the height of the water table and has consequences on many other environmental
251    factors. Changes in soil wetness and dryness is an important factor determining changes in
252    species composition in the long run, considering the fact that tropical trees are long-lived.
253    However, one cannot predict precisely which species will change their distributions following
254    changes in rainfall. Different species react differently to the drought. Then, neutral theory
255    (Hubbell 2001) predicts that changes in species composition have a strong random component,
256    with the constraint that the species adapted to greater wetness are more likely to expand if rainfall
257    increases whereas those more adapted to dry conditions are more likely to regress. This question
258    was discussed in depth by Condit et al. (1996). Legendre et al. (2010, Fig. 4) illustrated the
259    changes to two species at BCI, *Poulsenia armata* and *Beilschmiedia pendula*, between 1983 and
260    1995. The first one decreased in most quadrats where it was present whereas the second increased
261    in abundance. Chisholm et al. (2014) analysed changes in tree abundance in 12 forests across the
262    world over periods of 6–28 years and pointed out the importance of the variance in environmental
263    drivers in determining the changes in community composition.

264         A significant space-time interaction was found in the analysis of the seven censuses
265    conducted at BCI between 1985 and 2015, meaning that the spatial structure of the multi-species
266    community has changed significantly among censuses, confirming statistically the observation of
267    the field scientists.

268         Among the Temporal beta diversity indices (TBI) computed over all 1250 quadrats of the
269    BCI forest plot, the 5 quadrats that had the highest indices were found in the swamp habitat.
270    What is so special in this habitat? It seems to have been more strongly affected by the drought of
271    the 1980's and 1990's than the other habitats.

272         From 1985 to 2015, 35697 tree stems (or 14.9% of the 1985 survey counts) were lost in the
273    BCI forest plot excluding the swamp, whereas in habitat group 4 (the swamp), 1354 stems were
274    gained (or 48.4% compared to the 1985 survey). The tree community in the swamp reacted very
275    differently from the rest of the BCI plot to the drought this region of Panama suffered from 1982
276    to 1992. This is a major difference of the swamp community compared to the remainder of the
277    BCI forest plot. The B-C plots in Fig. 6 show these losses and gains in detail in the various
278    habitat groups.

279         Of the 1354 tree stems that were gained in the swamp, 595 belonged to the 7 species that
280    showed significant increases in that habitat (Table 2a). Most of these species had also increased
281    in the surrounding habitat group 1 (Table 2b). The drought created gaps in the forest canopy; the
282    few species that were favoured by the drought moved into the swamp and modified its species
283    composition.

284    ***B-C analysis: what have we learned?***

285    Analysis of the *B* and *C* components of the TBI dissimilarity between surveys has brought us to
286    the heart of the mechanisms by which communities change through time: *losses* (*b*) and *gains* (*c*)
287    of species, *losses* (*B*) and *gains* (*C*) of individuals of the various species. B-C analysis is
288    especially interesting in species-rich communities like the BCI forest, where we cannot examine
289    the changes in each species individually. B-C analysis can be applied to subgroups of sites, as

290    was done in this study for the 6 main habitat types of the BCI dynamics forest plot. It provided
291    detailed information on difference in dynamics between habitat types.

292          With this paper, we are hoping to encourage ecologists analysing other dynamics forest
293    plots to use TBI analysis to answer questions about the changes that have taken place in their
294    forests, either after gradual changes in environmental (e.g. climatic) conditions or as the result of
295    punctual events that may have affected the plots, e.g. hurricanes or ice storms.

## Ethics approval and consent to participate

Not applicable.

## Consent for publication

Not applicable.

## Availability of data and material

The BCI census data can be downloaded from Condit et al. (2012, 2017a). See the References section of the paper.

## Competing interests

The authors declare that they have no competing interests.

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## Authors' contributions

PL developed the methods of analysis, wrote the software, carried out the analyses of the BCI forest data and wrote most of the paper.

RC directed the field work at BCI since 1991, organized all aspects of the database, helped with the interpretation of the results, and wrote portions of the Discussion in the paper.

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393 Table 1. Basic information about the Barro Colorado Forest Dynamics plot (BCI) in Panama. For
394 more information, see Condit et al. (2017) and https://forestgeo.si.edu/sites/neotropics/barro-
395 colorado-island.

396 _____

397 • Location: Barro Colorado Island in Lake Gatun in the Panama canal, Panama

398 • Coordinates: 09°09' N, 79°51' W

399 • Principal investigators: Richard Condit, Stephen Hubbell and Robin Foster

400 • Plot size: 50 ha (1000 × 500 m), divided in 1250 (20 × 20 m) quadrats

401 • Average precipitation: 2581 mm/yr

402 • Average temperature: 27°C

403 • 120 – 160 m above sea level

404 • 8 surveys conducted in 1982+, 1985, 1990, 1995, 2000, 2005, 2010, 2015

405 • Number of tree species in the 8 censuses combined: 325

406 • 207719 tree stems $\geq$ 1 cm DBH[1] in the 2015 survey; 297 species

407 • In the 1985 census,

408     ➢ Mean number of species per 20 × 20 m quadrat: 53.5
409     ➢ Range of values of number of species per 20 × 20 m quadrat: [20, 84]

410 [1] DBH: diameter at breast height

411 _____

412

413 Table 2. (a) The 8 species that changed significantly in abundance in the 30 quadrats of group 4
414 (the swamp) from T1 (1985) to T2 (2015). (b) Changes in abundances of these 8 species in 500
415 quadrats of group 1 during the same time interval. A taxonomic data table archived in Condit et
416 al. (2017a) includes the family names and taxonomic authorities for all 455 species of the BCI
417 data base.

(a) Group 4, abundance data

| Species name | Family | Abundance at T1 | Abundance at T2 | Difference (T2 − T1) |
|---|---|---|---|---|
| *Alibertia edulis* | Rubiaceae | 10 | 45 | 35 |
| *Eugenia galalonensis* | Myrtaceae | 15 | 111 | 96 |
| *Guarea guidonia* | Meliaceae | 39 | 132 | 93 |
| *Simarouba amara* | Simaroubaceae | 21 | 67 | 46 |
| *Tabernaemontana arborea* | Apocynaceae | 49 | 148 | 99 |
| *Trichilia tuberculata* | Meliaceae | 132 | 322 | 190 |
| *Xylopia macrantha* | Annonaceae | 2 | 38 | 36 |
| *Bactris major* | Arecaceae | 245 | 65 | −180 |

(b) Group 1, abundance data

| Species name | Family | Abundance at T1 | Abundance at T2 | Difference (T2 − T1) |
|---|---|---|---|---|
| *Alibertia edulis* | Rubiaceae | 160 | 193 | 33 |
| *Eugenia galalonensis* | Myrtaceae | 472 | 965 | 493 |
| *Guarea guidonia* | Meliaceae | 383 | 474 | 91 |
| *Simarouba amara* | Simaroubaceae | 745 | 910 | 165 |
| *Tabernaemontana arborea* | Apocynaceae | 681 | 830 | 149 |
| *Trichilia tuberculata* | Meliaceae | 3724 | 2421 | −1303 |
| *Xylopia macrantha* | Annonaceae | 121 | 415 | 294 |
| *Bactris major* | Arecaceae | 16 | 6 | −10 |

15

462   Fig. 1. Map of the BCI forest dynamics plot habitat classification proposed by Harms et al.
463   (2001). The plot is divided into 1250 quadrats of size (20 m × 20 m).

464   Fig. 2. The BCI plot divided into 1250 quadrats. The LCBD index values are represented in
465   shades of grey; darker is higher. The quadrats with indices significant at the 0.05 significance
466   level have a blue rim. After Holm correction for multiple testing (1250 simultaneous tests), the
467   quadrats that were still significant at the 0.05 level are represented with a red rim. (a) 1985
468   survey; (b) 2015 survey.

469   Fig. 3. Number of tree stems in the BCI forest plot recorded during 7 surveys from 1985 to 2015.

470   Fig. 4. Map of TBI indices, group 4 (swamp). Circle radii are proportional to the TBI index
471   values. Circle fill colours: gold, $C > B$ (gains); white, $B = C$; grey, $B > C$ (losses). Rim colours:
472   red, adjusted p-value ≤ 0.05; green, unadjusted p-value ≤ 0.05 but adjusted p-value > 0.05; black,
473   p-value not significant at 0.05 level.

474   Fig. 5. B-C plot for species abundance data, 1250 quadrats (dots) of the BCI forest. Green line
475   with slope of 1: line where gains equal losses. The red line is drawn parallel to the green line (i.e.
476   with a slope of 1) and passing through the centroid of the points. Its position below the green line
477   indicates that, on average, species losses dominated gains between 1985 and 2015. Dot fill
478   colours correspond to habitat types; habitat colour codes are the same as in Fig. 1. Red arrow:
479   direction where $D = (B+C)$ increases.

480   Fig. 6. B-C plots for species abundance data, six habitat types. In all habitat types except group 4,
481   the green line is above the red line, indicating that species losses dominated gains from 1985 to
482   2015. In group 4 (the swamp) on the contrary, the red line is above the green line, indicating that
483   gains dominated losses in this habitat. See Fig. 5 where the construction of the green and red
484   lines is described. Symbol fill colours correspond to habitat types; habitat colour codes are the
485   same as in Fig. 1.

486

487   Plate 1. The swamp near the centre of the BCI forest plot. The swamp is seasonal; it is inundated
488   during the wet season. Stepping stones installed by researchers are visible in the picture. The oil
489   palm, *Elaeis oleifera*, is a conspicuous indicator species of the swamp community. Photo P.
490   Legendre, 4 February 2015.

Harms *et al*. (2001) BCI habitat classification
Group 1 – Old forest, Low plateau
Group 2 – Old forest, High plateau
Group 3 – Old forest, Slope
Group 4 – Old forest, Swamp
Group 5 – Old forest, Streamside
Group 6 – Young forest
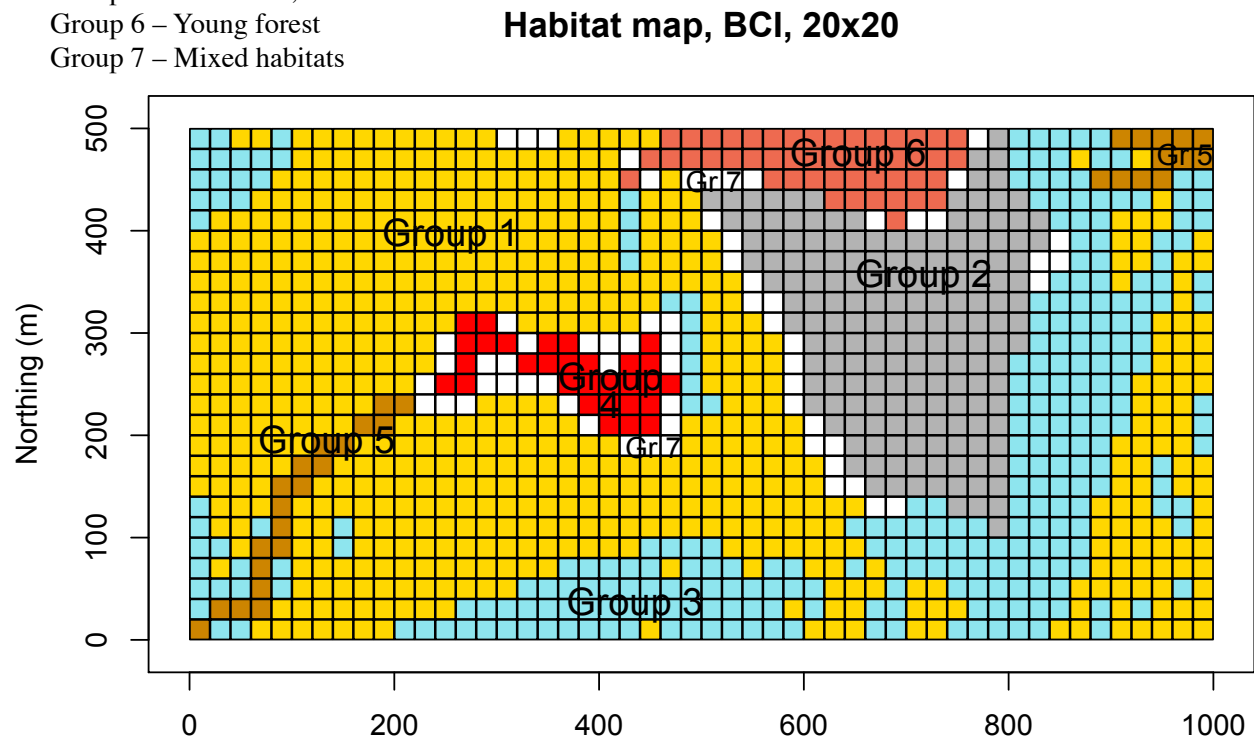Group 7 – Mixed habitats

**Habitat map, BCI, 20x20**



Fig. 1. Map of the BCI forest dynamics plot habitat classification proposed by Harms et al. (2001). The plot is divided into 1250 quadrats of size (20 m × 20 m).
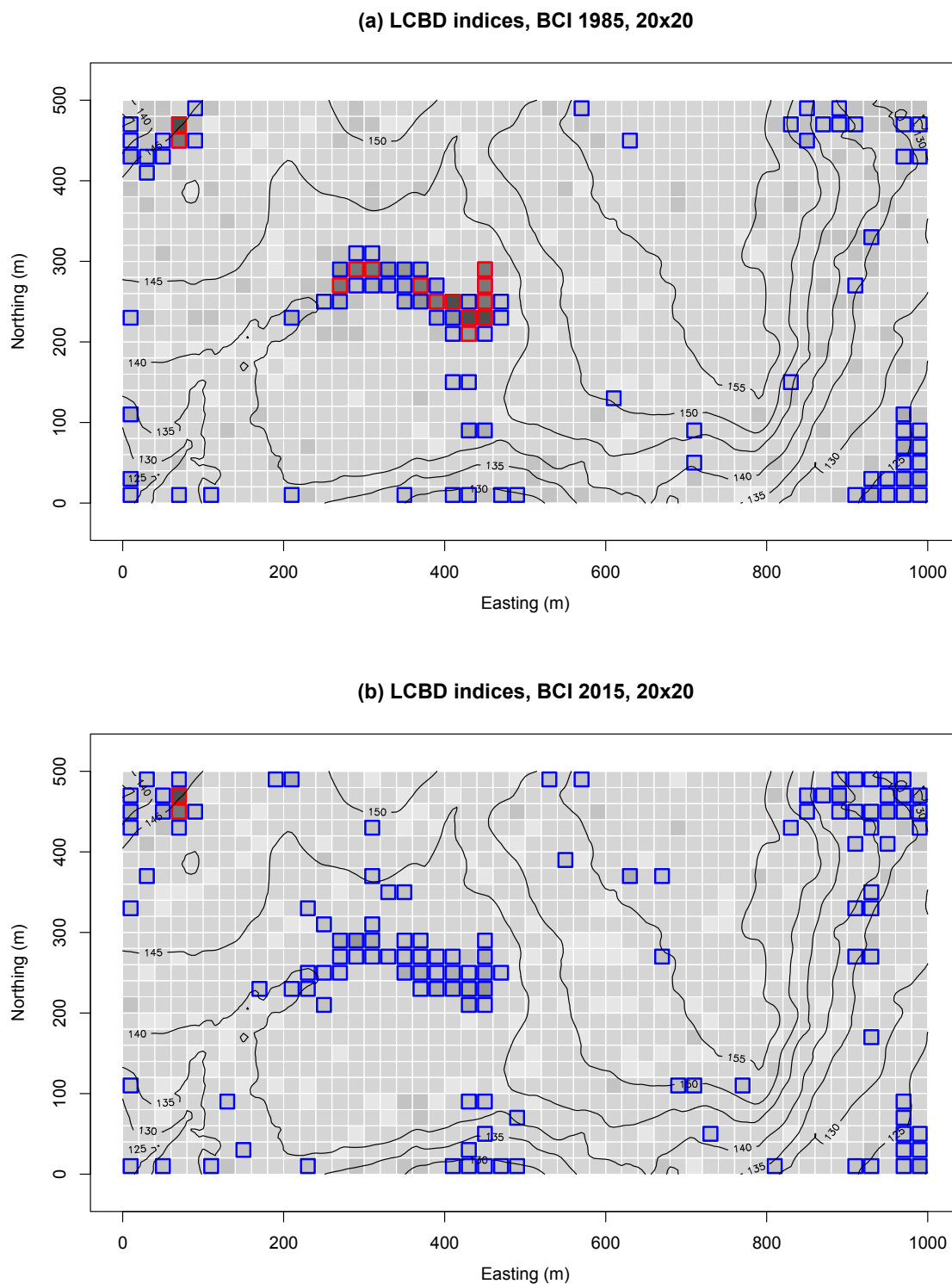
**(a) LCBD indices, BCI 1985, 20x20**



**(b) LCBD indices, BCI 2015, 20x20**

Fig. 2. The BCI plot divided into 1250 quadrats. The LCBD index values are represented in shades of grey; darker is higher. The quadrats with indices significant at the 0.05 significance level have a blue rim. After Holm correction for multiple testing (1250 simultaneous tests), the quadrats that were still significant at the 0.05 level are represented with a red rim. (a) 1985 survey; (b) 2015 survey.
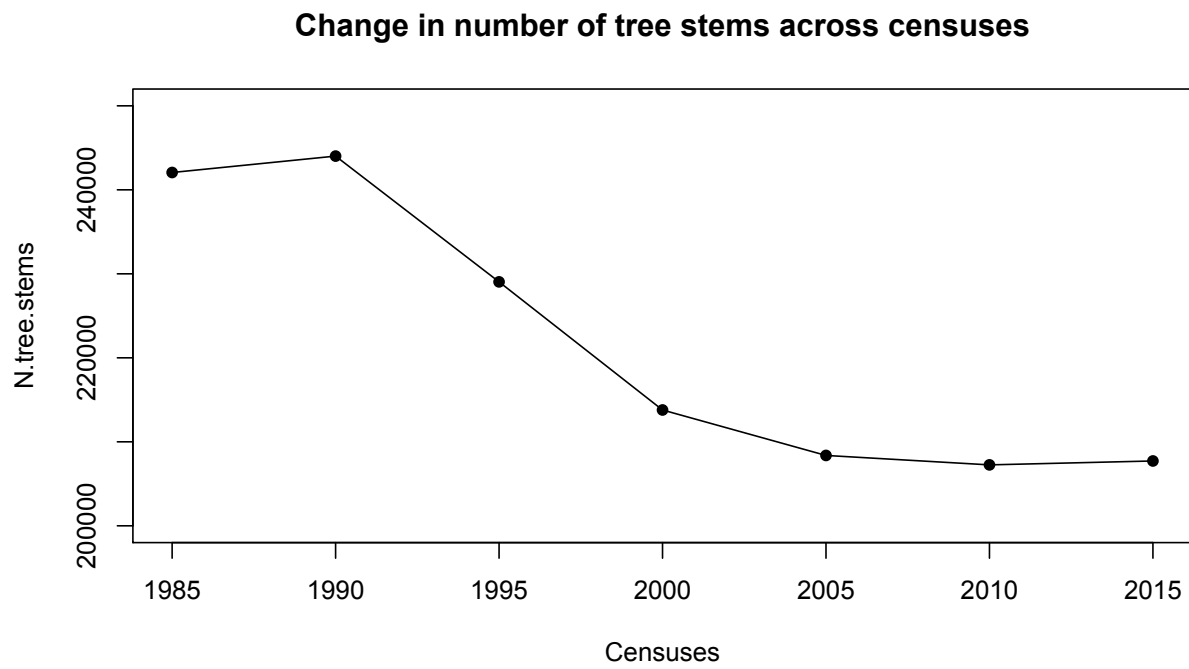
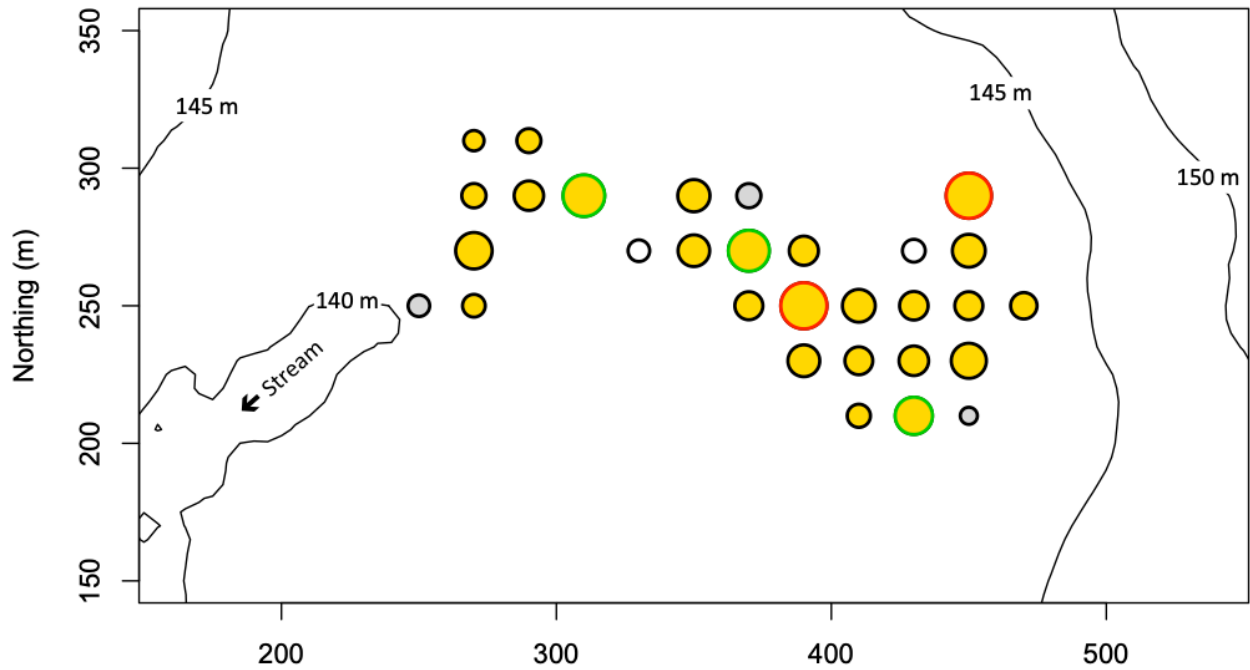Fig. 3. Number of tree stems in the BCI forest plot recorded during 7 surveys from 1985 to 2015.

Fig. 4. Map of TBI indices, group 4 (swamp). Circle radii are proportional to the TBI index values. Circle fill colours: gold, $C > B$ (gains); white, $B = C$; grey, $B > C$ (losses). Rim colours: red, adjusted p-value $\leq 0.05$; green, unadjusted p-value $\leq 0.05$ but adjusted p-value $> 0.05$; black, p-value not significant at 0.05 level.
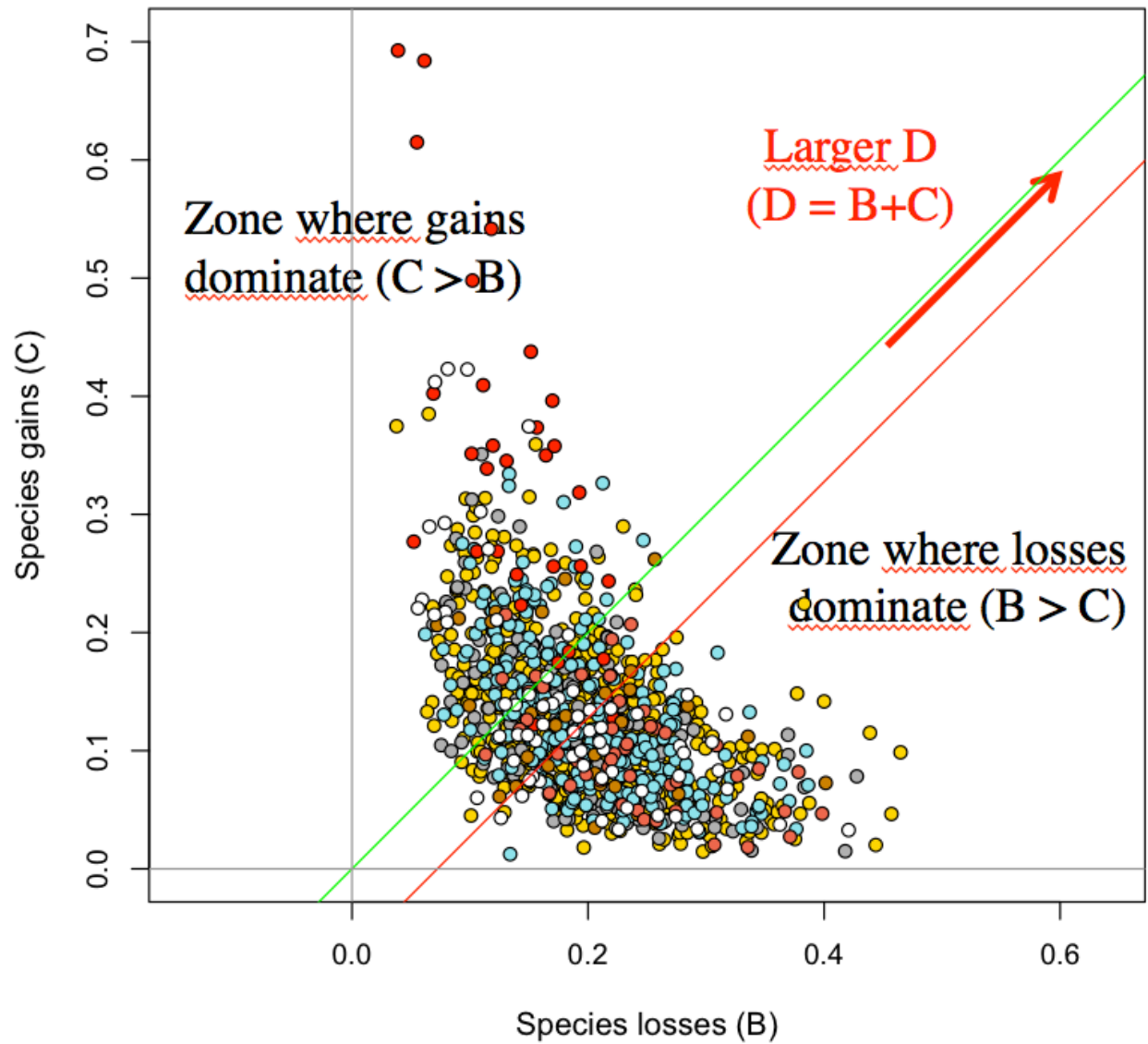
Fig. 5. B-C plot for species abundance data, 1250 quadrats (dots) of the BCI forest. Green line with slope of 1: line where gains equal losses. The red line is drawn parallel to the green line (i.e. with a slope of 1) and passing through the centroid of the points. Its position below the green line indicates that, on average, species losses dominated gains between 1985 and 2015. Dot fill colours correspond to habitat types; habitat colour codes are the same as in Fig. 1. Red arrow: direction where $D = (B+C)$ increases.
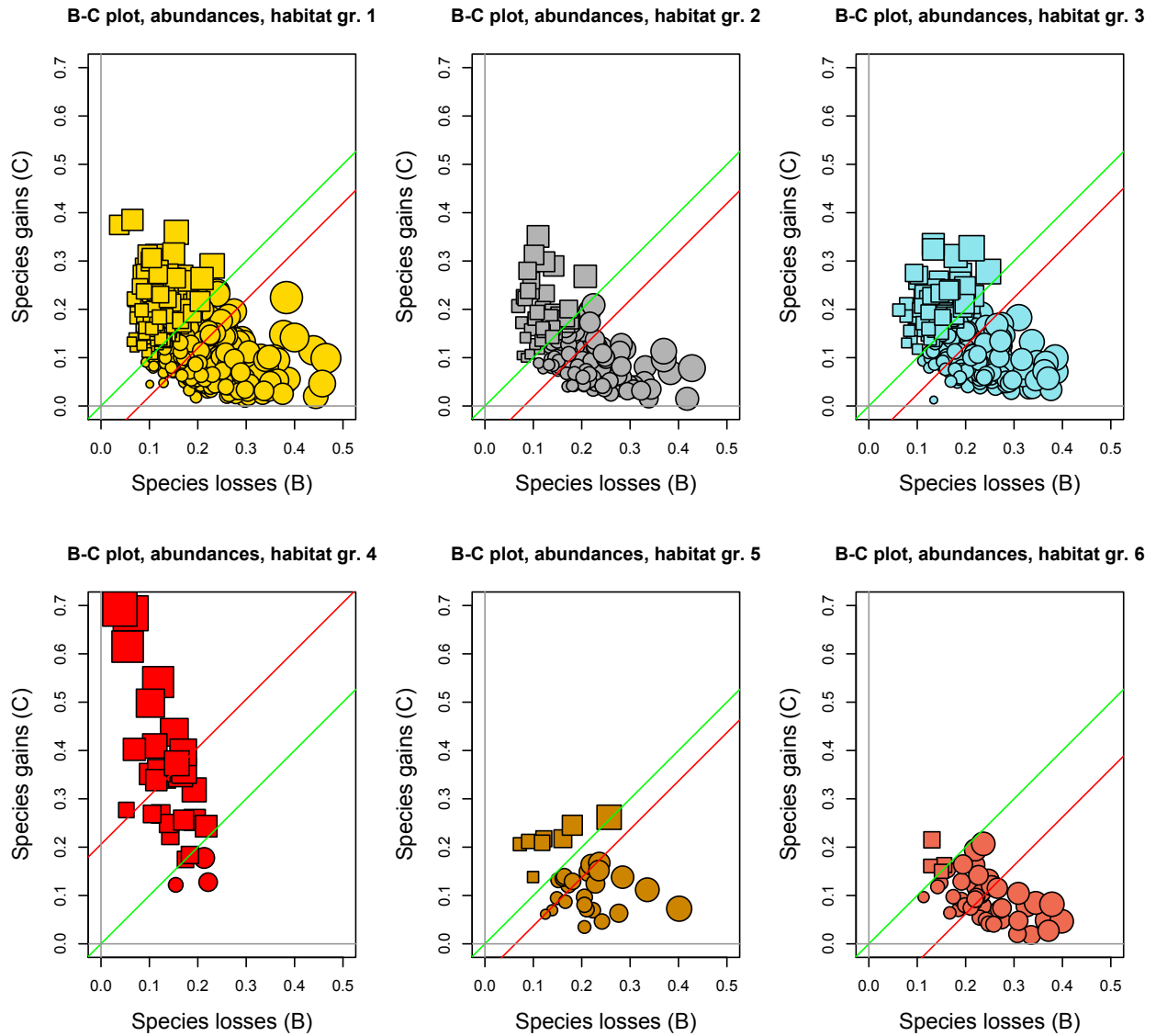
Fig. 6. B-C plots for species abundance data, six habitat types. In all habitat types except group 4, the green line is above the red line, indicating that species losses dominated gains from 1985 to 2015. In group 4 (the swamp) on the contrary, the red line is above the green line, indicating that gains dominated losses in this habitat. See Fig. 5 where the construction of the green and red lines is described. Symbol fill colours correspond to habitat types; habitat colour codes are the same as in Fig. 1.

Plate 1. The swamp near the centre of the BCI forest plot. The swamp is seasonal; it is inundated during the wet season. Stepping stones installed by researchers are visible in the picture. The oil palm, *Elaeis oleifera*, is a conspicuous indicator species of the swamp community. Photo P. Legendre, 4 February 2015.

*Supporting information to:*

Legendre P, Condit R (2019) Spatial and temporal analysis of beta diversity in the Barro Colorado Island forest dynamics plot, Panama. *Forest Ecosystems* (in press).

## Appendix S1

TBI ANALYSIS OF GROUP 4 (THE SWAMP) USING THE TBI() FUNCTION IN R

TBI analysis of the community composition (abundance) data observed in the 30 (20 m × 20 m) quadrats of habitat group 4 during the 1985 (T1) and 2015 (T2) surveys at BCI.

The swamp (Group 4) was an identified habitat category in the Harms et al. (2001) habitat classification of the BCI forest; it contains 30 sites. The numbers of the swamp quadrats in the BCI data base, divided into 1250 (20 m × 20 m) quadrats, are the following:

```
group.4
 [1] 313 338 339 340 341 365 366 390 414 439 440 463 464 465 487 488 489 511
[19] 512 513 536 537 538 539 561 562 563 564 565 588
```

## Results of calculations with R function TBI()

*TBI analysis for habitat group 4 (swamp), abundance data; percentage difference D*

```
( out = TBI(BCI.20.2[group.4,], BCI.20.8[group.4,], method="%diff", nperm=9999, ,
test.BC=TRUE, test.t.perm=TRUE) )


-----
$TBI
 [1] 0.3489583 0.3663912 0.5892256 0.3920705 0.3292308 0.4761905 0.3886792 0.6700000
 [9] 0.3492063 0.5111111 0.5204678 0.4527027 0.6597222 0.3908629 0.5142857 0.7452830
[17] 0.4712644 0.3744493 0.4500000 0.5294118 0.6000000 0.4776119 0.4608696 0.3675214
[25] 0.2764228 0.5660377 0.4530612 0.5301205 0.7316017 0.4266212

$p.TBI
 [1] 0.9579 0.9250 0.0587 0.8662 0.9754 0.4988 0.8713 0.0033 0.9534 0.3202 0.2738
[12] 0.6182 0.0051 0.8721 0.3066 0.0001 0.5223 0.9150 0.6429 0.2401 0.0443 0.4948
[23] 0.5722 0.9262 0.9975 0.1114 0.6166 0.2272 0.0003 0.7396

$p.adj
 [1] 1.0000 1.0000 1.0000 1.0000 1.0000 1.0000 1.0000 0.0924 1.0000 1.0000 1.0000
[12] 1.0000 0.1377 1.0000 1.0000 0.0030 1.0000 1.0000 1.0000 1.0000 1.0000 1.0000
[23] 1.0000 1.0000 1.0000 1.0000 1.0000 1.0000 0.0087 1.0000

$BCD.mat
        B/(2A+B+C)  C/(2A+B+C)  D=(B+C)/(2A+B+C)  Change
Site.1  0.22135417  0.1276042       0.3489583       -
Site.2  0.14325069  0.2231405       0.3663912       +
Site.3  0.15151515  0.4377104       0.5892256       +
Site.4  0.12334802  0.2687225       0.3920705       +
Site.5  0.05230769  0.2769231       0.3292308       +
Site.6  0.13095238  0.3452381       0.4761905       +
Site.7  0.13962264  0.2490566       0.3886792       +
Site.8  0.05500000  0.6150000       0.6700000       +
```

```
Site.9  0.17460317  0.1746032      0.3492063    0
Site.10 0.19259259  0.3185185      0.5111111    +
Site.11 0.11111111  0.4093567      0.5204678    +
Site.12 0.10135135  0.3513514      0.4527027    +
Site.13 0.11805556  0.5416667      0.6597222    +
Site.14 0.21319797  0.1776650      0.3908629    -
Site.15 0.16428571  0.3500000      0.5142857    +
Site.16 0.06132075  0.6839623      0.7452830    +
Site.17 0.06896552  0.4022989      0.4712644    +
Site.18 0.10572687  0.2687225      0.3744493    +
Site.19 0.19375000  0.2562500      0.4500000    +
Site.20 0.17156863  0.3578431      0.5294118    +
Site.21 0.10204082  0.4979592      0.6000000    +
Site.22 0.11940299  0.3582090      0.4776119    +
Site.23 0.21739130  0.2434783      0.4608696    +
Site.24 0.18376068  0.1837607      0.3675214    0
Site.25 0.15447154  0.1219512      0.2764228    -
Site.26 0.16981132  0.3962264      0.5660377    +
Site.27 0.11428571  0.3387755      0.4530612    +
Site.28 0.15662651  0.3734940      0.5301205    +
Site.29 0.03896104  0.6926407      0.7316017    +
Site.30 0.17064846  0.2559727      0.4266212    +


$BCD.summary
 mean(B/den) mean(C/den)  mean(D)    B/(B+C)   C/(B+C) Change
    0.137376     0.34327 0.480646 0.2858153 0.7141847    +


$t.test_B.C
              mean(C-B)     Stat     p.param p.perm   p<=0.05
Paired t.test  0.205894 6.031982 1.459043e-06 0.0001        *


$BC
[1] NA
-----



# List of output elements in the output file of function TBI

summary(out)

-----
            Length Class      Mode
TBI         30     -none-     numeric
p.TBI       30     -none-     numeric
p.adj       30     -none-     numeric
BCD.mat      4     data.frame list
BCD.summary  6     data.frame list
t.test_B.C   5     data.frame list
BC           1     -none-     logical
-----
```

**Appendix S2**

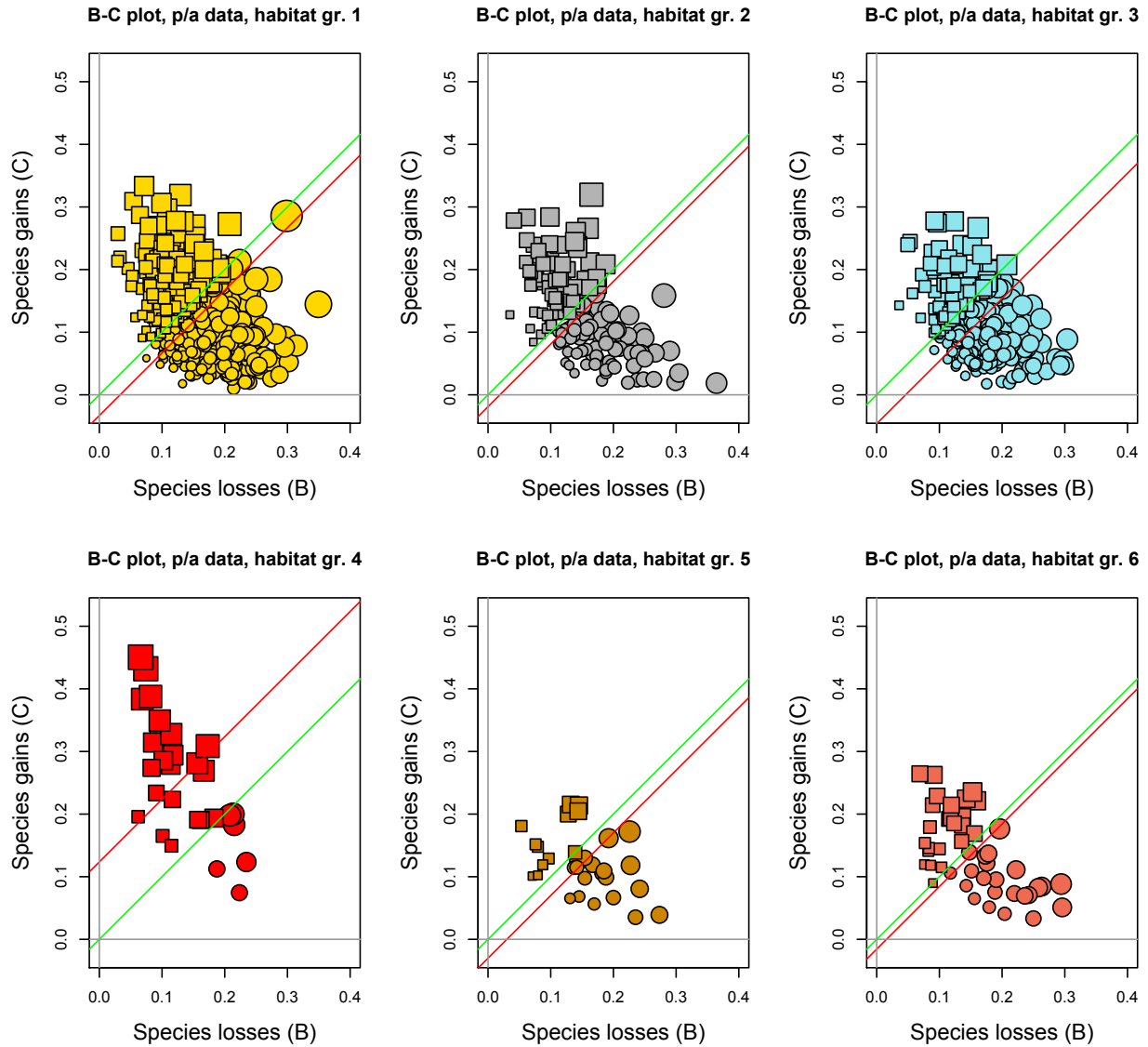B-C PLOTS, OCCURRENCE (PRESENCE-ABSENCE) DATA



Fig. S2.1. B-C plots for species occurrence (presence-absence) data, six habitat types. In all habitat types except group 4, the green line is above the red line, indicating that species losses dominated gains from 1985 to 2015. In group 4 (the swamp) on the contrary, the red line is above the green line, indicating that gains dominated losses in this habitat. See Fig. 5 where the construction of the green and red lines is described. Symbol fill colours correspond to habitat types; habitat colour codes are the same as in Fig. 1 of the main paper.