

1 Putting floristic thermophilization in forests into a conservation
2 biology perspective: beyond mean trait approaches

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18 **Key message:** the use of mean characteristics of communities to infer absolute
19 species variations may well constitute another “silent clash of paradigms” (Austin,
20 1999) in community ecology. We discuss this issue based on a recent paper on
21 floristic thermophilization in forests.

22

23 Fifteen years ago, Austin (1999) denounced the lack of communication and
24 coherence between different paradigms in ecology – with an emphasis on
25 community ecology. I gave a further example of this short-coming related to the
26 analysis and interpretation of biotic homogenization (Gosselin 2012): while mean
27 trait approaches related to niche theory have been used to quantify within-
28 community biotic homogenization, they have no clear bearing on the extirpation
29 of specialist species in a conservation biology context – despite what is often
30 claimed. Hereafter, I discuss yet another, similar example of inconsistency
31 between ecological paradigms, with the aim to ultimately better connect them.
32 De Frenne et al. (2013) have proposed an interesting temporal analysis with
33 respect to climate change of 1,409 vegetation plots in European and North
34 American forests. They found that the species composition on the plots indicates a
35 “thermophilization” over time, i.e. an increase in mean species thermal
36 preference. The authors also reveal a negative correlation between change in
37 forest canopy cover and thermophilization. As regards plot species richness, it
38 was stable in Europe and increasing in North America.

39 Although the study is interesting, I have serious doubts about the interpretation of
40 the results. Indeed, the authors state that “these changes [related to
41 thermophilization] reflect concurrent declines in species adapted to cooler
42 conditions and increases in species adapted to warmer conditions” (p. 18561). To
43 draw these conclusions, however, the authors do not analyze the species richness
44 or abundance of cold-adapted or warmth-adapted species; rather they interpret the
45 cold (fifth percentile) and warm (95th percentile) extremes of the floristic
46 temperature distribution of each plot as indicated by species thermal preferences.
47 This method of interpretation is based on Figure S4 in De Frenne et al. (2013) and
48 is problematic in two respects. The first limitation (L1) is that this method of
49 interpretation only considers species that have a similar level of “specialization”
50 with respect to temperature. The second limitation (L2) is due to the fact that the
51 method used is relative: exactly the same thermophilization statistics would be
52 obtained even if we replicated each species in the community n times. As with
53 any other mean trait approach (Gosselin 2012), De Frenne et al.’s results for
54 thermophilization may therefore have no direct link with actual declines and
55 increases in cold-adapted and warmth-adapted species – if we interpret these
56 declines and increases in terms of absolute frequency or absolute abundance
57 changes of these species. Only analyses of absolute metrics (species richness,
58 abundance...) for more precisely defined groups of species or multi-species
59 analyses of abundance will indicate what is actually occurring (Gosselin 2012).
60 For example, the results in Europe could just as well be explained by (i) an
61 increase in warmth-adapted species and a decrease in cold-adapted species, as

62 proposed by De Frenne et al., (ii) a decrease in cold-adapted species and an
63 increase in generalist species; (iii) an increase in warmth-adapted species and a
64 decrease in generalist species; (iv) an increase in all the species groups, but with a
65 higher relative increase in warmth-adapted species and (v) a decrease in all the
66 species groups, but with a lower relative increase in warmth-adapted species (cf.
67 Figures 1 and 2 based on simulations described in Supplementary Material 1).
68 Points (ii) and (iii) above illustrate (L1) while points (iv) and (v) are related to
69 (L2).

70 Similarly, the link between canopy cover variation and thermophilization has no
71 direct bearing on the absolute variation in species abundance or richness,
72 whatever their temperature preference, contrary to what De Frenne et al. state –
73 e.g. “the increase in warm-adapted species was consistently lower in plots that
74 increased in canopy cover compared with plots that became more open over
75 time”. Yet De Frenne et al. do not analyze the relationship between canopy cover
76 variation and changes in species richness or absolute abundance of species. The
77 net effect of variations in canopy cover on floristic diversity can be due to many
78 mechanisms other than temperature – such as light, water balance... – and can be
79 negative in some circumstances (Kwiatkowska 1994; Spyreas and Matthews 2006
80) and/or depend on ecological groups (Barbier et al. 2009, Zilliox and Gosselin
81 2014) and ecological contexts (Zilliox and Gosselin 2014).

82 This means that ecologists treating conservation issues based on mean trait
83 analyses – or other metrics based on relative abundance – should take care to
84 consider absolute metrics as well – e.g. richness, abundance and viability. Indeed,

85 while niche theory in community ecology could to some extent be coherent with
86 mean trait approaches, the two main paradigms of conservation biology – the
87 minimum viable population paradigm and the declining population paradigm
88 (Caughley 1994) – require more absolute metrics as exemplified by cases (iv) and
89 (v) above. Otherwise, we may very well witness another silent clash of paradigms,
90 similar to the one deplored by Austin (1999).

91

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98

99 **References:**

- 100 Austin MP (1999). A silent clash of paradigms: some inconsistencies in
101 community ecology. *Oikos* 86:170-178. doi: 10.2307/3546582
- 102 Barbier S, Chevalier R, Loussot P, Bergès L, Gosselin F (2009) Improving
103 biodiversity indicators of sustainable forest management: tree genus abundance
104 rather than tree genus richness and dominance for understory vegetation in French
105 lowland oak hornbeam forests. *For Ecol Manag* 258:S176-S186. doi:
106 10.1016/j.foreco.2009.09.004

107 Caughley, G. (1994) Directions in conservation biology. *Journal of Animal*
108 *Ecology* 63:215-244. doi: 10.2307/5542

109 De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G,
110 Vellen M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J, Decocq
111 GM, Dierschke H, Eriksson O, Gilliam FS, Hédli R, Heinken T, Hermy M (2013)
112 Microclimate moderates plant responses to macroclimate warming. *Proc Nat Acad*
113 *Sci USA* 110:18561-18565. doi: 10.1073/pnas.1311190110

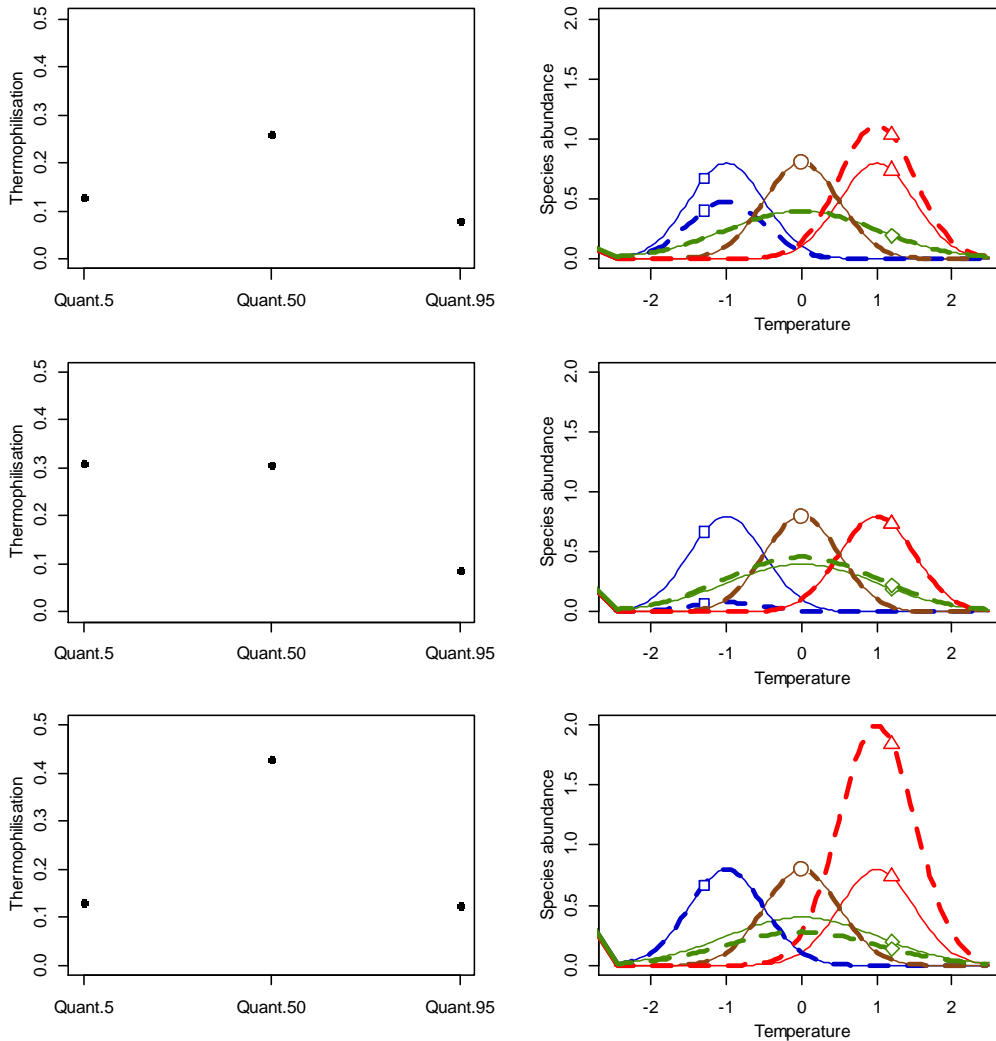
114 Gosselin F (2012) Improving Approaches to the Analysis of Functional and
115 Taxonomic Biotic Homogenization: beyond Mean Specialization. *J Ecol*
116 100:1289-1295. doi: 10.1111/j.1600-0587.2013.00279.x

117 Kwiatkowska AJ (1994) Changes in the species richness, spatial pattern and
118 species frequency associated with the decline of oak forest. *Vegetatio* 112:171-
119 180. doi: 10.1007/BF00044691

120 Spyreas G, Matthews JW (2006) Floristic conservation value, nested understory
121 floras, and the development of second-growth forest. *Ecol Appl* 16:1351-1366.
122 doi: 10.1890/1051-0761

123 Zilliox C, Gosselin F (2014) Tree species diversity and abundance as indicators of
124 understory diversity in French mountain forests: Variations of the relationship in
125 geographical and ecological space. *For Ecol Manag* 321:105-116. doi:
126 10.1016/j.foreco.2013.07.049

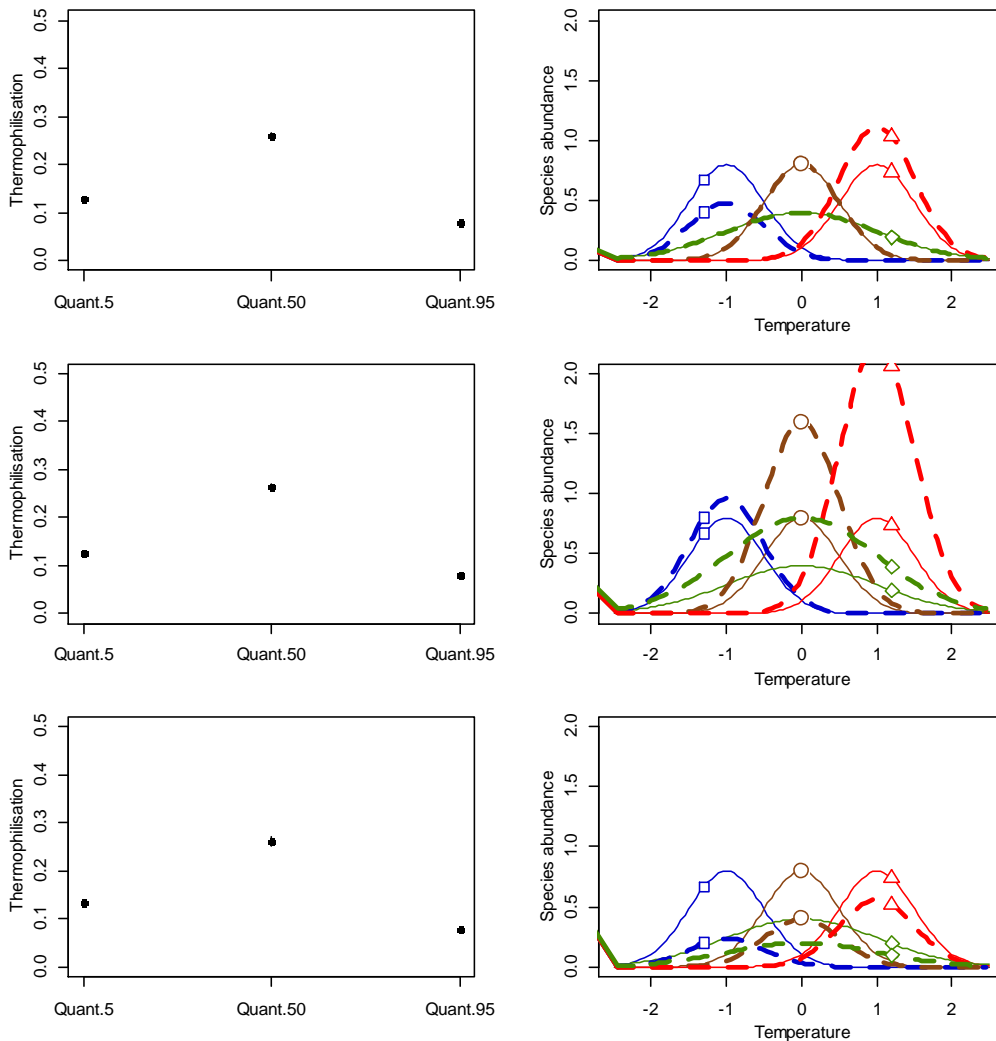
127



128

129 Figure 1. Three scenarios of floristic variation that give qualitatively similar
 130 results in terms of thermophilization – an increase of all three 5%, 50% and 95%
 131 quantiles of the floristic temperature distributions – as those observed by De
 132 Frenne et al. (2013) in Europe yet correspond to three different ecological
 133 interpretations: from top to bottom: (i) an increase in warmth-adapted species and
 134 a decrease in cold-adapted species, (ii) a decrease in cold-adapted species and an
 135 increase in generalist species; and (iii) an increase in warmth-adapted species and
 136 a decrease in generalist species. Left: thermophilization indices – i.e. differences

137 with original situations – for temperature quantiles 5%, 50% (median) and 95%.
138 Right: abundance – actually here proportional to the number of species – in the
139 four ecological groups simulated (temperature generalist in green with diamond
140 symbol, cold-adapted in blue with square symbol, intermediate temperatures
141 adapted in brown with circle symbol and warm-adapted species in red with
142 triangle symbol), in the past (thin plain curves) and now (thick dashed curves).
143



145

146 Figure 2. Three scenarios of floristic variation that give qualitatively similar
 147 results in terms of thermophilization – an increase of all three 5%, 50% and 95%
 148 quantiles of the floristic temperature distributions – as those observed by De
 149 Frenne et al. (2013) in Europe yet correspond to three different ecological
 150 interpretations: from top to bottom: (i) an increase in warmth-adapted species and
 151 a decrease in cold-adapted species, (ii) an increase in all the species groups; and
 152 (iii) a decrease in all the species groups. Left: thermophilization indices – i.e.

153 differences with original situations – for temperature quantiles 5%, 50% (median)
154 and 95%. Right: abundance – actually here proportional to the number of species
155 – in the four ecological groups simulated (temperature generalist in green with
156 diamond symbol, cold-adapted in blue with square symbol, intermediate
157 temperatures adapted in brown with circle symbol and warm-adapted species in
158 red with triangle symbol), in the past (thin plain curves) and now (thick dashed
159 curves).
160
161
162

163 **Supplementary Material**

164

```
165 ## # R code for simulations and associated graphics
166 #Functions to simulate Nplots of SR species each:
167 # and to analyze the 'floristic temperature' (FT) of these communities with
168 the same methods as de Frenne et al. (2013) PNAS 110: 18561-18565,
169 with rep samplings of species within communities to calculate
170 thermophilization statistics (median, 5th temperature percentile, 95th
171 temperature percentile).
172 ##### Note 1: de Frenne et al. use the mean rather than the median. We
173 here estimated both - which gave the same qualitative measures.
174 #####But we propose that the median seems more consistent, with regard
175 to the other quantiles (5% and 95%).
176
177 #####Note 2: In our simulations, these decreases and increases apply in
178 terms of species richness of these species groups - since the method by
179 de Frenne et al. is based on species occurrence and not species
180 abundance
181 #####but similar results should also apply if we had varied species
182 abundance.
183
184 #Communities are assumed to be composed of
185 # - cold-adapted,
186 # - meso-adapted,
187 # - warmth-adapted,
188 # - and temperature generalists,
189 #according to various proportions given by the argument "weights"
190
191 #generalist species have a niche standard deviation of width.gen
192 #and specialist species have a niche standard deviation of width.spe
193
194 samp.sp.type <- function(x,width.gen,width.spe,community){
195     toto<-sample(community,1)
196     res <- ifelse(toto==1,rnorm(1,-1,width.spe),
197                 ifelse(toto==2,rnorm(1,0,width.spe),
198                       ifelse(toto==3,rnorm(1,1,width.spe),rnorm(1,0,width.gen))))
199     return(res)
200 }
201
202 simul.T<-
203 function(weights=c(1,1,1,1),width.spe=0.5,width.gen=1,rep=5000,Nplots=1
204 400,SR=100)
205 {
206     res<-matrix(0,ncol=4,nrow=Nplots)
207     for (i in 1:Nplots)
```

```

208     {#sampling the community in the ith plot
209         community<-sample(4,SR,replace=T,prob=weights)
210         rest<-sapply(1:rep,
211             samp.sp.type,
212             width.gen,
213             width.spe,
214             community)
215         res[i,]<-c(quantile(rest,c(0.05,0.5,0.95)),mean(rest))
216     }
217     dimnames(res)[[2]]<-c("Th.C",
218         "Th.M",
219         "Th.W",
220         "Mean.Th")
221 return(res)
222 }
223
224 #example where the three cases:
225     #decrease in cold-adapted and increase in warmth-adapted;
226     #decrease in cold-adapted and increase in generalists;
227     #decrease in generalists and increase in warmth-adapted species
228 #give a similar signal in terms of significance of variation of 5%, 50% and
229 95% percentiles
230 #seed of pseudo-random numbers fixed to be able to replicate the results
231 #simulations:
232 set.seed(1)
233 FT.ref<-simul.T()
234
235
236 weight.coldhot <- c(0.6, 1, 1.4, 1)
237 weight.coldgen <- c(0.1, 1, 1, 1.15)
238 weight.hotgen <- c(1, 1, 2.5, 0.7)
239 list.weight.SM1 <- list(weight.coldhot, weight.coldgen, weight.hotgen)
240 list.weight.SM2 <- list(weight.coldhot, weight.coldhot*2,
241     weight.coldhot*0.5)
242
243 set.seed(1)
244 FT.1 <- simul.T(list.weight[[1]])
245 set.seed(1)
246 FT.2 <- simul.T(list.weight[[2]])
247 set.seed(1)
248 FT.3 <- simul.T(list.weight[[3]])
249 set.seed(1)
250 FT.4 <- simul.T(list.weight[[1]],SR=200)
251 set.seed(1)
252 FT.5 <- simul.T(list.weight[[1]],SR=50)
253

```

```

254 FT.list.SM1 <-list(FT.1, FT.2, FT.3)
255
256 FT.list.SM2 <-list(FT.1, FT.4, FT.5)
257
258 #results of simulations:x
259 list.Th.SM1 <- lapply(FT.list.SM1,
260                       function(df,df.ref) as.data.frame(df - df.ref),
261                       df.ref = FT.ref)
262 list.Th.obs.SM1 <- lapply(FT.list.SM1,
263                           function(df,df.ref) apply(df, 2, mean) - apply(df.ref, 2, mean),
264                           df.ref = FT.ref)
265
266 list.Th.SM2 <- lapply(FT.list.SM2,
267                       function(df,df.ref) as.data.frame(df - df.ref),
268                       df.ref = FT.ref)
269 list.Th.obs.SM2 <- lapply(FT.list.SM2,
270                           function(df,df.ref) apply(df, 2, mean) - apply(df.ref, 2, mean),
271                           df.ref = FT.ref)
272
273 fit.lm.CI <- function(var,df){
274 lm.M <- lm(as.formula(paste(var, ' ~ 1')), data = df)
275 return(c(coefficients(lm.M),
276          confint(lm.M)))
277 }
278
279 fit.lm.3quantiles <- function(df,
280                               vars = c('Th.C', 'Th.M', 'Th.W')){
281
282 list.lm.res <- lapply(vars, fit.lm.CI, df)
283 names(list.lm.res) <- vars
284 return(list.lm.res)
285 }
286
287 list.res.lm.SM1 <- lapply(list.Th.SM1, fit.lm.3quantiles)
288
289 list.res.lm.SM2 <- lapply(list.Th.SM2, fit.lm.3quantiles)
290
291 ###
292
293 plot.abundance.change <- function(vec.weights){
294 x1<-seq(-2.5,2.5,length.out=10)
295 #x3<-seq(-2.5,2.5,length.out=20)
296 #x2<-seq(-1.5,1.5,length.out=20)
297 #x4<-seq(-0.5,2.5,length.out=20)
298 x2<-x1
299 x3<-x1

```

```

300 x4<-x1
301
302 x1<--1.3
303 x2<-0
304 x3<-1.2
305 x4<-1.2
306
307
308 curve(dnorm(x, -1, 0.5), xlim = c(-2.5, 2.5), ylim = c(0, 2),
309       xlab = 'Temperature', ylab = 'Species abundance', col = 'blue3', lwd = 1.5)
310 points(x1,dnorm(x1, -1, 0.5), xlim = c(-2.5, 2.5), ylim = c(0, 2),
311       xlab = 'Temperature', ylab = 'Species abundance', col = 'blue3', type = 'p',
312       pch=22, lwd = 1.5,cex=1.5,bg='white')
313
314
315
316
317 curve(dnorm(x, 0, 0.5), add = TRUE, col = 'chocolate4', lwd = 1.5)
318 points(x2,dnorm(x2, 0, 0.5), xlim = c(-2.5, 2.5), ylim = c(0, 2),
319       xlab = 'Temperature', ylab = 'Species abundance', col = 'chocolate4', type = 'p',
320       pch=21, lwd = 1.5,cex=2,bg='white')
321
322 curve(dnorm(x, 1, 0.5), add = TRUE, col = 'red', lwd = 1.5)
323 points(x4,dnorm(x4, 1, 0.5), xlim = c(-2.5, 2.5), ylim = c(0, 2),
324       xlab = 'Temperature', ylab = 'Species abundance', col = 'red', type = 'p',
325       pch=24, lwd = 1.5,cex=1.5,bg='white')
326
327 curve(dnorm(x, 0, 1), add = TRUE, col = 'chartreuse4', lwd = 1.5)
328 points(x3,dnorm(x3, 0, 1), xlim = c(-2.5, 2.5), ylim = c(0, 2),
329       xlab = 'Temperature', ylab = 'Species abundance', col = 'chartreuse4', type =
330       'p', pch=23, lwd = 1.5,cex=1.5,bg='white')
331
332 curve(vec.weights[1] *dnorm(x, -1, 0.5), add = TRUE, col = 'blue3', lty = 2, lwd =
333       3)
334 points(x1,vec.weights[1] *dnorm(x1, -1, 0.5), xlim = c(-2.5, 2.5), ylim = c(0, 2),
335       xlab = 'Temperature', ylab = 'Species abundance', col = 'blue3', type = 'p',
336       pch=22, lwd = 1.5,cex=1.5,bg='white')
337
338 curve(vec.weights[2] *dnorm(x, 0, 0.5), add = TRUE, col = 'chocolate4', lty = 2,
339       lwd = 3)
340 points(x2,vec.weights[2] *dnorm(x2, 0, 0.5), xlim = c(-2.5, 2.5), ylim = c(0, 2),
341       xlab = 'Temperature', ylab = 'Species abundance', col = 'chocolate4', type = 'p',
342       pch=21, lwd = 1.5,cex=2,bg='white')

```

```

343
344 curve(vec.weights[3] * dnorm(x, 1, 0.5), add = TRUE, col = 'red', lty = 2, lwd = 3)
345 points(x4,vec.weights[3] * dnorm(x4, 1, 0.5), xlim = c(-2.5, 2.5), ylim = c(0, 2),
346       xlab = 'Temperature', ylab = 'Species abundance', col = 'red', type = 'p',
347       pch=24, lwd = 1.5,cex=1.5,bg='white')
348
349 curve(vec.weights[4]*dnorm(x, 0, 1), add = TRUE, col = 'chartreuse4', lty = 2, lwd
350 = 3)
351 points(x3,vec.weights[4]*dnorm(x3, 0, 1), xlim = c(-2.5, 2.5), ylim = c(0, 2),
352       xlab = 'Temperature', ylab = 'Species abundance', col = 'chartreuse4', type =
353 'p', pch=23, lwd = 1.5,cex=1.5,bg='white')
354
355 }
356
357 plot.abundance.change(weight.coldhot)
358
359
360 ### Commands for Figure 1
361 par(mfrow = c(3, 2),mar= c(3.5, 4, 1, 2) + 0.1, mgp=c(2.2,1,0))
362 for (i in 1:3){
363
364     plot(1:3,c(list.res.lm.SM1[[i]]$Th.C[1],
365             list.res.lm.SM1[[i]]$Th.M[1],
366             list.res.lm.SM1[[i]]$Th.W[1]), xlim = c(1, 3),
367         ylab = 'Thermophilisation', xlab = NA,
368         xaxt = 'n', ylim = c(0, 0.5), col = 'black', pch = 16)
369     axis(1, 1:3, c('Quant.5', 'Quant.50', 'Quant.95'))
370     segments(1, list.res.lm.SM1[[i]]$Th.C[2], 1, list.res.lm.SM1[[i]]$Th.C[3])
371     segments(2, list.res.lm.SM1[[i]]$Th.M[2], 2, list.res.lm.SM1[[i]]$Th.M[3])
372     segments(3, list.res.lm.SM1[[i]]$Th.W[2], 3, list.res.lm.SM1[[i]]$Th.W[3])
373
374     plot.abundance.change(list.weight.SM1[[i]])
375
376 }
377 ### Commands for Figure 2
378 par(mfrow = c(3, 2),mar= c(3.5, 4, 1, 2) + 0.1, mgp=c(2.2,1,0))
379 for (i in 1:3){
380
381     plot(1:3,c(list.res.lm.SM2[[i]]$Th.C[1],
382             list.res.lm.SM2[[i]]$Th.M[1],
383             list.res.lm.SM2[[i]]$Th.W[1]), xlim = c(1, 3),
384         ylab = 'Thermophilisation', xlab = NA,
385         xaxt = 'n', ylim = c(0, 0.5), col = 'black', pch = 16)
386     axis(1, 1:3, c('Quant.5', 'Quant.50', 'Quant.95'))

```

```

387     segments(1, list.res.lm.SM2[[i]]$Th.C[2], 1, list.res.lm.SM2[[i]]$Th.C[3])
388     segments(2, list.res.lm.SM2[[i]]$Th.M[2], 2, list.res.lm.SM2[[i]]$Th.M[3])
389     segments(3, list.res.lm.SM2[[i]]$Th.W[2], 3, list.res.lm.SM2[[i]]$Th.W[3])
390
391     plot.abundance.change(list.weight.SM2[[i]])
392
393 }
394
395 ### here are the numerical results: each has four components:
396 #(i) Quantile 5%; (ii) Quantile 50% (=median); (iii) Quantile 95%; and (iv)
397 mean
398
399 #reference/baseline situation:
400 apply(FT.ref,2,mean)
401 #-1.539968245 0.003256743 1.543673240 0.002439712
402
403
404 #new situations (each to be compared with the reference situation):
405 #decrease in cold-adapted and increase in warmth-adapted;
406 apply(FT.list.SM1[[1]],2,mean)
407 #-1.4125214 0.2628160 1.6236205 0.2000333
408
409
410 #decrease in cold-adapted and increase in generalists;
411 apply(FT.list.SM1[[2]],2,mean)
412 #-1.2290590 0.3094626 1.6316034 0.2788521
413
414 #decrease in generalists and increase in warmth-adapted species
415 apply(FT.list.SM1[[3]],2,mean)
416 #-1.4082757 0.4333396 1.6685698 0.2899387
417
418
419 #increase in all the species groups
420 apply(FT.list.SM2[[2]],2,mean)
421 #-1.4150345 0.2664850 1.6251364 0.2023492
422
423 #decrease in all the species groups
424 apply(FT.list.SM2[[3]],2,mean)
425 #-1.4071107 0.2650027 1.6228678 0.2012783
426

```