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## Latitudinal phytoplankton distribution and the neutral theory of biodiversity

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### Abstract:

**Aim** : Recent studies have suggested that global diatom distributions are not limited by dispersal, in the case of both extant species and fossil species, but rather that environmental filtering explains their spatial patterns. Hubbell's neutral theory of biodiversity provides a framework in which to test these alternatives. Our aim is to test whether the structure of marine phytoplankton (diatoms, dinoflagellates and coccolithophores) assemblages across the Atlantic agrees with neutral theory predictions. We asked: (1) whether intersite variance in phytoplankton diversity is explained predominantly by dispersal limitation or by environmental conditions; and (2) whether species abundance distributions are consistent with those expected by the neutral model.

**Location** : Meridional transect of the Atlantic (50° N–50° S).

**Methods** : We estimated the relative contributions of environmental factors and geographic distance to phytoplankton composition using similarity matrices, Mantel tests and variation partitioning of the species composition based upon canonical ordination methods. We compared the species abundance distribution of phytoplankton with the neutral model using Etienne's maximum-likelihood inference method.

**Results** : Phytoplankton communities are slightly more determined by niche segregation (24%), than by dispersal limitation and ecological drift (17%). In 60% of communities, the assumption of neutrality in species' abundance distributions could not be rejected. In tropical zones, where oceanic gyres enclose large stable water masses, most communities showed low species immigration rates; in contrast, we infer that communities in temperate areas, out of oligotrophic gyres, have higher rates of species immigration.

**Conclusions** : Phytoplankton community structure is consistent with partial niche assembly and partial dispersal and drift assembly (neutral processes). The role of dispersal limitation is almost as important as habitat filtering, a fact that has been largely overlooked in previous studies. Furthermore, the polewards increase in immigration rates of species that we have discovered is probably caused by water mixing conditions and productivity.

**Keywords**: Atlantic Ocean ; beta diversity ; diatom ; dispersal ; neutral theory ; plankton

49 **INTRODUCTION**

50

51 Unlike sessile species or those dwelling on islands, oceanic planktonic species have no  
52 apparent barriers to dispersal (Cermeño & Falkowski, 2009). It also appears that  
53 planktonic species are broadly distributed, both in space and in time. Planktonic species  
54 also exhibit some of the most striking examples of explosive population growth  
55 (blooms) and of fine niche specialization (d'Ovidio *et al.*, 2010). Ecologists have long  
56 debated whether the regional distribution of species arises from dispersal limitation  
57 (MacArthur & Wilson, 1967) or from niche differentiation (Hutchinson, 1957). The  
58 neutral theory of biodiversity (Hubbell, 2001) has generated a great deal of attention  
59 because it provides an integrative framework in which to test these alternatives  
60 (Duivenvoorden *et al.*, 2002). Initially, tests and applications of the neutral theory of  
61 biodiversity and biogeography have been restricted to tropical forests (e.g. Condit *et al.*,  
62 2002; Duivenvoorden *et al.*, 2002; Chave *et al.*, 2006; Chust *et al.*, 2006a), but since  
63 then they have also been applied in marine ecology (e.g. Dornelas *et al.*, 2006; Martiny  
64 *et al.*, 2011), and more specifically to planktonic species assemblages (Alonso *et al.*,  
65 2006; Pueyo, 2006a,b; Dolan *et al.*, 2007; Vergnon *et al.*, 2009; Irigoien *et al.*, 2011).  
66 However, these latter works have only tested the neutral model partially because they  
67 did not take into account explicitly the migration rate of species.

68

69 The neutral model of biodiversity developed by Hubbell (1997, 2001) was inspired by  
70 MacArthur & Wilson's (1967) theory of island biogeography. In Hubbell's model, all  
71 individuals are assumed to have the same prospects for reproduction and death  
72 (neutrality). The variability in relative abundances across species is solely due to  
73 demographic stochasticity or 'ecological drift'. This model further assumes a separation

74 of spatial scales: demographic processes occur at the local scale of an ecological  
75 community, where species may go locally extinct through demographic drift. The local  
76 diversity is replenished by immigration at rate  $m$  of propagules from a regional species  
77 pool. In this large regional pool, drift may also cause species to go extinct, and novel  
78 species arise through speciation, such that  $\theta$  new species are produced every generation  
79 in this regional pool. If  $m = 1$ , the local community is a random (Poisson) sample of the  
80 regional pool. In contrast, if  $m$  is close to zero, the local community is virtually isolated  
81 from the regional pool. Hubbell's neutral model thus assumes that limited dispersal,  
82 rather than niche specialization, is the main explanation for spatial structure across  
83 ecological communities. Under this model, the local species abundance distribution is  
84 thus defined by only two model parameters  $\theta$ , and  $m$ . A spatially-explicit version of  
85 Hubbell's model has also been developed (Chave & Leigh, 2002), in which dispersal  
86 from one locale to another is limited by the geographical distance between these sites.  
87 In such a model, taxonomic cross-site similarity (i.e. the opposite of  $\beta$ -diversity)  
88 declines logarithmically with increasing geographical distance (Hubbell, 2001; Condit  
89 *et al.*, 2002; Chave & Leigh, 2002).

90

91 In contrast, niche theory assumes that differences in species composition among  
92 communities is caused by heterogeneity in the environment or limiting resources, and  
93 by environmental filtering of species according to their environmental requirements,  
94 such as oceanographic conditions, and competition for resources such as nutrient  
95 concentrations for marine phytoplankton. In niche-based models, species are able to  
96 coexist by avoiding competition through resource and environmental partitioning  
97 (Gause, 1934; Chesson, 2000). Testing neutral theory against niche theory has proven  
98 challenging, because both environmental variables and species distributions tend to be

99 spatially autocorrelated (Legendre *et al.*, 2005). On the one hand, species distributions  
100 are most often aggregated spatially because of biotic processes such as reproduction and  
101 death. On the other hand, the pelagic environment is primarily structured by ocean  
102 currents and oceanographic processes causing spatial gradients. Statistical techniques  
103 have been developed to partition variation of diversity due to environmental variability  
104 and due to dispersal limitation (Legendre, 1993; Legendre *et al.*, 2005; Chust *et al.*,  
105 2006b).

106

107 Recently, Cermeño & Falkowski (2009) have offered a thought-provoking analysis of  
108 global patterns of fossil diatom diversity. They suggested that diatom distributions over  
109 the oceans show no evidence of dispersal limitation either at present or over long time  
110 scales, but rather that environmental filtering explains these spatial distributions. This  
111 view is in line with the Baas-Becking hypothesis that ‘everything is everywhere – the  
112 environment selects’. More evidence in support for this conclusion has been gathered by  
113 Cermeño *et al.* (2010). However, this view contradicts findings for lake diatoms where  
114 the potential for dispersal-related community structuring has been shown (Verleyen *et*  
115 *al.*, 2009). Also, an analysis of the genetic structure of populations of a marine diatom,  
116 *Pseudo-nitzschia pungens*, is consistent with a strong isolation by distance pattern,  
117 suggesting that dispersal limitation may be an important factor in explaining the spatial  
118 structure of extant diatom communities (Casteleyn *et al.*, 2010). These few statistical  
119 analyses offer a quantitative glimpse of the relative roles of environment and dispersal  
120 for diatom diversity (Verleyen *et al.*, 2009; Cermeño *et al.*, 2010). Further, the  
121 implications of these alternative interpretations for species abundance distributions have  
122 not yet been examined in light of Hubbell’s neutral theory.

123

124 Here we examine the structure of communities of three phytoplankton groups (diatoms,  
125 dinoflagellates, and coccolithophores), along a transect across the Atlantic Ocean from  
126 nearly 50° North to 50° South, to ascertain the extent to which the structure is consistent  
127 with niche assembly or dispersal (neutral) assembly. This latitudinal transect allows for  
128 large biological diversity and strong environmental gradients to be covered. All three  
129 phytoplankton groups behave as passive organisms and occupy the same trophic level.  
130 We seek to understand whether marine phytoplankton comply with neutral theory  
131 predictions of the distribution of relative species abundance and of spatial turnover in  
132 diversity. The following null hypotheses were formulated to address our main question:  
133 1) According to the neutral theory, and when species are dispersal limited, the similarity  
134 of phytoplankton species composition should decrease with geographic distance, and  
135 the distance decay in similarity is expected to be more important than oceanographic  
136 conditions and nutrient concentrations. Here, we assess the relative contribution of  
137 dispersal limitation and environmental factors to the explanation of the variance in  
138 phytoplankton assemblages. We note that niche assembly mechanisms and neutral  
139 processes of drift and dispersal can occur simultaneously, so that results indicating a  
140 contribution of dispersal limitation, while supporting the neutral model, do not preclude  
141 a role for niche differentiation in phytoplankton assemblages. However, not finding a  
142 role of dispersal limitation does not provide any information on the validity, or lack  
143 there of, of the neutral model. 2) Assuming neutrality, the phytoplankton species  
144 abundance distribution should fit the distribution expected from Hubbell's neutral  
145 model. As the neutral theory applies to metacommunities, where local communities  
146 interact with each other by an immigration rate, the test has been performed in three  
147 regions (see also Cermeño *et al.*, 2010). Thus, we test, for the first time, the predictions

148 of neutral theory for the spatial turnover in species composition and for relative species  
149 abundance in three of the most important phytoplankton groups.

150

## 151 **MATERIAL AND METHODS**

152

### 153 *The AMT surveys and datasets*

154

155 The Atlantic Meridional Transect (AMT) is an ocean observation programme that  
156 undertakes biological, chemical and physical oceanographic research over a latitudinal  
157 transect of the Atlantic ocean from nearly 50° North to 50° South (Fig. 1), a distance of  
158 over 13,500 km (Robinson *et al.*, 2006). This transect crosses a range of biome types  
159 from sub-polar to tropical and from eutrophic shelf seas and upwelling systems to  
160 oligotrophic mid-ocean gyres. We analysed phytoplankton data from the first three  
161 AMT surveys, on-board the research ship James Clark Ross: AMT1 (which took place  
162 from 21 September to 24 October 1995), AMT2 (between 22 April and 28 May 1996),  
163 and AMT3 (between 20 September and 25 October 1996). AMT1 and AMT3 sailed  
164 from the UK to Falkland Islands, whereas AMT2 sailed from Falkland Islands to the  
165 UK. The AMT surveys included 25 sampling stations, each separated by 4° latitude  
166 from the next station.

167

168 Data from AMT surveys are available from the British Oceanographic Data Center  
169 (BODC; <http://www.amt-uk.org/data.aspx>) and is described in Robins *et al.* (1996a,b)  
170 and Bale (1996). Specifically, chemical and phytoplankton data were sampled at 7-m  
171 depth waters using a rosette (i.e. water sampling device) fitted with 12 10-litre General  
172 Oceanics water bottles. Physical and optical data were obtained with a CTD (Neil

173 Brown Mark IIIB, Instrument Systems, Inc.). Environmental data considered in our  
174 analysis encompasses physical variables (sea surface temperature, salinity), optical  
175 variables (down-welling irradiance at Photosynthetically Active Radiation (PAR)  
176 wavelengths, percentage of irradiance at sampling depth, surface solar radiation) and  
177 nutrients: nitrate+nitrite ( $\text{NO}_3+\text{NO}_2$ ), nitrite ( $\text{NO}_2$ ), phosphate ( $\text{PO}_4$ ), and silicate ( $\text{SiO}_4$ )  
178 concentrations. The percentage of surface irradiance at the sampling depth was inferred  
179 from the spectral diffuse attenuation coefficient of light (K) at PAR wavelengths.  
180 Geographic data were: latitude and longitude.

181

182 For the collection and identification of phytoplankton, 100 ml samples were taken at  
183 each station and preserved in lugol's iodine solution (Robins, 1996b). Examination of  
184 the samples was conducted following Uthermol's sedimentation technique under an  
185 inverted microscope (Robins, 1996b). The sampling procedure and volume used is the  
186 standard one for phytoplankton, considered adequate for repeatable characterizations of  
187 oceanic phytoplankton communities (Lund *et al.*, 1958). Previous studies using these  
188 three AMT datasets (and two other ones, AMT4 and AMT5) showed qualitatively  
189 similar productivity-diversity patterns, which indicates that 100 ml sample provides a  
190 reasonable representation of the phytoplankton community diversity (e.g. Irigoien *et al.*,  
191 2004). Phytoplankton (diatoms, dinoflagellates, and coccolithophorids) were  
192 taxonomically classified based on morphological characters at species level, and in  
193 some cases at genus level. For the present analysis, the species abundance per 100 ml  
194 sample volume was considered in order to work with count data (i.e. number of  
195 individuals). Overall, diatoms are the most diverse of the three phytoplankton groups  
196 (from 83 to 92 diatom species per survey, 35 to 42 dinoflagellate species, and 34-38  
197 coccolithophore species), see Table 1. However, coccolithophores showed the highest

198 average species richness per station (9.8), followed by diatoms (8.3) and dinoflagellates  
199 (6.5). Among coccolithophores, the most abundant species was the bloom forming  
200 *Emiliana huxleyi* in all three surveys. In contrast, the most abundant diatom and  
201 dinoflagellate species varied from one survey to the next. In particular, diatoms varied  
202 markedly in abundance and dominance; for instance, the most abundant species on  
203 AMT1 was *Thalassiosira gracilis* with 6144.6 individuals per ml, all present on a single  
204 station, and absent on both AMT2 and AMT3.

205

#### 206 *Spatial species turnover*

207

208 The relative contribution of environmental factors and geographic distance to  
209 phytoplankton composition was estimated using similarity matrices, Mantel tests and  
210 variation partitioning of the species composition across sites based upon canonical  
211 ordination methods (Legendre & Legendre, 1998). The Jaccard index was used to  
212 measure the compositional similarity between pairs of stations. The Jaccard index is the  
213 number of species shared between the two plots, divided by the total number of species  
214 observed. Distance matrices for environmental variables and geographic distance were  
215 measured by the Euclidean distance between values at two stations. We used Mantel  
216 tests (Legendre & Legendre, 1998) to determine the correlation between species  
217 similarity matrices and environmental and geographic distance. The Mantel test is a  
218 nonparametric test based on a bootstrap randomization of the matrices, to determine how  
219 frequently the observed similarity would arise by chance. This test computes a statistic  
220  $r_M$  which measures the correlation between two matrices. The rate of change in species  
221 similarity with increasing geographic distance was calculated by fitting a linear model.  
222 Also, the latitudinal range of a species was defined as the distance between the observed



223 latitudinal extremes of its occurrence. From the individual species ranges, average  
224 latitudinal ranges were then computed for each phytoplankton group. To test the  
225 correlation between species similarity and environmental distance, we first selected the  
226 best subset of environmental variables, such that the Euclidean distance of scaled  
227 environmental variables would have the maximum correlation with community  
228 dissimilarities, using the *vegan* package (Oksanen et al. 2011) implemented in the R  
229 2.13.1 language (R Development Core Team, 2011). We then compared the  $2^p - 1$   
230 possible models, where  $p$  is the number of environmental variables, for each AMT  
231 survey and phytoplankton group. Only environmental variables with values in all  
232 stations were considered in the initial model. Subsequently, a partial Mantel test was  
233 undertaken to determine the relative contribution of environmental distance (after model  
234 selection) and geographic distance in accounting for species variation.

235

236 We partitioned the variance of phytoplankton composition across stations to determine  
237 the relative contribution of environmental factors and spatial pattern. Species spatial  
238 pattern, as a result of aggregation because of biotic processes, were modelled with third-  
239 degree polynomial of geographic coordinates of latitude ( $X$ ) and longitude ( $Y$ ):  $X$ ,  $Y$ ,  
240  $X*Y$ ,  $X^2$ ,  $Y^2$ ,  $X^2*Y$ ,  $Y^2*X$ ,  $X^3$  and  $Y^3$  (cubic trend surface analysis, Legendre 1993). The  
241 total intersite variation in species abundance was decomposed into four components:  
242 pure effect of environment, pure effect of geographical distance, combined variation  
243 due to the joint effect of environment and geographical distance, and unexplained  
244 variation. Since partitioning on distance matrices (Mantel approach) underestimates the  
245 amount of variation in community composition (Legendre *et al.*, 2005), we used a  
246 canonical (i.e. constrained) ordination analysis (ter Braak & Šmilauer, 1998) to estimate  
247 a proportion of the variance of the original phytoplankton table of abundances (sites by

248 species). Canonical ordination analysis is a method to reduce the variation in  
249 community composition in which the axes are constrained to be linear combinations of  
250 explanatory variables. More specifically, species are assumed to have unimodal  
251 response surfaces with respect to explanatory gradients. The variance partitioning  
252 analysis, detailed in Legendre *et al.* (2005), proceeds in two steps. First, we selected the  
253 best two canonical correspondence models (one for environmental variables, the other  
254 for spatial terms) using a stepwise procedure and based upon the Akaike Information  
255 Criterion (AIC), with the *vegan* package (Oksanen, 2011) implemented in the R 2.13.1  
256 language (R Development Core Team, 2011). Subsequently, a partial canonical analysis  
257 (ter Braak & Šmilauer, 1998) was undertaken to determine the relative contribution of  
258 environmental factors and spatial terms in accounting for species variation. Specifically,  
259 the partial canonical analysis estimates the contribution of environmental factors in  
260 accounting for species variation by removing the effect of the spatial term covariable.  
261 Because of the presence of environmental missing values (at 29 sites) and low number  
262 of stations per AMT survey for this type of analysis, the variation partitioning was  
263 undertaken for the overall three AMT surveys (46 sites) restricting the analysis to six  
264 environmental variables whose values were available for all sites: sea surface  
265 temperature, salinity, percentage of irradiance, NO<sub>2</sub>, PO<sub>4</sub>, and SiO<sub>4</sub>.

266

### 267 *Neutral theory*

268

269 One radical step toward the construction of a mathematically tractable community  
270 model is Hubbell's theory of biodiversity (Hubbell, 2001). This theory is radical in  
271 assuming that all individuals have the same prospects of reproduction and death  
272 irrespective of their age, size and of the species to which they belong. Hubbell (2001)

273 modeled local communities in which each death is replaced, with probability  $1-m$ , by an  
274 offspring of a randomly chosen individual in the local community, regardless of species,  
275 and with probability  $m$ , by an immigrant from the regional species pool. The species of  
276 immigrant is determined by the relative abundance of species in the regional pool. In  
277 Hubbell's original model, community size remains constant, but in later versions, the  
278 size of the local community can vary about a stochastic mean size (Volkov *et al.* 2003).  
279 Hence, the species composition fluctuates due to stochastic drift only, but not because  
280 of habitat selection or of interspecific competition. The local community is embedded in  
281 and connected via migration to the geographic area occupied by the regional species  
282 pool, the metacommunity, of size  $J_M$  (the number of individuals in the regional pool), so  
283 that a fraction  $m$  of recruits has immigrated from the regional pool rather than being the  
284 offspring of local parents. The local community reaches a dynamic equilibrium between  
285 stochastic local species extinction and species replenishment through immigration. At  
286 the scale of the regional pool, a similar dynamics occurs; diversity is maintained  
287 because extinction is balanced by speciation. Speciation in the regional species pool is  
288 modeled simply by assuming that each new recruit has a small probability  $\nu$  of yielding  
289 an altogether new species, so that  $\theta = \nu \times J_M$  new species appear in the system on  
290 average each generation. Hubbell's (2001) neutral model, thus, has two parameters: the  
291 regional diversity parameter  $\theta$  and the immigration rate  $m$ . Etienne (2005) has formally  
292 shown that  $\theta$  can jointly be estimated with  $m$  from empirical species abundance data  
293 using a maximum likelihood framework.

294

295 Jabot & Chave (2011) have proposed a test of neutrality building upon Etienne's (2005)  
296 maximum-likelihood (ML) inference method. Briefly, for any species abundance  
297 distribution, a ML estimate of the neutral parameters  $\theta$  and  $m$  may be obtained. Using

298 Hubbell's model as a null model, neutral species abundance distributions are  
299 constructed, and only those with the same number of species as in the empirical dataset  
300 are retained, until one reaches one thousand simulated communities. These neutral  
301 species abundance distributions therefore have the same observed number of species  
302 and the same  $\theta$  and  $m$  as do the empirical species abundance distribution. To build a  
303 test, Shannon's index is then calculated for both the neutral species abundance  
304 distributions and for the empirical one. The rationale for our choice of Shannon's index  
305 as a summary statistic is further explained in Jabot and Chave (2011). If the empirical  
306 Shannon's index falls outside the distribution of neutral Shannon's indices, then  
307 neutrality is rejected. The empirical Shannon index was compared with this null  
308 distribution by a t-test. This test of neutrality is based on species abundance  
309 distributions only, but it is more robust than previous tests.

310

311 We explored the results of this neutrality test along the latitudinal axis by partitioning  
312 the global dataset into three regions: northern temperate zone ( $>25^\circ$ ), tropical zone  
313 (between  $>-25^\circ$  and  $<25^\circ$ ) and southern temperate zone ( $<-25^\circ$ ), see Fig. 1. The  
314 boundary of the northern zone with the tropical coincides with the Westerlies biome and  
315 Trade-Winds biome, respectively, defined by the Longhurst Biogeographical Provinces  
316 (VLIZ, 2009). The tropical zone so defined had a mean SST above  $24.5^\circ\text{C}$  (North of  
317 the equator) and above  $\sim 22^\circ\text{C}$  (South of the equator).

318

319 We estimated the neutral model parameters  $\theta$  and  $m$  together with confidence intervals  
320 and also performed the above test for the total dataset (including diatoms,  
321 coccolithophores and dinoflagellates). This inference was implemented in the Tetame  
322 software (Jabot *et al.*, 2008). Of the 75 samples, 8 had more than 50,000 individuals,

323 and this resulted in prohibitively long calculations (akin to finding the zeros of a  
324 polynomial of degree equal to the number of individuals, see Etienne 2005). For these 8  
325 samples, we picked a random sample of 50,000 individuals, and replicated this sampling  
326 procedure ten times to ensure its stability. In two cases, the neutral parameters could not  
327 be computed due to too small sample sizes. In a majority of tests, neutrality was not  
328 rejected; in such cases, assuming neutrality, we explored how the estimated immigration  
329 probability ( $m$ ) varied with latitude throughout the main Atlantic zones.

330

## 331 **RESULTS**

332

### 333 *Spatial species turnover*

334

335 Mean similarity among stations was highest for coccolithophores (0.29), followed by  
336 dinoflagellates (0.23) and diatoms (0.11), see Table 1. The geographic distance range  
337 occupied by a species (on average) is less in diatoms (3352.8 km) than in dinoflagellates  
338 (4784.1 km) and coccolithophores (6093.8 km) (Table 1). Similarity of the three  
339 phytoplankton groups decreases significantly ( $p < 0.001$ ) in all three groups with  
340 geographic distance (Fig. 2;  $r_M$  (diatoms) = 0.24-0.28;  $r_M$  (dinoflagellates) = 0.20-0.34,  
341  $r_M$  (coccolithophores) = 0.29-0.39, and in all three AMT surveys. The Mantel  
342 correlation between species similarity and environmental factors (0.37-0.74) was higher  
343 than with geographic distance (0.21-0.39), for the three phytoplankton groups and the  
344 three surveys (Table 2). The Mantel correlation between species similarity and  
345 geographic distance, partialling out environmental factors, was significant ( $p < 0.05$ ) for  
346 a majority of cases (in all three groups for AMT1 and AMT2).

347

348 The variation partitioning based upon canonical ordination analysis reveals that  
349 environment is the largest main-effect factor contributing to phytoplankton species  
350 variation (24%; Fig. 3). However, the spatial component accounted for almost as much  
351 variation (17%). However, the interaction of environment and distance explained even  
352 more of the variation (26%) than either of the main-effect factors, indicating a role for  
353 as yet unexplained covariance between environment and separation distance. In the case  
354 of diatoms, environment is clearly higher than the spatial terms (25% vs. 8%,  
355 respectively), whereas in dinoflagellates (17% vs. 18%) and coccolithophores (5% vs.  
356 6%) the two factors are approximately equivalent.

357

#### 358 *Neutral theory parameters and test*

359

360 The estimates of neutral parameters ( $\theta$  and  $m$ ) for each station are shown in Table 3 for  
361 the three defined latitudinal regions (see also Appendix S3 for parameters for each  
362 station). The test of fit of the phytoplankton species abundance distribution to the  
363 neutral communities indicates that the number of communities in which neutrality  
364 cannot be rejected is higher (45) than the number in which neutrality can be rejected  
365 (28) (Table 3). Communities for which neutrality could not be rejected made up a larger  
366 percentage of tropical communities (50 to 100%), than of communities in the northern  
367 (40 to 57%) or southern (17 to 71%) zones. Fig. 4 shows six examples of the empirical  
368 species abundance distribution compared with that expected by a neutral model given  
369 the local community parameters  $\theta$  and  $m$ . These examples are representative of  
370 communities in all three latitudinal zones and illustrate variation in the goodness of fit  
371 of the neutral expectation. Those communities whose abundance distributions were not

372 fit by the neutral model (e.g., Fig 4b,d,f), generally exhibit too many species in the  
373 doubling abundance classes of 3 to 16 individuals per species.

374

375 Because species abundance distribution matches neutral theory a majority of cases  
376 (60%), we went on in such cases to plot the immigration probability ( $m$ ) against latitude  
377 (Fig. 5a). This plot revealed that  $m$  is consistently lower in tropical zones than in  
378 temperate zones. In particular, the probability of immigration is a convex function of  
379 latitude ( $r^2 = 0.44$ , p-value  $< 0.0001$ ), with a minimum in the tropical zone. We used  
380 AIC to select the best-fitting polynomial function (up to 4th order). This result suggests  
381 that local plankton communities in the temperate zones receive more immigration from  
382 the metacommunity (regional species pool) than do tropical communities.

383

## 384 **DISCUSSION**

385

386 We tested two predictions of neutral theory against data on the community structure of  
387 three marine phytoplankton groups in a latitudinal transect of the Atlantic Ocean. First,  
388 the canonical ordination analysis and Mantel tests showed that environment and  
389 geographic distance explained variation in diversity for the three phytoplankton taxa  
390 (diatoms, dinoflagellates and coccolithophores). These analyses also indicated that  
391 environment is slightly more important than geographic distance. Second, the Shannon  
392 information test of the fit of neutral theory to observed relative species abundance  
393 distributions showed that neutral expectations can not be rejected for 60% of  
394 communities. These two findings suggest that phytoplankton communities result from a  
395 combination of niche and neutral processes, which is in accordance with the patterns  
396 found in an exhaustive phytoplankton time series dataset (Vergnon *et al.*, 2009). Similar

397 conclusions were reached in a study of phytoplankton communities in the Caribbean  
398 and Mediterranean seas; Pueyo (2006a) states that both neutral and non-neutral  
399 mechanisms co-occur. These recent findings and the results of this paper lead to a new  
400 perspective, that niche assembly is not the only, or even always the prevailing, assembly  
401 mechanism of plankton communities, in contrast to the views that emerge from  
402 previous, global-scale studies of fossil diatom assemblages (Cermeño & Falkowski,  
403 2009). To the best of our knowledge, ours is the only approach to combine three  
404 important analyses of the same dataset: (i) empirical estimation of dispersal limitation,  
405 (2) assessment of the relative contribution of environmental factors and dispersal  
406 limitation to community assembly; and (3) estimation of migration rate in the neutral  
407 model.

408

409 The estimation of dispersal limitation revealed slight differences between phytoplankton  
410 groups. On the one hand, the geographic distance range occupied by one species (on  
411 average) is less in diatoms than in dinoflagellates and coccolithophores (Table 1). This  
412 suggests that connectivity among population sites is low in diatoms. On the other hand,  
413 coccolithophore similarity has a correlation with geographic distance (i.e. distance  
414 decay) slightly higher (0.29-0.39) than in diatoms (0.24-0.28), which can be interpreted  
415 as high spatial structuring (i.e. patchiness). In a pure neutral metacommunity, high  
416 slopes in the distance decay and small ranges of geographic distance occupied by the  
417 species, are related and provide a measure of dispersal limitation. In our case, however,  
418 diatoms have the lowest latitudinal range and the lowest distance decay slope. This  
419 apparent paradox should be due to the fact that diatom occurrences are very low (2 to 3  
420 stations on average per AMT survey), with respect to coccolithophores (more than 7).  
421 The differential abundance of species, and differing species richness, make it difficult to



422 evaluate the significance of small differences in dispersal in the different groups.  
423 Although mobility, sedimentation and growth rates are known to differ among these  
424 phytoplankton groups (Broekhuizen, 1999), their functional similarity and co-  
425 occurrence in similar environments might result in similar dispersal rates at the  
426 community level. This is an aspect that requires further research. A limitation of our  
427 dataset is that samples were not repeatedly subsampled, to test for repeatability and the  
428 degree to which the species diversity present was accurately represented (Gotelli &  
429 Colwell, 2001). The difficulty of detecting the smallest organisms and finding the  
430 largest organisms, where are rare in finite volumes, is always problematic (e.g. Vergnon  
431 *et al.*, 2009). However, the consistent patterns between AMT surveys in our analysis  
432 and previous studies (Irigoiien *et al.*, 2004) allow us to conclude that community  
433 diversity is well captured and sampling biases are not important.

434

435 The three phytoplankton groups exhibited differences in community metrics, although  
436 similar patterns between AMT surveys. Coccolithophores are more diverse in tropical  
437 zone, decreasing slightly with latitude (see Appendix S1). Over the entire geographic  
438 dataset, they are less diverse than diatoms, although local (per sample) diversity is  
439 higher than diatoms. Both abundance and the number of species of coccolithophores are  
440 very constant across latitudes, compared with diatoms and dinoflagellates. Concerning  
441 the species response strength to the environment, canonical ordination analysis and  
442 Mantel tests were consistent in that the environment is slightly more important than  
443 geographic distance, although the results of the two statistical analyses differ slightly at  
444 the group level. At the current, relatively coarse level of analysis, it is not possible to  
445 determine which phytoplankton group responds most strongly to environment. The  
446 current wisdom is that diatoms are r-strategists associated with mixed waters and

447 unpredictable conditions (e.g. Margalef, 1978). However, all three taxa exhibit massive  
448 blooms, generally taking place in temperate, mixed water zones (Fig. 5b). In each of the  
449 three taxa, there is a single species responsible for blooms; among diatoms it is  
450 *Thalassiosira gracilis*; among dinoflagellates it is *Gymnodinium galeaeformae*, and  
451 among coccolithophores, it is *Emiliania huxleyii*, similar to the findings of Irigoien *et*  
452 *al.* (2004). During these massive bloom situations, species richness decreases  
453 (Appendix S2), in agreement with previous studies (e.g. Irigoien *et al.*, 2004), which is  
454 here interpreted as competitive exclusion (Huisman *et al.*, 1999) because of limiting  
455 resources. If this is the case, these exceptional situations escape from the neutral theory  
456 assumptions.

457

458 In comparison with other ecosystems, the pelagic environment and remote islands (e.g.  
459 islands *sensu stricto*, caves, basins, lakes, estuaries, forest remnants) are the two  
460 opposite extremes in terms of population connectivity. Whereas islands could be  
461 considered as adimensional points where connectivity is very limited, the pelagic zone  
462 could be seen as a three dimensional space with no barriers for marine plankton  
463 (Cermeño & Falkowski, 2009), except those imposed by physical heterogeneity (e.g.  
464 stratification) and continents. From this point of view, i.e. increasing space dimensions  
465 increases potential connectivity, land could act as a two dimensional space for sessile  
466 species (e.g. plants), whereas coastlines can limit the dispersal of their inhabitants (e.g.  
467 restricted intertidal organisms) in one dimension. For instance, whereas coastal fish  
468 species are more likely to remain close to their place of origin, oceanic animal species  
469 are highly mobile and live in a continuous habitat with high connectivity (Tittensor *et*  
470 *al.*, 2010). Within this general framework, our findings reveal, nevertheless, that overall  
471 phytoplankton assemblages are poorly but consistently spatially structured across the

472 Atlantic, indicating that dispersal limitation is playing a non negligible role in global  
473 oceanic primary-producer distribution. Our results on dispersal limitation and spatial  
474 community structure are intermediate between the strong barriers to dispersal evident in  
475 thermophilic Archaea (Whitaker *et al.*, 2003), and the other extreme of no limits to  
476 dispersal, expressed in the view that below 1 mm body size “everything is everywhere,  
477 but the environment selects” (Finlay, 2002). Unlike terrestrial plants, for which  
478 ecological drift is potentially a key factor on regional scales, marine phytoplankton  
479 species are nearly pan-distributed all over latitudes (at least for species described at the  
480 morphological level). Whether the morphologically described species include cryptic  
481 species (e.g Kooistra *et al.*, 2008), or ecotypes with adaptations at the molecular level  
482 (e.g. Johnson *et al.*, 2006), and to what extent the consideration of those would improve  
483 the percentage of the variance explained by the environment is an aspect that requires  
484 further research.

485

486 Another striking finding was that, when fitting the neutral model, immigration rates  
487 increase poleward, which is consistent for the three AMT surveys. In tropical zones,  
488 where oceanic gyres enclose large stable water masses, communities are relatively  
489 constant in species richness and abundance and have low immigration rates. In contrast,  
490 communities in temperate areas, out of the oligotrophic gyres, are dominated by  
491 blooming spatially-unstructured diatoms and show higher rates of species immigration.  
492 Thus, high species immigration probability from the metacommunity seems to be  
493 associated with areas of high water mixing and productivity.

494

495 **CONCLUSION**

496

497 Phytoplankton communities of diatoms, dinoflagellates and coccolithophores across the  
498 Atlantic Ocean are slightly more determined by niche differentiation (24%) than by  
499 dispersal limitation (17%). In 60% of communities from tropical to temperate ocean  
500 latitudes, neutrality assumption on the species abundance distribution could not be  
501 rejected. These two findings suggest that the observed structure of phytoplankton  
502 communities is consistent with a mechanism that combines both niche- and neutral-  
503 assembly processes. The consistent patterns between AMT surveys allow us to conclude  
504 that sampling biases are not important although our dataset was limited by the lack of  
505 repeatedly subsamples. We provide the first empirical evidence that the role of dispersal  
506 limitation and ecological drift is almost as important in structuring marine  
507 phytoplankton communities as niche assembly. Furthermore, we also found that in  
508 tropical zones, where oceanic gyres enclose large stable water masses, most  
509 communities were characterized as having low species immigration rates when fitting  
510 the neutral model. In contrast, communities in temperate areas, out of the oligotrophic  
511 gyres, show higher rates of species immigration.

512

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514

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526

## 527 **REFERENCES**

528

529 Alonso, D., Etienne, R. S. & McKane, A. J. (2006) The merits of neutral theory. *Trends*  
530 *in Ecology & Evolution*, **21**, 451-457.

531 Bale A.J. (1996) AMT-3 cruise report.

532 Broekhuizen, N. (1999) Simulating motile algae using a mixed Eulerian–Lagrangian  
533 approach: does motility promote dinoflagellate persistence or co-existence with  
534 diatoms? *J. Plankton Res.*, **21**, 1191–1216.

535 Casteleyn, G., Leliaert, F., Backeljau, T., Debeer, AE, Kotaki, Y., Rhodes, L.,  
536 Lundholm, N. Sabbe, K., & Vyverman, W. (2010) Limits to gene flow in a  
537 cosmopolitan marine planktonic diatom. *Proc Natl Acad Sci USA*, **107**, 12952 – 12957.

538 Cermeño, P., & Falkowski, P. G. (2009) Controls on Diatom Biogeography in the  
539 Ocean. *Science*, **325**, 1539-1541.

540 Cermeño, P., C. de Vargas, F. t. Abrantes, and P. G. Falkowski (2010) Phytoplankton  
541 Biogeography and Community Stability in the Ocean. *PLoS ONE*, **5**, e10037.

542 Cermeño, P., E. Maranon, D. Harbour, F. G. Figueiras, B. G. Crespo, M. Huete-Ortega,  
543 M. Varela, and R. P. Harris. 2008. Resource levels, allometric scaling of population

544 abundance, and marine phytoplankton diversity. *Limnology and Oceanography*, **53**,  
545 312-318.

546 Chave J, F. Jabot (2008) TeTame 2.1. Estimation of neutral parameters by maximum  
547 likelihood. <http://www.edb.ups-tlse.fr/equipe1/tetame.htm>.

548 Chave J., D. Alonso, R. S. Etienne (2006) Comparing models of species abundance.  
549 *Nature* 441:E1.

550 Chave, J. & Leigh, E.G (2002) A spatially explicit neutral model of beta-diversity in  
551 tropical forests. *Theor. Pop. Biol.*, **62**, 153-168.

552 Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol.*  
553 *Syst.*, **31**, 343–366.

554 Chust, G., A. Pérez-Haase, J. Chave, and J. L. Pretus (2006b) Floristic patterns and  
555 plant traits of Mediterranean communities in fragmented habitats. *Journal of*  
556 *Biogeography*, **33**, 1235-1245.

557 Chust, G., J. Chave, R. Condit, S. Aguilar, S. Lao, and R. Pérez (2006a) Determinants  
558 and spatial modeling of the tree B-diversity in a tropical forest landscape in Panama.  
559 *Journal of Vegetation Science*, **17**, 83-92.

560 Condit, R., Pitman, N., Leigh, E.G., Chave, J., Terborgh, J., Foster, R.B., Nunez, P.,  
561 Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P.  
562 (2002) Beta-diversity in tropical forest trees. *Science*, **295**, 666-669.

563 Dolan, J. R., Ritchie, M. R. & Ras, J. (2007) The neutral community structure of  
564 planktonic herbivores, tintinnid ciliates of the microzooplankton, across the SE Tropical  
565 Pacific Ocean. *Biogeosciences*, **4**, 297–310.

566 Dornelas, M., S. R. Connolly, & T. P. Hughes (2006) Coral reef diversity refutes the  
567 neutral theory of biodiversity. *Nature*, **440**, 80-82.

568 Duivenvoorden, J.F., Svenning, J.C. & Wright, S.J. (2002) Beta diversity in tropical  
569 forests. *Science*, **295**, 636-637.

570 Etienne, R.S. (2005) A new sampling formula for neutral biodiversity. *Ecology Letters*,  
571 **8**, 253-260.

572 Finlay, B. J. (2002) Global dispersal of free-living microbial eukaryote species. *Science*,  
573 **296**, 1061-1063.

574 Gause, G.F. (1934) *The Struggle for Existence*. Williams and Wilkins, Baltimore.

575 Gotelli, N. J. & Colwell, R. K. (2001) Quantifying biodiversity: procedures and pitfalls  
576 in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379-391.

577 Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in  
578 ecology. *Ecological Modelling*, **135**, 147 – 186.

579 Hubbell, S. P., F. L. He, R. Condit, L. Borda-de-Agua, J. Kellner, and H. ter Steege  
580 (2008) How many tree species and how many of them are there in the Amazon will go  
581 extinct? *Proceedings of the National Academy of Sciences of the United States of*  
582 *America*, **105**, 11498-11504.

583 Hubbell, S.P. (1997) A unified theory of biogeography and relative species abundance  
584 and its application to tropical rain forests and coral reefs. *Coral Reefs*, **16**, S9–S21.

585 Hubbell, S.P. (2001) *A unified neutral theory of biodiversity and biogeography*.  
586 Princeton University Press, Princeton, NJ.

587 Huisman, J., Jonker, R. R., Zonneveld, C. & Weissing, F. J. (1999) Competition for  
588 light between phytoplankton species: experimental tests of mechanistic theory. *Ecology*,  
589 **80**, 211–222.

590 Hutchinson, G.E. (1957) Concluding remarks. *Cold Spring Harbor Symposia on*  
591 *Quantitative Biology*, **22**, 415–427.

592 Irigoien, X., G. Chust, J. A. Fernandes, A. Albaina, & L. Zarauz (2011) Factors  
593 determining mesozooplankton species distribution and community structure in shelf and  
594 coastal waters. *Journal of Plankton Research*, **33**, 1182-1192.

595 Irigoien, X., J. Huisman, et al. (2004) Global biodiversity patterns of marine  
596 phytoplankton and zooplankton. *Nature*, **429**, 863-867.

597 Jabot, F., & J. Chave (2009) Inferring the parameters of the neutral theory of  
598 biodiversity using phylogenetic information and implications for tropical forests.  
599 *Ecology Letters*, **12**, 239-248.

600 Jabot, F., & J. Chave (2011) Analyzing Tropical Forest Tree Species Abundance  
601 Distributions Using a Nonneutral Model and through Approximate Bayesian Inference.  
602 *American Naturalist*, **178**, E37-E47.

603 Jabot F., Etienne R.S. & Chave J. (2008) Reconciling neutral community models and  
604 environmental filtering: theory and an empirical test. *Oikos*, **117**, 1308-1320.

605 Johnson, Z. I., E. R. Zinser, et al. (2006) Niche partitioning among *Prochlorococcus*  
606 ecotypes along ocean-scale environmental gradients. *Science*, **311**, 1737.

607 Kooistra, W. H. C. F., D. Sarno, et al. (2008) Global Diversity and Biogeography of  
608 *Skeletonema* Species (Bacillariophyta). *Protist*, **159**, 177-193.

609 Legendre, P., D. Borcard, & P. R. Peres-Neto (2005) Analyzing beta diversity:  
610 Partitioning the spatial variation of community composition data. *Ecological*  
611 *Monographs*, **75**, 435-450.

612 Legendre, P. & Legendre, L. (1998) *Numerical ecology*. Elsevier, Amsterdam.

613 Legendre, P. (1993) Spatial autocorrelation: trouble or new paradigm? *Ecology*, **74**,  
614 1659-1673.



615 Lund, J.W.G., Kipling, C. & Le Cren, E.D. (1958) The inverted microscope method of  
616 estimating algal numbers and statistical basis of estimations by counting.  
617 *Hydrobiologia*, **11**, 143-170.

618 MacArthur, R.H., Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton  
619 University Press.

620 Margalef, R. (1978) Life forms of phytoplankton as survival alternatives in an unstable  
621 environment. *Oceanol. Acta*, **1**, 493–509.

622 Martiny, J.B.H., Eisen, J.A., Penn, K., Allison, S.D., Horner-Devine, M.C. (2011)  
623 Drivers of bacterial beta-diversity depend on spatial scale. *Proc Natl Acad Sci USA*,  
624 **108**, 7850-7854.

625 Oksanen, J., (2011) *Multivariate Analysis of Ecological Communities in R: vegan*  
626 *tutorial*. pp. 43.

627 d'Ovidio, F., De Monte, S., Alvain, S., Dandoneau, Y., Lévy, M. (2010) Fluid  
628 dynamical niches of phytoplankton types. *Proc Natl Acad Sci USA* 107:18366–18370.

629 Pueyo, S. (2006a) Diversity: between neutrality and structure. *Oikos*, **112**, 392-405.

630 Pueyo, S. (2006b) Self-similarity in species-area relationship and in species abundance  
631 distribution. *Oikos*, **115**, 582-582.

632 Robins, D.B. et al. (1996a) AMT-1 cruise report and preliminary results. NASA  
633 technical memorandum 104566, vol. 35.

634 Robins, D.B. et al. (1996b) AMT-2 cruise report.

635 Robinson, C., A. J. Poulton, P. M. Holligan, A. R. Baker, G. Forster, N. Gist, T. D.  
636 Jickells, G. Malin, R. Upstill-Goddard, R. G. Williams, E. M. S. Woodward, & M. V.  
637 Zubkov (2006) The Atlantic Meridional Transect (AMT) Programme: A contextual  
638 view 1995-2005. *Deep Sea Research Part II: Topical Studies in Oceanography*, **53**,  
639 1485-1515.

640 Schluter, D. (2001) Ecology and the origin of species, *Trends in Ecology & Evolution*,  
641 **16**, 372-380.

642 Telford, R.J., Vandvik, V. & Birks, H.J.B. (2006) Dispersal limitations matter for  
643 microbial morphospecies. *Science*, **312**, 1015-1015.

644 ter Braak, C.J.F & Šmilauer, P. (1998) CANOCO reference manual and user's guide to  
645 Canoco for Windows: Software for canonical community ordination (version 4).  
646 Microcomputer Power, Ithaca, NY, US.

647 R Development Core Team (2011) R: A Language and Environment for Statistical  
648 Computing, Vienna, Austria, ISBN 3-900051-07-0, <http://www.R-project.org>.

649 Tittensor, D.P., Mora, C., Jetz, W., Lotze, H.K., Ricard, D., Vanden Berghe, E. &  
650 Worm, B. (2010) Global patterns and predictors of marine biodiversity across taxa.  
651 *Nature*, **466**, 1098-U1107.

652 Vergnon, R., Dulvy, N.K. & Freckleton, R.P. (2009) Niches versus neutrality:  
653 uncovering the drivers of diversity in a species-rich community. *Ecology Letters*, **12**,  
654 1079-1090.

655 Verleyen, E., W. Vyverman, M. Sterken, D. A. Hodgson, A. De Wever, S. Juggins, B.  
656 Van de Vijver, V. J. Jones, P. Vanormelingen, D. Roberts, R. Flower, C. Kilroy, C.  
657 Souffreau, & K. Sabbe (2009) The importance of dispersal related and local factors in  
658 shaping the taxonomic structure of diatom metacommunities. *Oikos*, **118**, 1239-1249.

659 VLIZ (2009) Longhurst Biogeographical Provinces. Available online at  
660 <http://www.vliz.be/vmdcdata/vlimar/downloads.php>.

661 Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003) Neutral theory and  
662 relative species abundance in ecology. *Nature*, **424**, 1035-1037.

663 Whitaker, R.J., Grogan, D.W. & Taylor, J.W. (2003) Geographic Barriers Isolate  
664 Endemic Populations of Hyperthermophilic Archaea. *Science*, **301**, 976-978.

665

666 **BIOSKETCH**

667

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671 of climate change in marine and coastal ecosystems, and on scale-dependent processes

672 in ecology.

673

674 **Figure legends**

675

676 Fig. 1. Oceanographic sampling stations corresponding to AMT1, AMT2, and AMT3  
677 overlain on a satellite image of ocean colour (blue, green, yellow and red represent  
678 increasing values of sea surface chlorophyll-a concentration; mean annual of 2010,  
679 MODIS sensor). Arrows indicate the main Atlantic oceanographic gyres.

680

681 Fig. 2. Species similarity against the distance between stations for each AMT (AMT-1  
682 in (a), AMT-2 in (b), and AMT-3 in (c), and for the three phytoplankton groups  
683 (diatoms, dinoflagellates and coccolithophores). Species similarity was averaged at  
684 1000 km interval. Error values are the standard deviation divided by two.

685

686 Fig. 3. Variation partitioning (%) of species composition, based on constrained  
687 correspondence analysis, according to spatial terms and environmental determinants, for  
688 each phytoplankton group.

689

690 Fig. 4. Empirical species abundance distributions and that expected under neutral model  
691 of six communities using Preston plots. Grey bars show the binned abundance classes  
692 (i.e. 1, 2, 3-4, 5-8, 9-16, ...), and black circles represent the expected number of species  
693 for each abundance class under neutral model with maximum likelihood estimation of  $\theta$   
694 and  $m$  parameters, and  $J$  individuals. *a*) Northern station AMT3.4 ( $J = 2294$ ,  $\theta = 3.75$ ,  $m$   
695  $= 0.45$ ,  $p = 0.114$ ); *b*) Northern station AMT1.4 ( $J = 3224$ ,  $\theta = 3.46$ ,  $m = 0.52$ ,  $p = 0.$   
696  $003$ ); *c*) Tropical station AMT3.9 ( $J = 1548$ ,  $\theta = 3.91$ ,  $m = 0.26$ ,  $p = 0.344$ ); *d*) Tropical  
697 station AMT3.12 ( $J = 7052$ ,  $\theta = 3.82$ ,  $m = 0.54$ ,  $p = 0.009$ ); *e*) Southern station AMT2.5  
698 ( $J = 3436$ ,  $\theta = 7.69$ ,  $m = 0.099$ ,  $p = 0.167$ ); *f*) Southern station AMT1.20 ( $J = 2692$ ,  $\theta =$

699 4.63,  $m = 0.44$ ,  $p < 0.001$ ). Communities in the left side ( $a$ ,  $c$  and  $d$ ) fitted to neutral  
700 model according to the test ( $p > 0.05$ ), and communities in the right side ( $b$ ,  $d$  and  $f$ ) did  
701 not fit to neutral model ( $p < 0.05$ ).

702

703 Fig. 5. ( $a$ ) Immigration rate ( $m$ ) and ( $b$ ) overall abundance across latitude for each AMT  
704 survey. Fitted curve is a 4<sup>th</sup> order polynomial model (for  $m$ ,  $r^2=0.44$ ,  $p<0.0001$ ; for  
705 abundance,  $r^2=0.54$ ,  $p<0.0001$ ), selected with AIC comparing four polynomial models  
706 from first to 4<sup>th</sup> order.

707

708 Table 1. Statistics of community structure of phytoplankton groups and AMT surveys.  
 709 Abundance is the total number of individuals (per 100 ml) in all stations and for all  
 710 species.

711

|  | Diatoms | Dinoflagellates | Coccolithophores |
|--|---------|-----------------|------------------|
| Mean species richness per station                        | 8.25    | 6.53            | 9.77             |
| Species richness (AMT1)                                  | 92      | 35              | 34               |
| Species richness (AMT2)                                  | 83      | 38              | 35               |
| Species richness (AMT3)                                  | 83      | 42              | 38               |
| Abundance (AMT1)   | 683648  | 23282           | 94110            |
| Abundance (AMT2)   | 1563014 | 7120            | 109535           |
| Abundance (AMT3)   | 568879  | 5674            | 104262           |
| Mean similarity (AMT1)                                   | 0.095   | 0.221           | 0.325            |
| Mean similarity (AMT2)                                   | 0.107   | 0.229           | 0.241            |
| Mean similarity (AMT3)                                   | 0.119   | 0.231           | 0.308            |
| Mean similarity (AMT1-3)                                 | 0.107   | 0.227           | 0.291            |
| Mean number of sites where a species is present (AMT1)   | 2.46    | 4.40            | 7.76             |
| Mean number of sites where a species is present (AMT2)   | 2.45    | 3.89            | 6.31             |
| Mean number of sites where a species is present (AMT3)   | 2.29    | 4.66            | 7.09             |
| Mean number of sites where a species is present (AMT1-3) | 2.40    | 4.32            | 7.05             |
| Mean range of latitudes occupied (AMT1, in km)           | 4385.9  | 5776.0          | 7285.0           |
| Mean range of latitudes occupied (AMT2, in km)           | 3078.7  | 3511.2          | 4934.7           |
| Mean range of latitudes occupied (AMT3, in km)           | 2593.7  | 5065.1          | 6061.8           |

712

713

714

715 Table 2. Mantel and partial Mantel tests between species similarity and environmental  
 716 determinants and geographical distance, for each AMT survey and phytoplankton  
 717 group. Irrad: Irradiance, Sol: Solar radiance.

|      |            | Mantel <i>r</i>                          | <i>p</i> -value | Terms selected | Terms entered                 |  |
|------|------------|--|-----------------|----------------|-------------------------------|--|
| AMT1 | Diatoms    | Jacc × Environ.                          | 0.42            | .001           | Temperature, Irrad            | NO <sub>3</sub> +NO <sub>2</sub> , NO <sub>2</sub> , PO <sub>4</sub> , Salinity, SiO <sub>4</sub> , Temperature, Irrad       |
|      |            | Jacc × Distance                          | 0.25            | .001           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.38            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.15            | .009           |                               |  |
|      | Dinoflag.  | Jacc × Environ.                          | 0.58            | .001           | NO <sub>2</sub>               | NO <sub>3</sub> +NO <sub>2</sub> , NO <sub>2</sub> , PO <sub>4</sub> , Salinity, SiO <sub>4</sub> , Temperature, Irrad       |
|      |            | Jacc × Distance                          | 0.33            | .001           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.53            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.14            | .047           |                               |  |
|      | Coccolith. | Jacc × Environ.                          | 0.74            | .001           | NO <sub>2</sub> , Temperature | NO <sub>3</sub> +NO <sub>2</sub> , NO <sub>2</sub> , PO <sub>4</sub> , Salinity, SiO <sub>4</sub> , Temperature, Irrad       |
|      |            | Jacc × Distance                          | 0.39            | .001           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.68            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.15            | .030           |                               |  |
| AMT2 | Diatoms    | Jacc × Environ.                          | 0.38            | .001           | Temperature                   | NO <sub>3</sub> +NO <sub>2</sub> , NO <sub>2</sub> , PO <sub>4</sub> , Salinity, SiO <sub>4</sub> , Temperature, Irrad , Sol |
|      |            | Jacc × Distance                          | 0.29            | .001           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.32            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.19            | .005           |                               |  |
|      | Dinoflag.  | Jacc × Environ.                          | 0.37            | .001           | NO <sub>2</sub> , Temperature | NO <sub>3</sub> +NO <sub>2</sub> , NO <sub>2</sub> , PO <sub>4</sub> , Salinity, SiO <sub>4</sub> , Temperature, Irrad , Sol |
|      |            | Jacc × Distance                          | 0.34            | .001           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.23            | .005           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.18            | .004           |                               |  |
|      | Coccolith. | Jacc × Environ.                          | 0.60            | .001           | Temperature                   | NO <sub>3</sub> +NO <sub>2</sub> , NO <sub>2</sub> , PO <sub>4</sub> , Salinity, SiO <sub>4</sub> , Temperature, Irrad , Sol |
|      |            | Jacc × Distance                          | 0.32            | .001           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.55            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.16            | .014           |                               |  |
| AMT3 | Diatoms    | Jacc × Environ.                          | 0.46            | .001           | Temperature                   | Salinity, Temperature  |
|      |            | Jacc × Distance                          | 0.24            | .004           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.41            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.07            | .199           |                               |  |
|      | Dinoflag.  | Jacc × Environ.                          | 0.47            | .001           | Temperature                   | Salinity, Temperature  |
|      |            | Jacc × Distance                          | 0.21            | .011           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.43            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.04            | .323           |                               |  |
|      | Coccolith. | Jacc × Environ.                          | 0.56            | .001           | Temperature                   | Salinity, Temperature  |
|      |            | Jacc × Distance                          | 0.29            | .001           |                               |  |
|      |            | Jacc × Environ. (Distance partially out) | 0.51            | .001           |                               |  |
|      |            | Jacc × Distance (Environ. partially out) | 0.10            | .091           |                               |  |

718

719 Table 3. Test of fitting phytoplankton Species Abundance Distribution (SAD) to the  
 720 neutral model for the three AMT surveys and zones. S: species richness; N: total sum of  
 721 the number of individuals; H: Shannon's index of diversity;  $\theta$ : the fundamental  
 722 biodiversity parameter;  $m$ : species immigration probability of a local community from  
 723 the metacommunity. S, H,  $\theta$ , and  $m$  are the mean values for the corresponding zone. See  
 724 Appendix S3 for values for each station.

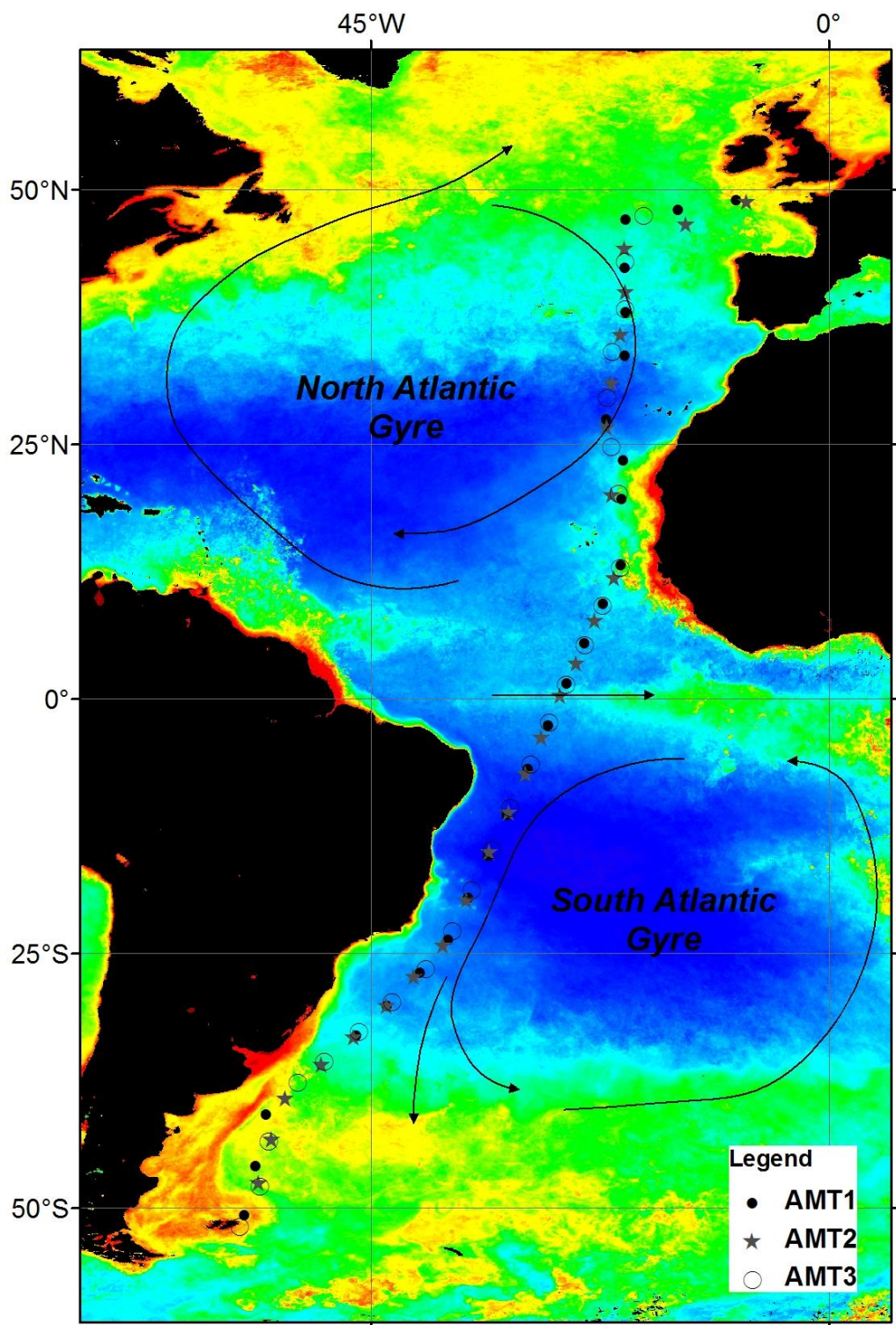
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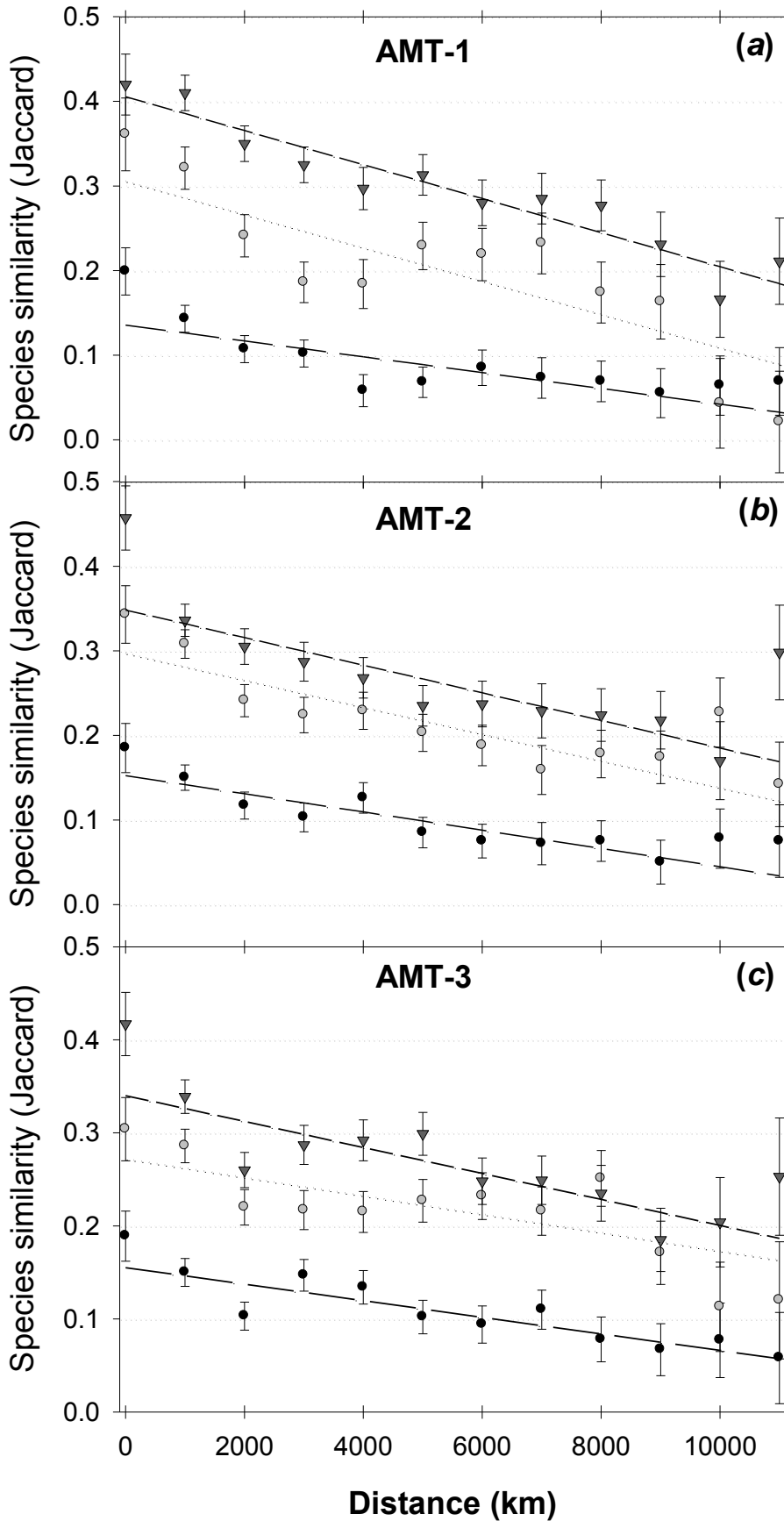
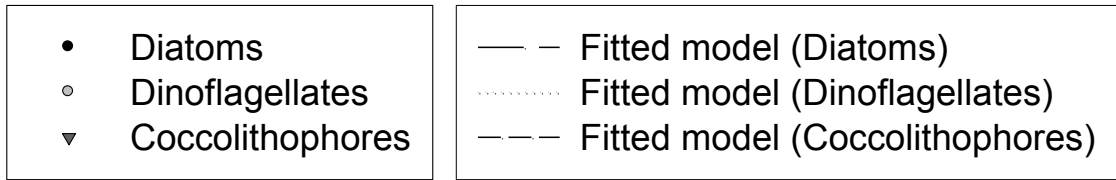
|                | Zone     | Number of stations | S    | N       | H    | $\theta$ | $m$  | Number of stations with Neutral SAD ( $p>0.05$ ) |
|----------------|----------|--------------------|------|---------|------|----------|------|--|
| AMT1           | Northern | 7                  | 24.9 | 2755.1  | 1.57 | 4.15     | 0.45 | 4  |
|                | Tropical | 12                 | 20.9 | 2921.9  | 1.53 | 3.77     | 0.36 | 6  |
|                | Southern | 6                  | 35.2 | 13326.0 | 1.45 | 5.52     | 0.42 | 1  |
| AMT2           | Northern | 7                  | 22.6 | 12914.0 | 1.34 | 3.22     | 0.53 | 4  |
|                | Tropical | 11                 | 17.6 | 1137.9  | 1.92 | 4.02     | 0.15 | 11   |
|                | Southern | 7                  | 28.7 | 7161.6  | 1.77 | 5.28     | 0.21 | 4  |
| AMT3           | Northern | 5                  | 25.0 | 5776.6  | 1.54 | 4.16     | 0.45 | 2  |
|                | Tropical | 10                 | 25.0 | 5210.6  | 1.81 | 4.32     | 0.23 | 8  |
|                | Southern | 7                  | 23.4 | 10910.8 | 1.35 | 3.29     | 0.51 | 5  |
| <b>Overall</b> |          | <b>73</b>          |      |         |      |          |      | <b>45</b>  |

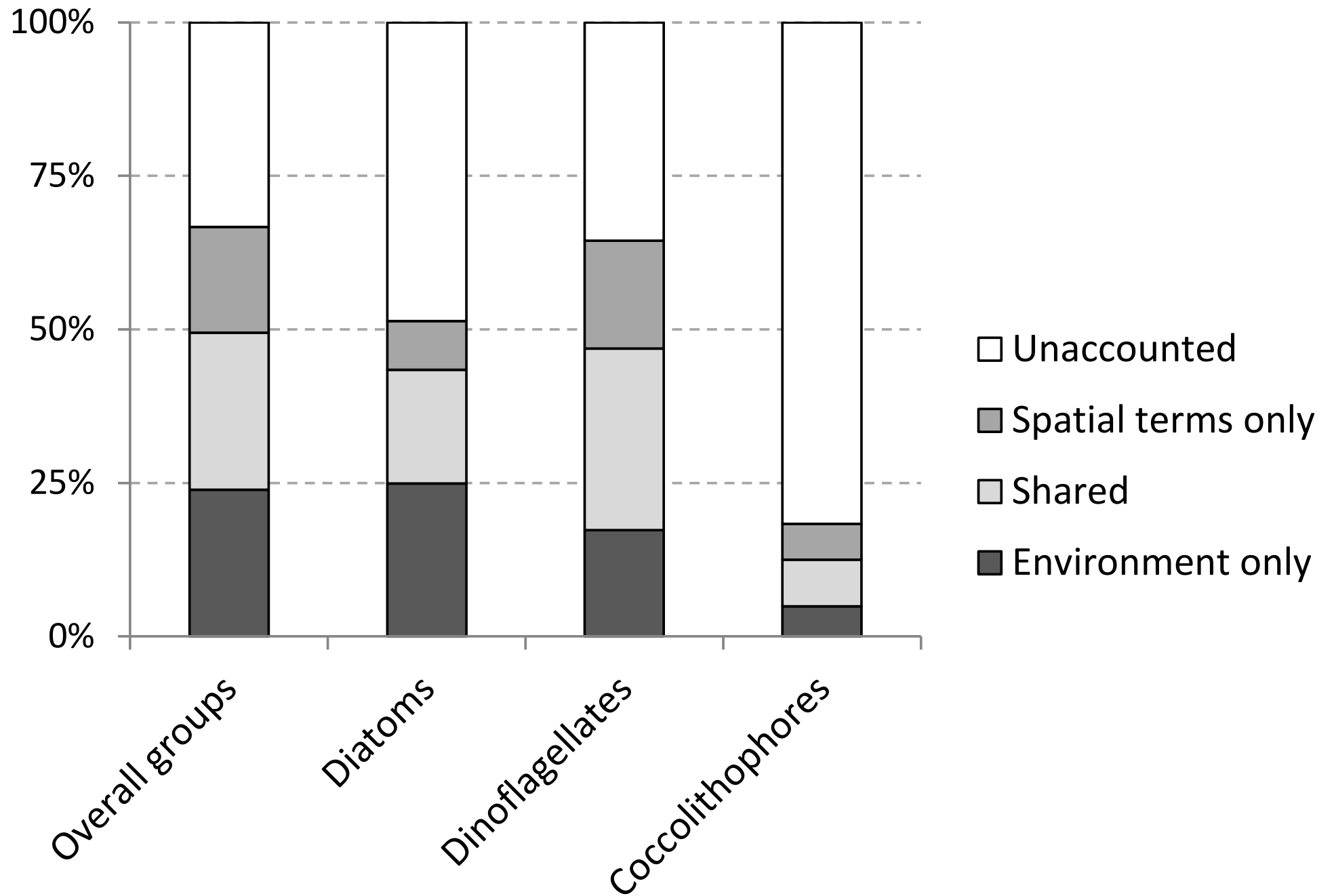
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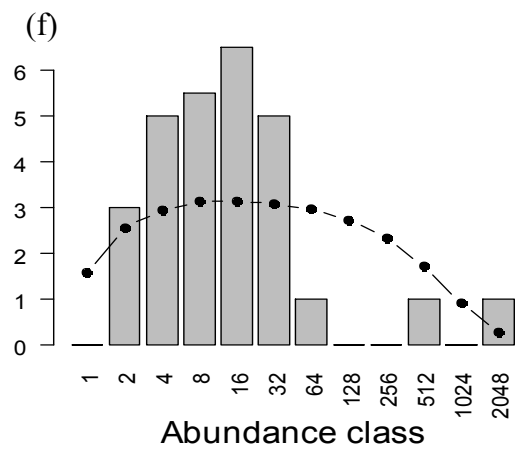
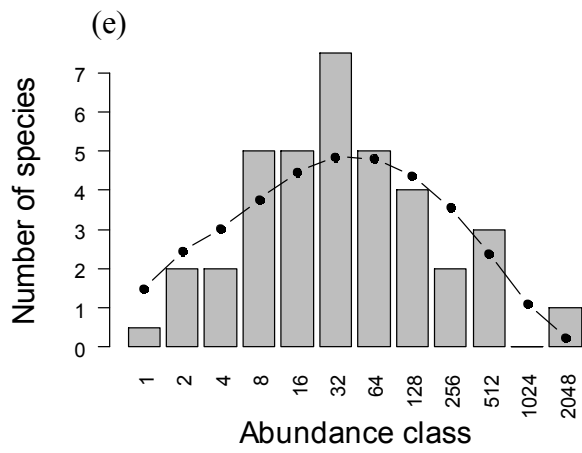
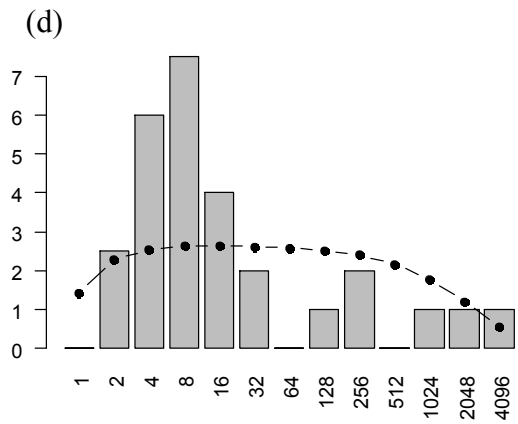
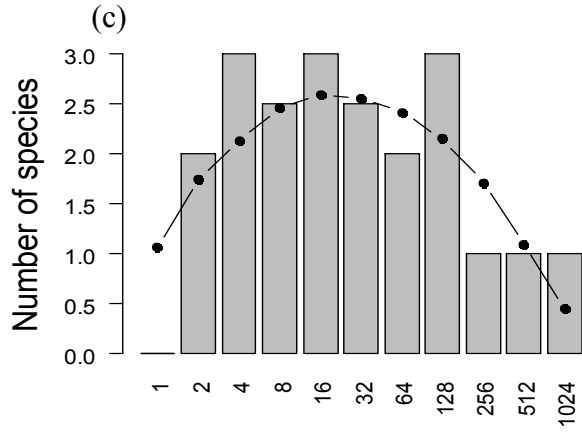
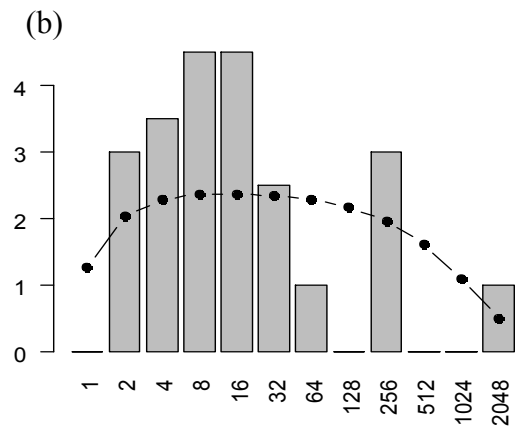
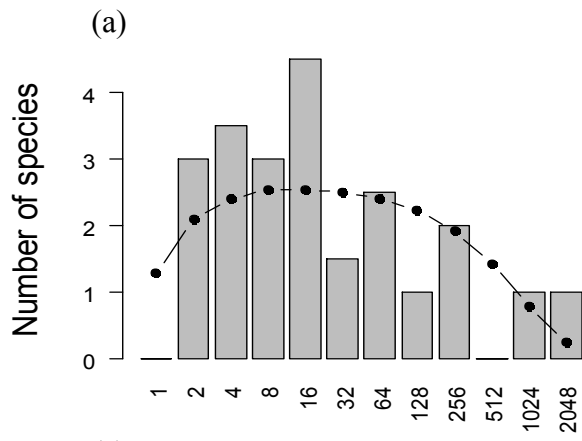
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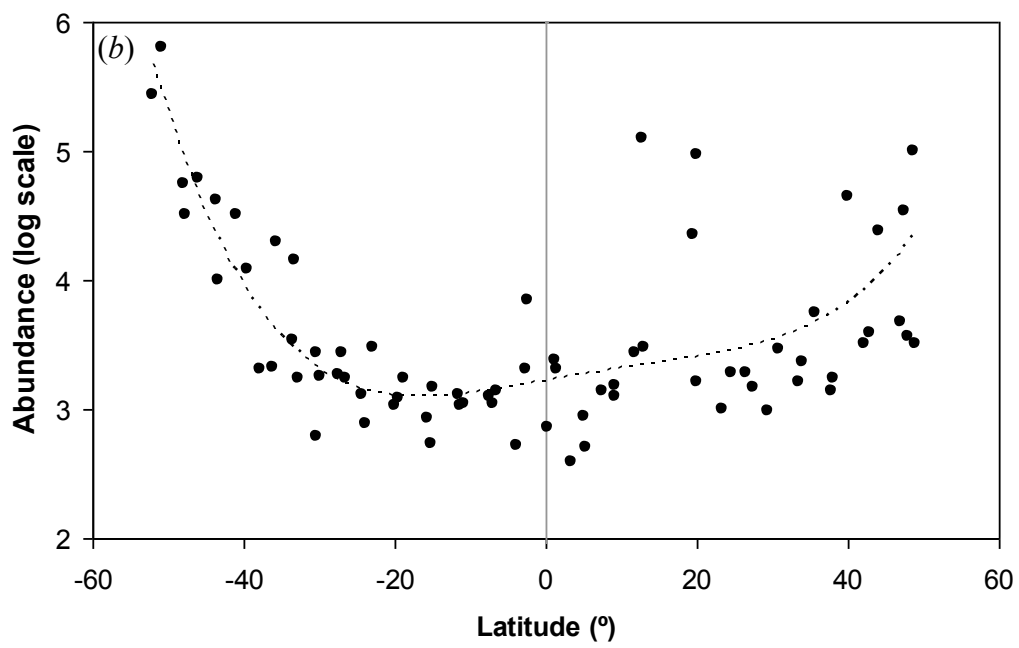
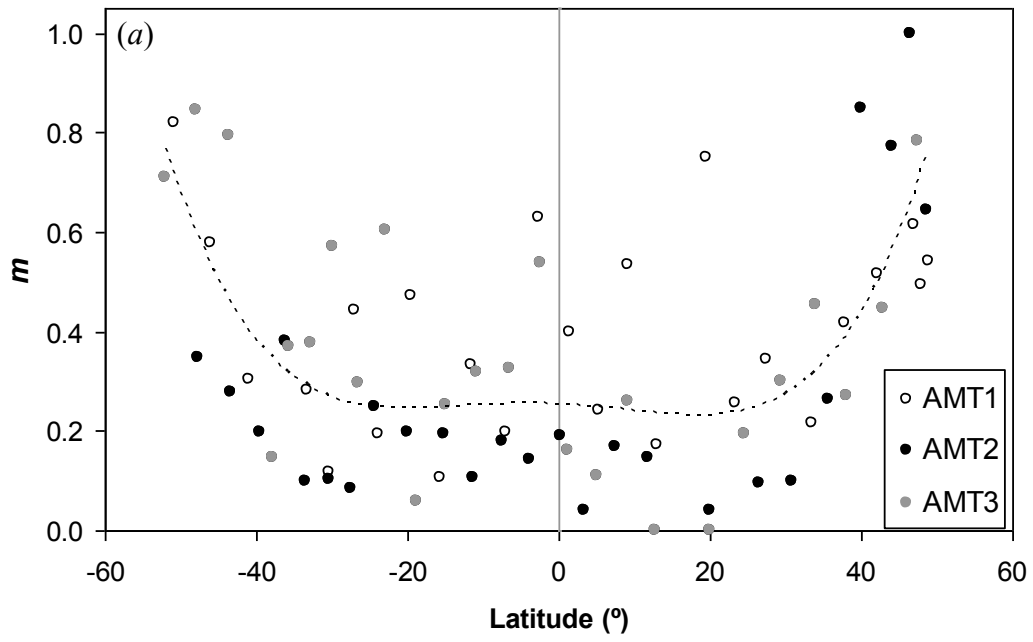


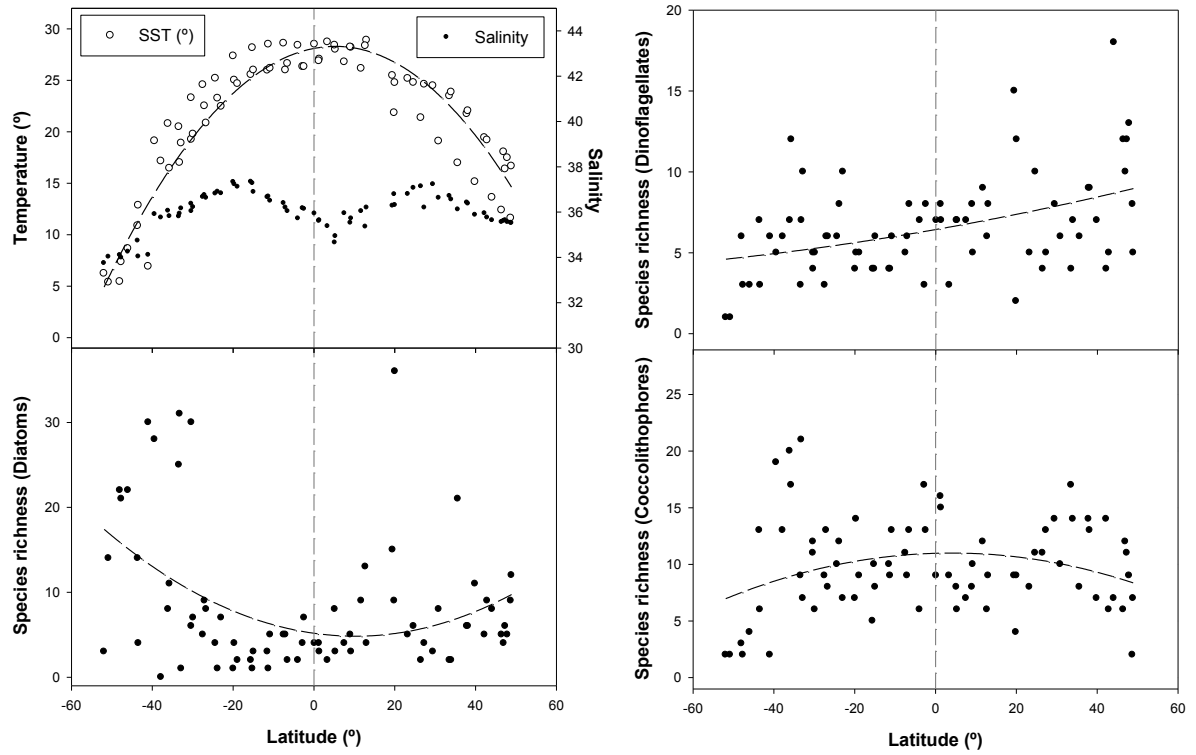




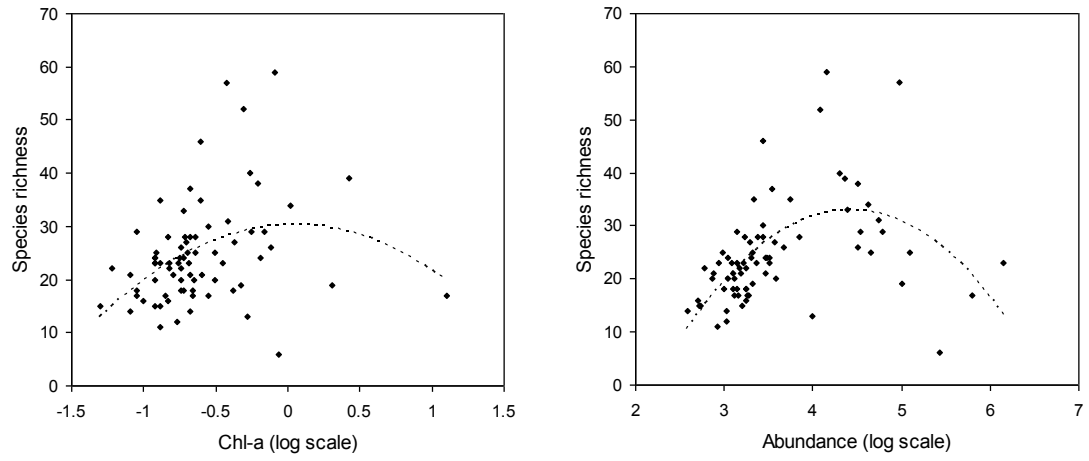








Appendix S1. Latitudinal patterns of sea surface temperature, salinity, and species richness of diatoms, dinoflagellates and coccolithophorids.



Appendix S2. Unimodal relation of phytoplankton species richness across biomass ( $r^2 = 0.15$ , p-value=0.003) and abundance ( $r^2 = 0.34$ , p-value<0.001).

Appendix S3. Test of fitting phytoplankton species abundance distributions to the neutral model for the each sampling station.  $J$ : total sum of the number of individuals;  $S$ : species richness;  $H$ : Shannon's index of diversity;  $\theta$ : the fundamental biodiversity parameter;  $m$ : species immigration probability of a local community from the metacommunity;  $p$ -value: probability of the neutrality test based upon Shannon's index.

| Zone          | AMT survey and station | $J$    | $S$ | $H$   | $\theta$ | $m$     | $p$ -value |
|---------------|------------------------|--------|-----|-------|----------|---------|------------|
| Northern zone | AMT1.1                 | 3196   | 24  | 1.155 | 3.63541  | 0.54153 | 0.009      |
| Northern zone | AMT1.2                 | 3647   | 27  | 1.583 | 4.13152  | 0.49229 | 0.050      |
| Northern zone | AMT1.3                 | 4718   | 26  | 1.723 | 3.69217  | 0.61449 | 0.141      |
| Northern zone | AMT1.4                 | 3224   | 23  | 0.939 | 3.46402  | 0.51623 | 0.003      |
| Northern zone | AMT1.5                 | 1391   | 29  | 2.065 | 5.64489  | 0.41876 | 0.082      |
| Northern zone | AMT1.6                 | 1641   | 23  | 1.836 | 4.44645  | 0.21660 | 0.092      |
| Northern zone | AMT1.7                 | 1469   | 22  | 1.665 | 4.03803  | 0.34346 | 0.073      |
| Tropical      | AMT1.8                 | 998    | 18  | 1.814 | 3.57938  | 0.25734 | 0.256      |
| Tropical      | AMT1.9                 | 22635  | 38  | 0.850 | 4.41010  | 0.74953 | 0.000      |
| Tropical      | AMT1.10                | 2975   | 21  | 1.730 | 3.58023  | 0.17204 | 0.163      |
| Tropical      | AMT1.11                | 1250   | 18  | 1.120 | 3.07614  | 0.53425 | 0.013      |
| Tropical      | AMT1.12                | 509    | 16  | 1.973 | 3.74556  | 0.24146 | 0.414      |
| Tropical      | AMT1.13                | 2068   | 25  | 1.360 | 4.30817  | 0.39897 | 0.004      |
| Tropical      | AMT1.14                | 2040   | 24  | 1.387 | 3.90031  | 0.62754 | 0.017      |
| Tropical      | AMT1.15                | 1110   | 20  | 1.344 | 4.16201  | 0.19894 | 0.010      |
| Tropical      | AMT1.16                | 1314   | 17  | 1.455 | 3.00126  | 0.33475 | 0.118      |
| Tropical      | AMT1.17                | 842    | 11  | 1.559 | 2.26946  | 0.10769 | 0.406      |
| Tropical      | AMT1.18                | 1197   | 23  | 2.022 | 4.29514  | 0.47035 | 0.260      |
| Tropical      | AMT1.19                | 760    | 21  | 1.719 | 4.97221  | 0.19558 | 0.029      |
| Southern zone | AMT1.20                | 2692   | 28  | 0.960 | 4.63056  | 0.44443 | 0.000      |
| Southern zone | AMT1.21                | 2758   | 46  | 2.728 | 10.51770 | 0.11720 | 0.133      |
| Southern zone | AMT1.22                | 14506  | 59  | 2.167 | 8.70780  | 0.28042 | 0.005      |
| Southern zone | AMT1.23                | 32179  | 35  | 1.366 | 4.59466  | 0.30258 | 0.011      |
| Southern zone | AMT1.24                | 61663  | 29  | 1.297 | 3.12250  | 0.57787 | 0.036      |
| Southern zone | AMT1.25                | 630258 | 15  | 0.170 | 1.54189  | 0.82094 | 0.000      |
| Southern zone | AMT2.1                 | 32454  | 26  | 0.651 | 2.96950  | 0.34781 | 0.002      |
| Southern zone | AMT2.2                 | 9873   | 13  | 1.228 | 1.54473  | 0.27934 | 0.357      |
| Southern zone | AMT2.3                 | 12255  | 52  | 2.080 | 8.03276  | 0.19643 | 0.007      |
| Southern zone | AMT2.4                 | 2129   | 35  | 1.813 | 6.54618  | 0.38104 | 0.008      |
| Southern zone | AMT2.5                 | 3436   | 37  | 2.452 | 7.69979  | 0.09899 | 0.167      |
| Southern zone | AMT2.6                 | 608    | 22  | 2.424 | 6.72432  | 0.10233 | 0.561      |
| Southern zone | AMT2.7                 | 1830   | 17  | 1.751 | 3.43551  | 0.08314 | 0.240      |
| Tropical      | AMT2.8                 | 1304   | 20  | 1.944 | 3.85101  | 0.24988 | 0.313      |
| Tropical      | AMT2.9                 | 1053   | 12  | 1.666 | 2.17805  | 0.19631 | 0.541      |
| Tropical      | AMT2.10                | 532    | 15  | 1.519 | 3.52518  | 0.19569 | 0.066      |
| Tropical      | AMT2.11                | 1058   | 14  | 1.783 | 2.95684  | 0.10465 | 0.437      |
| Tropical      | AMT2.12                | 1238   | 21  | 2.055 | 4.37661  | 0.18101 | 0.323      |
| Tropical      | AMT2.13                | 515    | 15  | 1.992 | 3.81080  | 0.14274 | 0.471      |
| Tropical      | AMT2.14                | 729    | 20  | 2.032 | 4.75005  | 0.18881 | 0.208      |
| Tropical      | AMT2.15                | 388    | 14  | 2.223 | 5.84715  | 0.04129 | 0.871      |
| Tropical      | AMT2.16                | 1390   | 18  | 1.844 | 3.52581  | 0.16668 | 0.314      |
| Tropical      | AMT2.17                | 2706   | 30  | 2.108 | 5.86781  | 0.14536 | 0.097      |
| Tropical      | AMT2.18                | 1604   | 15  | 1.929 | 3.50292  | 0.04005 | 0.548      |
| Northern zone | AMT2.19                | 1918   | 17  | 1.860 | 3.30704  | 0.09655 | 0.379      |



|               |         |         |    |       |         |         |       |
|---------------|---------|---------|----|-------|---------|---------|-------|
| Northern zone | AMT2.20 | 2914    | 24 | 2.168 | 4.62893 | 0.09789 | 0.386 |
| Northern zone | AMT2.21 | 5566    | 35 | 2.090 | 5.59426 | 0.26337 | 0.108 |
| Northern zone | AMT2.22 | 44709   | 24 | 0.864 | 2.65332 | 0.84951 | 0.013 |
| Northern zone | AMT2.23 | 24292   | 33 | 1.169 | 3.72220 | 0.77140 | 0.008 |
| Northern zone | AMT2.24 | 1423869 | 10 | 0.160 | 1.05899 | 1.00000 | 0.016 |
| Northern zone | AMT2.25 | 101299  | 17 | 1.074 | 1.56579 | 0.64474 | 0.168 |
| Northern zone | AMT3.1  | 34057   | 26 | 0.803 | 3.31893 | 0.78361 | 0.006 |
| Northern zone | AMT3.2  | 3888    | 20 | 1.602 | 2.87015 | 0.44806 | 0.245 |
| Northern zone | AMT3.3  | 1727    | 28 | 1.795 | 5.45832 | 0.26896 | 0.028 |
| Northern zone | AMT3.4  | 2294    | 23 | 1.664 | 3.74597 | 0.45542 | 0.114 |
| Northern zone | AMT3.5  | 974     | 25 | 1.860 | 5.39180 | 0.29832 | 0.032 |
| Tropical      | AMT3.6  | 1930    | 28 | 2.149 | 5.58667 | 0.19335 | 0.168 |
| Tropical      | AMT3.7  | 94326   | 51 | 0.737 | na      | 0.00031 | 0.000 |
| Tropical      | AMT3.8  | 125084  | 18 | 0.077 | na      | 0.00008 | 0.000 |
| Tropical      | AMT3.9  | 1548    | 21 | 1.990 | 3.91312 | 0.25849 | 0.344 |
| Tropical      | AMT3.10 | 866     | 23 | 2.394 | 6.10525 | 0.11066 | 0.565 |
| Tropical      | AMT3.11 | 2373    | 28 | 2.240 | 5.46656 | 0.16028 | 0.296 |
| Tropical      | AMT3.12 | 7052    | 28 | 1.195 | 3.81965 | 0.53635 | 0.009 |
| Tropical      | AMT3.13 | 1392    | 23 | 1.798 | 4.35725 | 0.32602 | 0.110 |
| Tropical      | AMT3.14 | 1114    | 24 | 1.973 | 4.88359 | 0.31718 | 0.118 |
| Tropical      | AMT3.15 | 1464    | 18 | 1.469 | 3.27231 | 0.25196 | 0.076 |
| Tropical      | AMT3.16 | 1742    | 16 | 1.734 | 3.43278 | 0.05887 | 0.257 |
| Tropical      | AMT3.17 | 3046    | 24 | 1.134 | 3.62876 | 0.60225 | 0.007 |
| Southern zone | AMT3.18 | 1761    | 22 | 1.656 | 3.94985 | 0.29796 | 0.073 |
| Southern zone | AMT3.19 | 1789    | 18 | 1.642 | 2.83822 | 0.57197 | 0.260 |
| Southern zone | AMT3.20 | 1740    | 18 | 1.456 | 2.99142 | 0.37682 | 0.102 |
| Southern zone | AMT3.21 | 19936   | 40 | 1.752 | 5.10525 | 0.37098 | 0.036 |
| Southern zone | AMT3.22 | 2060    | 19 | 1.734 | 3.50460 | 0.14671 | 0.169 |
| Southern zone | AMT3.23 | 42038   | 33 | 1.187 | 3.84918 | 0.79323 | 0.008 |
| Southern zone | AMT3.24 | 55292   | 28 | 1.073 | 3.56535 | 0.84672 | 0.011 |
| Southern zone | AMT3.25 | 273563  | 5  | 0.339 | 0.51678 | 0.70993 | 0.291 |